MATERNAL STRATEGIES IN VERVET MONKEYS

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ABSTRACT

I studied free-ranging vervet monkeys (*Chlorocebus aethiops*) in South Africa using focal animal sampling to test current theories of reproduction and maternal investment. Mothers cope with the energetic costs of lactation by feeding more than non-lactating females and targeting higher nutrient quality items as their infant ages. The dynamic nature of mother-infant interactions is highlighted, with infants spending less time in contact while the mother is moving and foraging. Other troop members "allomother" the infant primarily in the infant's first couple of months. The length of investment is explored, with greater length of interbirth interval in low nutrient quality environments, larger troop sizes and higher survival rates. Maternal dominance rank and infant sex significantly influenced time in ventral contact, with low-ranking daughters spending more time in contact than high-ranking daughters. The findings from this thesis highlight the complex interaction of ecological and social conditions on maternal investment.

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LIST OF ABBREVIATIONS

RST= Riverside Troop

RBM= Riverbend Mob

D.O.B.= Date of birth

D.O.D. = Date of death/disappearance

ITE = Intertroop encounter

IBI= Interbirth interval

SE= standard error

SD= standard deviation

CI= confidence interval

REML= Restricted maximum likelihood

I.D. = identification

CHAPTER ONE. INTRODUCTION

1.1. OVERVIEW

Reproduction is the ultimate goal of an animal's life. To be successful in this endeavor, animals must survive, mate, and rear offspring to maturity, three activities which often have conflicting demands (Dunbar, 1988). Female mammals typically have greater demands of rearing offspring compared to males due to the costs associated with gestation and lactation (Glittleman & Thompson, 1988). Primate mothers are faced with the additional challenge of caring for dependent offspring, characterized by a relatively long lactation period associated with late weaning, and with high investment in individual offspring (Martin, 1995). As stated by Martin (1995), "primate reproduction is geared to 'quality rather than quantity'"(p.19), which probably occurred early in the line of primate ancestry (Ross & Jones, 1999). For example, most primate taxa give birth to singletons rather than twins and larger litters. Slow reproductive turnover is one of the defining characteristics of the primate order (Martin, 1995). A lengthy lactation period also permits flexibility in reproductive strategies and maternal care. As a result, primates utilize various reproductive and investment strategies to cope with the costs of lactation. As continued investment in the current offspring delays production of future offspring, the 'decision' to stop investing is crucial: halting investment too early may result in offspring death, investing too long could result in a significant reduction in lifetime reproductive output.

A final additional challenge faced by most primate mothers is the need to obtain

sufficient energy for themselves and their offspring in complex social and ecological

settings (Altmann 1980), while having to coordinate their behaviour with other members

of their social group (Dunbar 1988). While group living offers several advantages, one

disadvantage is having to coordinate behaviour where others' needs are different.

The goal of this thesis is to test current theories of reproductive and parental investment

in a seasonally breeding Old-World monkey: the vervet. Specifically, I examine how

females cope with the energetic costs of lactation through readjustments of their time

budgets and nutrient quality of their targeted diet items. I investigate mother-infant

behavioural dynamics, and how the influence of other troop members affects this

dynamic. Finally, I explore patterns of differential investment in offspring based on

maternal activity, maternal rank and infant sex.

1.2. LACTATION COSTS

Lactation is the most energetically expensive phase of reproduction for female mammals,

with energy intake ranging 66-188% higher than non-lactating females (Glittleman &

Thompson, 1988). These demands are extended in primates, which have particularly

long periods of lactation. For example, in savanna baboons, Altmann et al. (1977)

highlighted the prevalence of motherhood during an adult female's life by noting that

females spent over half their adult years in postpartum amenorrhea caring for a dependent

infant. Therefore, the strategies of obtaining enough energy for coping with the costs of lactation may differ in primates compared to other mammals.

Large bodied mammals, such as certain pinniped species, store fat during pregnancy and fast during lactation (Boness & Don Bowen, 1996); females can lose up to 42% of their body weight (Costa, Boeuf, Huntley, & Ortiz, 1986). The lactation period in these animals can be extremely short (e.g.,in the hooded seal, weaning occurs fours days after birth), with high infant birth weights and high daily infant growth rates. Thus, infants are weaned at a comparable weight to other phocids that either park their young to forage during lactation or that forage with their young at sea (Bowen, Oftedal, & Boness, 1985). Milk quality is extremely high in species with short, intense periods of lactation (Ortiz, La Boeuf, & Costa, 1984).   An advantage to this strategy is that it minimizes the costs of body maintenance while nursing, allowing mothers to return to sea to quickly to feed and begin gestating another offspring, unencumbered by a following pup (Ortiz et al., 1984).

Most mammals, however, are unable to accumulate large fat stores to fuel lactation like the pinnipeds, and must pursue other strategies. One common strategy for mammals with highly precocial young is for the infant to follow the mother very soon after birth (for example, in ungulates). In these species, milk is often dilute, with low fat content, much like in species that carry their young with them (Shaul, 1963). In mammalian species that have slightly less precocial young that are not able to travel with their mother shortly after birth, another strategy exhibited is for mothers to leave the young for periods of time while they forage unencumbered by a clinging or following offspring. In species that

"park" their infants, females have highly concentrated milk, with a very high fat content (Shaul, 1963), which places more energy demands on the mother. Lastly, only in some mammalian orders are infants carried (dorsally or ventrally) as the mother forages (Ross, 2001). In species where infants that are carried by or follow their mothers, allowing an "on demand" nursing schedule, mothers have dilute milk and low fat content (Shaul, 1963), lowering the energetic demands placed on the mother.

Primates, as a group, exhibit the last two strategies referred to above, with some prosimian species leaving their infants in nests or tree holes (eg. tarsier, bush baby, aye ayes), and other prosimian species (eg. many lemur species) as well as monkeys and apes carrying their infants while they forage (Ross, 2001). Within the primate taxa, species which park their infants wean their infants earlier than in species which carry their infants (Ross, 2001).   As a result, in species that carry their infants, mothers are faced with the challenge of foraging with a potentially interfering offspring over a longer period.

1.3. BIRTH SEASONALITY

One common reproductive strategy in the primates is birth seasonality. Lancaster and Lee (1965) define a birth season as "a discrete period of the year to which all births are confined", whereas a birth peak is, "the period of the year in which a high proportion of births but not all births are concentrated," (p.488).   As reviewed by Lindburg (1987), most primates exhibit either birth seasonality or a birth peak. This has more recently been confirmed for New World primates by Di Bitetti and Janson (2000), who reviewed

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birth seasonality in neotropic primates and noted that most monkeys show some degree of birth seasonality. In the Old-World monkeys, birth seasonality is nearly universal among cercopithecines living more than 20°C from the equator, with only one known exception (*Papio ursinus)* and is common for cercopithecines living close to the equator (the exceptions are the mangabeys, the Papio baboons, the gelada baboon and the crab-eating macaque) (Lindburg, 1987).

Food availability is suggested to be the most important ultimate cause of birth seasonality or birth peaks with the highest food availability timed to coincide with different reproductive events (Butynski, 1988; Di Bitetti & Janson, 2000). High availability of nutrient quality has been found to correspond with conception (eg. baboons Altmann, 1980; Bercovitch & Harding, 1993; Cheney et al., 2006; gelada: Dunbar, 1984), gestation and later, lactation (eg. rhesus and langur monkeys Lancaster & Lee, 1965), birth (eg. East African baboon Lancaster & Lee, 1965), and peak lactation (eg. cappuchins Carnegie, Fedigan, & Melin, 2011; vervets Lee, 1987). Other ultimate explanations of seasonal births or birth peaks are thermoregulatory costs (Dunbar, Hannah-Stewart, & Dunbar, 2002) and responses to the social stress of allomothering (M. Kavanagh, 1983). It is worth noting that the timing of conception with food availability may actually be more of a proximate explanation than an ultimate one; that is, it is possible that females are simply regaining condition (for example, weight lost during pregnancy) as a result of increased food availability, and are then able to conceive.

As noted above, vervets are seasonal breeders, although provisioning can lead to 'off-season' breeding (Lee, Brennan, Else, & Altmann, 1986). In a review of guenon birth seasonality, Butynski noted that food availability was highest following the wettest months of the year, with births occurring in vervet monkeys between the end of the dry season and end of the wet season, depending on the rainfall distribution. In areas of low (35-101 cm) rainfall, the middle of the birth season corresponds to 0.5 to 2 months prior to peak food abundance, meaning peak lactation and therefore greatest nutritional stress on the mothers corresponds with the period of peak food abundance (Butynski, 1988). Among the Amboseli vervets, for example, Lee (1987) found that peak nutritional quality corresponded with peak lactation, and suggested an ultimate explanation for birth seasonality in terms of ensuring that mothers obtained sufficient nutrients during the most reproductively stressed phase of reproduction.

1.4. ALTMANN'S MATERNAL FEEDING TIME BUDGET MODEL

In order to compensate for the increased nutrient demands of a growing infant, a mother needs to consume increasingly more calories than a non-lactating female. Assuming that nutrient quality stayed the same over the course of lactation, Altmann (1980) proposed an elegant model of feeding time allocation for mothers, taking into consideration both mother and infant energy demands. Several studies have found support for increased maternal feeding time with increasing infant age (Altmann, 1980; Dunbar & Dunbar, 1988; Kenyatta, 1995), although the model has shown often a relatively poor quantitative fit (see Chapter Three). As is usual in such cases, the model makes several simplifying

assumptions. By examining the deviations from the proposed model and the violations of the assumptions, conflicting demands can be assessed as a means of determining why a female may not be behaving in a predicted manner. For example, when Barrett et al. (2006a) tested Altmann's model in chacma baboons, they found lactating females increased resting (rather than foraging) time, and suggested resting time served to increase time spent vigilant. Considering the high rates of infanticide in their baboon population, selection appears to have favoured increased vigilant rates in lactating females over maintaining body condition.

1.5. MATERNAL INVESTMENT

The previous section examined how mothers cope with the demands of lactation. However, lifetime reproductive success is measured by the number of surviving offspring, with continued investment in one offspring potentially interfering with the production of other offspring. This inevitably requires a trade-off between investment in current versus future offspring (Trivers, 1972): females must invest sufficiently in offspring to ensure their survival, while at the same time retain the capacity to invest in future offspring. An example of how continued investment in the current offspring delays investment in future offspring is lactational anoestrus, where females are unable able to resume cycling until suckling frequencies and milk production decrease. Therefore the 'decision' of how much investment to provide to the current offspring is an important one, particularly in seasonally breeding species where continued investment in current offspring will delay reproduction for an entire year until the following mating

season. For the purpose of this thesis, I will use Trivers' (1972) definition of investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring" (p.139).

1.5.1. WEANING CONFLICT

Trivers (1974) extended Hamilton's (1964) theory of kin selection and suggested that parents and offspring should disagree on both the amount and duration of parental investment. This parent-offspring conflict stems from fact that all offspring share an average of 50% of the their genes with their mother, and an average of 25-50% of genes with current/future siblings, but 100% of their genes with themselves. As a result, the point at which the costs of continued investment in current offspring outweigh the benefits is reached earlier in mothers than it is in offspring. Mothers are therefore selected to halt investment at a stage when infants have been selected to continue to elicit more. Trivers (1974) suggests this is why "weaning conflict" occurs. Bateson (1994), however, has argued the relationship between mother and offspring and maternal investment is dynamic, with both mother and offspring continually evaluating each other's condition. Therefore, rather than mothers and offspring disagreeing on the amount of investment, they converge on the optimum amount that the offspring should receive and there is no conflict. The decision to stop investing is thus a response of environmental, maternal and infant condition. Individual differences that may influence investment include environmental conditions, infant sex and maternal dominance rank,

behavioural "meshing" of mother and infant (where the infant matches its activity to its mothers, nursing while it is most convenient to the mother), and allocare provided by other individuals.

1.5.2. LENGTH OF INVESTMENT

Environmental parameters can influence the amount of investment in individual offspring, and in turn, the inter-birth interval and total reproductive fitness. For example, in captive/food provisioned troops females tend to give birth earlier, have lower inter-birth intervals and higher infant growth rates (Altmann & Alberts, 2003; Lee & Bowman, 1995; Lee, Majluf, & Gordon, 1991). Lee et al. (1991) noted that infant weaning weight was roughly the same between food enhanced and food restricted groups, due to a longer lactation period in the food restricted groups. For example, using data over a thirty year period, Altmann and Alberts (2003) found that offspring growth rates in Lodge Troop, which had access to human food, was almost double that of the neighbouring troops. In a study of red deer hinds, Loudon et al. (1983) demonstrated that hinds in lower nutrient quality environment produce lower milk yields, and as a result, the infants of hind in lower quality environment grow slower and suckle more frequently, which extends lactation anoestrous. In vervet monkeys, Hauser and Fairbanks (1988) noted that time in ventral contact decreased most rapidly in a swamp environment (which is high in nutrient quality) compared to dry woodland (which is low in nutrient quality) and captive conditions. As well, inter-birth interval was roughly one year in the swamp environment

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compared to two years in the dry woodland   Comparing investment between populations can highlight environmental influences on reproductive parameters.

1.5.3. TIMING

In accordance with Bateson (1994) argument outlined in section 1.5.1, Dunbar (1988) and Altmann (1980) suggest that, rather than weaning tantrums always representing the manifestation of an underlying genetic conflict of interest, such behavior may often be related to the timing of the infant's access to milk. They emphasized that, particularly among ground dwelling primates, infants that cling ventrally to their mothers interfere with a mother's activity such as feeding, especially as the infant gets larger. As a result, it is suggested that females attempt to train their infants to nurse when it is convenient for them, such as when the mother is resting or engaging in social activities (see Chapter Four).

1.5.4. INVESTMENT BASED ON MATERNAL RANK AND INFANT SEX

In 1973, Trivers and Willard hypothesized differential selection on birth sex ratios and investment based on maternal condition. For polygynous animals, a male in good condition can potentially produce many more offspring than a female in good condition, whereas the opposite is true for individuals in poor condition. For example, in red deer sons of dominant females had greater lifetime reproductive success than daughters of dominant females, whereas in subordinate females, daughters have greater reproductive

success than sons (Clutton-Brock, Albon, & Guiness, 1984). Therefore, Trivers and Willard (1973) proposed that females in poor condition will bias investment towards daughters, whereas females in good condition would bias investment towards sons, which would maximize their reproductive success and increase their fitness. The bias can occur through sex-biased birth ratios or differential post-natal investment. Support for the Trivers-Willard hypothesis has come from studies examining sex and rank differences in birth sex-ratio (red deer: Clutton-Brock et al., 1984; rhesus macaques: Meikle, Tilford, & Vessey, 1984; Babary macaque: Paul & Kuester, 1990), although several studies that have looked for a rank related sex difference have not found one (eg. rhesus macaques: Berman, 1988; vervets: Cheney, Seyfarth, Andelman, & Lee, 1988), but see Clutton Brock and Iason (1986) for a review.

An alternative to the Trivers and Willard hypothesis is the local resource competition hypothesis, first proposed by Clark (1978) and then expanded by Silk. Originally as proposed by Clark (1978), a higher male biased sex ratio may be expected in species that compete with female relatives for resources. Silk (1983) expanded on the local resource competition hypothesis by suggesting females may reduce the probability of other females successfully rearing daughters. As a consequence of aggression directed towards female offspring, females who are unable to defend their daughters (ie. low ranking females) would be expected to have a male biased sex ratio, with all females investing more in their daughters than sons. A male biased sex ratio has been found in low ranking females for various populations: rhesus macaques (Gomendio, 1990; Silk, 1983; Simpson & Simpson, 1982), bonnet macaques (Silk, 1983), and yellow baboons (Altmann, 1980).

Interestingly, the reverse has been found to occur in primate groups with male philopatry (eg. spider monkeys McFarland Symington, 1987). The main distinction between the two hypotheses is the predicted effect rank has on reproductive success for the two sexes: for the local resource competition hypothesis, high rank should have the greatest effect on the reproductive success of the offspring sex that remains in the troop. In female philopatric societies, daughters typically inherit their mother's rank while males disperse to a new troop and no longer receive benefits from their mother's high rank; therefore, it suggests high ranking females would most influence the reproductive success of daughters. Females raising daughters may also benefit from their daughter's help in the future as allies (the "advantaged daughter" hypothesis) (Altmann 1980).

Whether it is the Trivers-Willard hypothesis or the local resource competition hypothesis, both are based on the premise that mothers will bias investment toward one sex versus the other, depending on the mother's condition. Both hypotheses suggest this bias will maximize inclusive fitness, since greater investment in one offspring could potentially produce greater number of grand-offspring.

1.5.5. ALLOMOTHERING

In addition to infants playing an active role in determining the amount of investment they receive, other individuals outside of the mother-infant pair may influence investment levels. One such influence is allomothering: the handling and care of infants by individuals other than the mother incurs a variety of costs and benefits. Across

taxonomic levels, the amount of allomothering is positively correlated to post-natal growth rate (Ross & MacLarnon, 1995), which therefore allows mother to wean their infants earlier. In a group of captive vervets, Fairbanks et al. (1990) found that the time infants that spent being allomothered significantly reduced interbirth interval. Hrdy (1976) summarizes allomothering as mechanism to allow foraging freedom, with mothers depositing infants with another individual and going to feed. Additional benefits include increased protection from predators for infants and reduced caretaking costs for the mother (as reviewed by Chism, 2000). However, increased costs include the danger of injury to the infant by incompetent handling, reduced opportunity to nurse (with the danger of "aunting to death" Hrdy, 1976), and a higher risk of predation if abandoned. The benefits of allomothering for the 'aunt' is assumed to be practice for motherhood, particularly for juvenile females (Lancaster, 1971).

Within the cercopithecines, many guenon mothers permit infant handling while baboon and macaque mothers restrict contact (Chism, 2000). Cercopithecines with early allomothering are characterized by birth seasonality, rapid rates of infant development and shorter periods of interbirth intervals, compared to cercopithecines without early allomothering (Chism, 2000). Vervet mothers are typically relaxed, allowing others to handle their infants at a young age and even leaving their infants with juvenile females (Lancaster, 1971). Allomothering typically occurs in the first three months of an infant's life (Lee, 1983), corresponding with the change of the black natal coat to the grey coat (see Chapter 2).

1.6. RESEARCH AIMS

Motherhood is costly, specifically the nutritional demands of lactation. The purpose of this thesis is to examine the strategies to cope with those costs. In Chapter Three, I will examine the nutritional quality of targeted diet items throughout motherhood. If Lee's (1987) findings are collaborated, then targeted food items should be of highest nutritional quality at peak lactation, which Lee (1987) defines as infant months one to two. In addition to food of high nutritional quality being available when mothers are most nutritionally stressed, lactating females may also be targeting higher quality nutritional items compared to non-lactating females, which will also be explored in Chapter Three. Furthermore, females may increase their caloric intake by increasing the amount of time they spend feeding in relation to their growing infant's nutritional demands, which is tested using Altmann's (1980) proposed maternal feeding time budget model. I will test the generality of Altmann's predicted model using my collected data and identify potential erroneous assumptions of the model associated with my study population. If females aren't increasing the among of time foraging as predicted by Altmann's model, changes in other activity levels with infant age will indicate potential conflicting demands. Furthermore, I will compare activity budgets of lactating females to non-lactating females to tease out differences due to infant demands rather than seasonal influences. I will also incorporate temperature and precipitation into a maternal feeding time budget model and determine the best predictor variables for maternal feeding time in Chapter Three.

In Chapter Four, the levels of investment (as measured by time in ventral contact) in individual offspring is evaluated in response to environmental conditions, infant sex, maternal dominance, maternal activity, and allocare provided by other individuals. I will compare investment in current offspring and delay in future offspring (as measured by inter-birth interval) in my troops at Samara to the Amboseli vervet monkey troops. The Trivers-Willard hypothesis and local resource competition hypothesis both predict that mothers will bias investment toward one sex versus the other, depending on the mother's condition in order to maximize inclusive fitness. Therefore, one of the objectives of Chapter Four is to determine if there is differential investment towards infant sex for mothers of different ranks, and if there is, whether the difference is as predicted by the Trivers-Willard hypothesis or the local resource competition hypothesis.   In addition, the gradual termination of investment (the weaning process) will be explored in relation to maternal activity, and whether maternal rejections reflect training the infant to nurse at opportune times. Lastly, in Chapter Four I will examine the rate of allomothering as the infant ages, as well as the maternal activity of the mother while the infant is off ventral contact.

My research aims for this thesis:

1. Test Altmann's maternal feeding time budget model during lactation

    a. Determine the deviations from the model

    b. Assess the violations of model assumptions

    c. Assess differences in time allocation between lactating and non-lactating females

d. Incorporate seasonal effects into a maternal feeding time budget model

2. Identify differences in individual investment levels based on current evolutionary hypotheses

   a. Examine the rate of decrease of infant contact and proximity to its mother over the infant's first seven months

   b. Qualitatively compared investment in my study troops to Amboseli vervet troops.

   c. Consider differences in investment based on maternal rank and infant sex

   d. Test the influence of maternal activity on infant contact times

   e. Explore the influence of allomothering on infant independence

The specific hypotheses and predictions tested are stated and explored in Chapters Three and Four. Chapter Two presents the study site and methods. Chapter Five summarizes the research findings and its implications.

CHAPTER TWO. STUDY SITE AND METHODS

2.1. INTRODUCTION

Vervet monkeys (*Chlorocebus aethiops*) are found in savanna regions throughout Africa, from Senegal to Ethiopia and Sudan to the tip of South Africa (Tappen, 1960), as well as on the colonized Caribbean islands of St. Kitts, Nevis and Barbados (Fedigan & Fedigan, 1988). They are part of the subfamily *Cercopithecinae,* which are the cheek pouch monkeys (Grubb et al., 2003). Originally classified as guenons in the *Cercopithecus* genus (Tappen, 1960), they have recently been suggested to be placed within their own genus, *Chlorocebus* (Grubb et al., 2003; Tosi, Melnick, & Disotell, 2004). The superspecies *aethiops* is known by several common names including vervets, green monkeys, grivets and tantalus monkeys (Fedigan & Fedigan, 1988). Other than baboons, they are "the most widely distributed and abundant of all African monkeys" (Struhsaker 1967b). The only limits for population expansion seem to be the availability of water and the presence of trees for sleeping (Fedigan & Fedigan, 1988).

Vervet monkeys are semi-terrestrial, foraging and moving equally well on the ground and in the trees, though they sleep up in the trees at night (Struhsaker, 1967b). They live in multi-male, multi-female groups (Struhsaker, 1967b), ranging in size from 5 to 76 individuals, with a mean of roughly 25 (Fedigan and Fedigan 1988). Females remain in their natal groups and males migrate roughly every 2.5 to 3 years (Cheney & Seyfarth, 1983; Henzi & Lucas, 1980; Struhsaker, 1967b). Typically the adult sex ratio is 1.5 females to one male in each troop (Fedigan and Fedigan 1988). Linear dominance

hiearchies are usually present within the troops (Struhsaker, 1967a), and are relatively stable in females and more variable in males (Bramblett, Bramblett, Bishop, & Coelho Jr., 1982).

Vervets are territorial with ranges varying from 13 to 178 hectares (Fedigan & Fedigan, 1988; Struhsaker, 1967c). The size of terrirotry seems to be dependent on the habitat quality and vegetation type (De Moor & Steffens, 1972; Struhsaker, 1967b). As opportunistic omnivores, vervets feed on a wide variety of plant species, insects and occasionally bird eggs and chicks (Struhsaker, 1967b). Various species of *Acacia* are an important component of the African monkeys' diet (eg. *Acacia xanthophloia* and *Acacia tortilla*) (Struhsaker, 1967b; Whitten, 1983; Wrangham & Waterman, 1981).

2.1.1. PHYSICAL FEATURES

Females reach an adult mass of 2.5 to 3.5kg and an average body length of 37cm, and males weigh 4.1 to 5.8 kg and an average body length of 41 cm (Bolter & Zihlman, 2006; Turner, Anapol, & Jolly, 1994, 1997). Females stop growing and reach sexual maturity when they are approximately three years old (Turner et al., 1997) and typically have their first infant when they are between three and five years old (Fairbanks & McGuire, 1984). Females usually give birth to a single offspring (Horrocks, 1986; Struhsaker, 1967a). Males on average reach sexual maturity around five years of age (Horrocks, 1986) at which point they typically stop growing (Turner et al., 1997).

Infants are born with black natal coats and pink faces, and begin getting a darker face colour when they are about one month old, a brow band when they are roughly two months old, and their adult grey fur when they are approximately three months old (Seier, 1986; Struhsaker, 1971, personal observation). The average birth weight is 358 g with a range of 233 to 488 g (Seier, 1986). Infants get their canines at 46 to 47 days of age and their first set of molars at 64 to 66 days of age (Seier, 1986). No sexual dimorphism in weight is apparent until about 39 months (Seier, 1986), though females have been noted to develop more rapidly on certain behavioural variables (Lee, 1984).

2.1.2. MATING AND BIRTH SEASONS

In wild populations of vervets, there is often a clear mating and birth season. In Amboseli, Kenya, the May to October copulation season corresponds with the dry season and the birth season is October to March, with a peak in November (Struhsaker, 1967b). The two rain periods in Amboseli are between November and December and March through May, and Struhsaker (1967) suggests it is the increase in food availability following the March rainy season that facilitates the transition to solid foods by infants. Lee (1987) found the highest nutritional quality corresponded with peak lactation frequencies and suggested the seasonal decline in food quality serves as a proximate cue for initiating weaning conflict. In contrast to the seasonal Amboseli births, the vervets (*Cercopithecus aethiops sabaeus*) in Barbados give birth throughout the year with a peak between April and July (Horrocks, 1986). The vervets in our study population are similar to the Amboseli vervets, with the most copulations occurring between April and August,

with a peak in May (Freeman, 2012). Gestation is approximately 165 days (Rowell, 1970) with an interbirth interval in the wild in the range of one to two years (Lee, 1984) (but captive populations can reproduce in one year or less (Fairbanks & McGuire, 1984; Rowell & Richards, 1979; Seier, 1986). Weaning is a slow and gradual process with the highest frequencies of rejection activities directed towards the infant when the infant is roughly three months old (Lee, 1984; Struhsaker, 1971), and continuing until suckling is terminated, typically when the infant is between eight and twelve months (Horrocks, 1986; Lee, 1987).

2.1.3 INFANTS

Juveniles, sub-adult females and adult females are attracted to young infants and frequently handle, groom and carry the infants (Lancaster, 1971; Struhsaker, 1967a). If the infant is clinging ventrally to a caretaker, other individuals may groom the caretaker while pulling on and trying to handle the infant (Lancaster, 1971). Generally adult males show little interest or response to infants, but do allow infants to climb over them (Struhsaker, 1967a, personal observation). Infanticide is rare in vervets although there have been exceptions such as cross-group infanticide, when males from one troop killed infants from another troop during intertroop encounters (Cheney & Seyfarth, 1987). Another exception occurred during the study when on one occasion, an infant jumped on a resident adult male's tail and the adult male turned around and grabbed the infant's neck in his jaws and then ran roughly 5m with the infant. The mother and other females

in the area chased the male and the male dropped the infant; the infant subsequently bled

out and died within 15 minutes (personal observation).

2.2. STUDY SITE

I conducted my study at Samara Game Reserve, in the Eastern Province of South Africa

(32 22^0 S, 24 52^0 E). The site is in the semi-arid karoo approximately 40 km from the

town of Graaff-Reinet (see Fig. 2.1). This population has been studied since 2008.
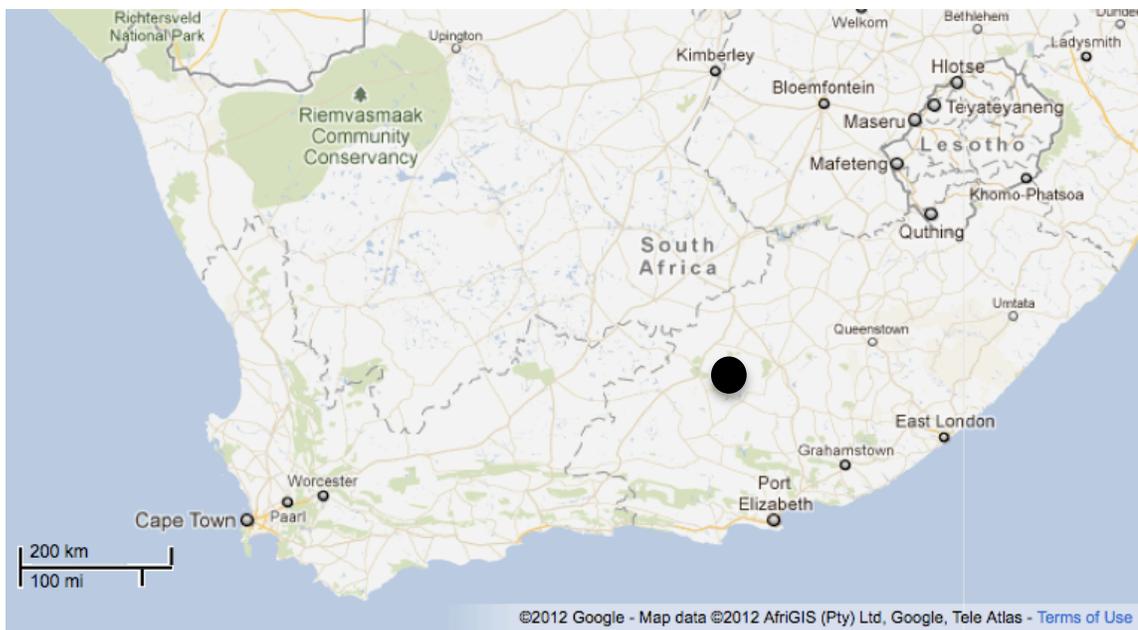
Fig. 2.1: Map of South Africa, study location indicated by the black dot. (Google, 2012)

The area is dominated by *Acacia karoo* woodland centered on the riverbeds, where the

rivers flow intermittently following a heavy rainfall (McDougall, Forshaw, Barrett, &

Henzi, 2010). The Milk River runs through the study site (see Fig. 2.2). Most monkey

troops in the area are centered on the riverbed and are larger than the average troop size,

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(mean=40) though there are still a few smaller troops (mean=12) that utilize the water

holes (Pasternak et al., 2011).

Fig. 2.2: The study site. (Google Maps)

In addition to vervets, buffalo (*Syncerus caffer*), white rhino (*Ceratotherium simum*),

zebra (*Equus burchellii*), giraffe (*Giraffa camelopardalis*), kudu **(***Tragelaphus*

strepsiceros), gemsbok (*Oryx Gazella Gazella), red hartebeest (*Alcelaphus buselaphus*),

duiker (*Sylvicapra grimmia), springbok (Antidorcas marsupialis*) and eland

(*Taurotragus oryx*) are also found on the reserve, along with chacma baboons (*Papio*

ursinus), aardvark (*Orycteropus afer*), warthog (*Phacochoerus africanus*), cape

porcupine (*Hystrix africaeaustralis)*, scrub hare (*Lepus saxatilis*), and meerkat (*Suricata suricatta).* Potential predators and animals of possible risk include the land carnivores cheetah (*Acinonyx jubatus*), caracal (*Caracal caracal*) and jackal (*Canis mesomelas*)), birds of prey (martial eagle (*Polemaetus bellicosus)* and black eagle (*Ictinaetus malayensis*)), and venomous snakes (specifically puff adders (*Bitis arietans*), cape cobra (*Naja nivea*) and boomslang (*Dispholidus typus*)). I didn't witness any predator attacks during my study although two monkeys (a female adult and a two year old juvenile) were found dead in the sleep site from confirmed puff adders bites.

2.3. CLIMATE

Mean annual rainfall in the area is 330 mm with most rain falling in the summer months (December-March) (McDougall et al., 2010). There was very little rain for the first few months of the study (the rainfall throughout the study duration is noted in Fig. 2.3a, courtesy of the South African Weather Service), which along with the draught conditions at the time, meant almost no standing water available. Heavy rains in January and February created flowing rivers or left many puddles for the hot summer months and by mid-April, there was a flowing river that remained for the duration of the study. Mean monthly temperature ranged from a low of $3.3^{\circ}\text{C} - 17.3^{\circ}\text{C}$ and a maximum of $18.7^{\circ}\text{C} - 33.^{\circ}\text{C}$ (see Figure 2.3b).
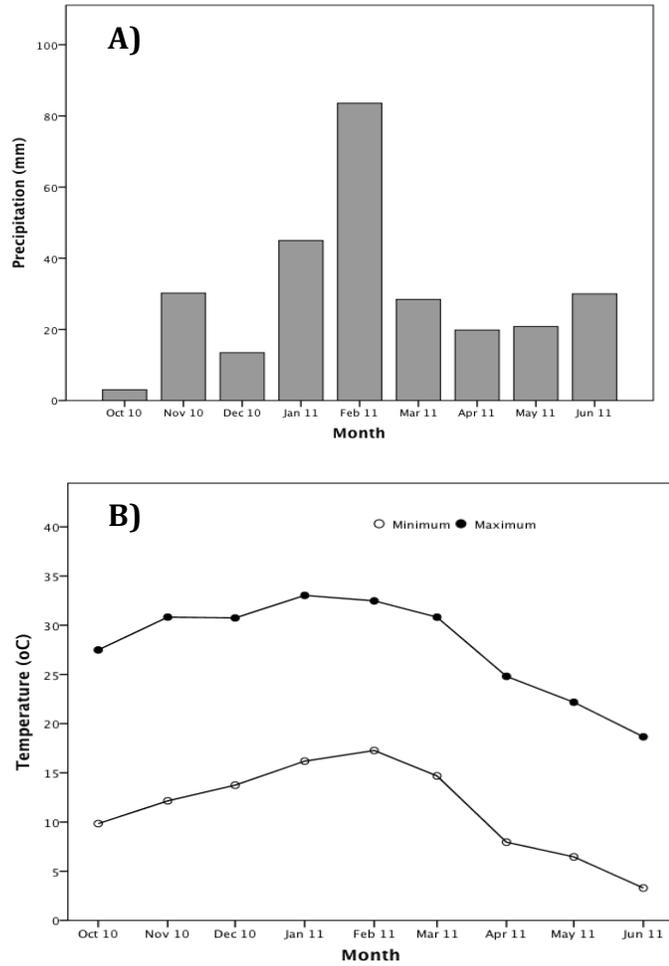
Figure 2.3: A) Monthly rainfall for the study period and B) Monthly mean maximum and minimum temperatures for the study season (October 2010 – June 2011).

2.4. STUDY ANIMALS

I collected data from two troops of monkeys: Riverside Troop (RST) and Riverbend Mob (RBM). They have been under observation since September 2008. The females and juveniles are generally well habituated; migrant males are often skittish but habituated

over time. Adult individuals were individually recognizable through facial and other

markings. The age group classification for the two troops is listed in Table 2.1.

Table 2.1: Age group classification for the two study troops in October 2010 (before the
birth season).

AGE/SEX CLASS	RIVERSIDE TROOP (RST)	RIVERBEND MOB (RST)
Adult males	14	9
Adult females	20	14
Juveniles	33	18
2009 infants	5	8
Total	**72**	**49**

The two troops occupy overlapping territories along the Milk River. Four adjacent troops

occupied bordering or overlapping territories along the riverbed: Happy Campers (HC),

South West Troop (SWT), Picnic Troop (PT) and Lodge Troop (LT).

2.4.1. RIVERSIDE TROOP (RST)

Riverside troop maintained a single sleeping site consisting of several tall trees. They

had intertroop encounters (ITEs) with Picnic Troop (PT), Southwest Troop (SWT) and

RBM. In February, three to four of the females without young infants and a couple of

juveniles would split away from the troop to forage, rest and groom until meeting up with

the rest of the troop before returning to sleep site at the end of the day. By May, the

entire troop split up during the day with individuals or small groups spread throughout the home range. A few males occasionally joined the troop in the 2011 mating season, with only two males immigrating into the troop by the end of the mating season.

2.4.2. RIVERBEND MOB (RBM)

Riverbend mob consistently used two different sleeping sites. Their territory overlapped with Picnic Troop, Lodge Troop and RST. The monkeys in RBM tended to stick together, though they were more widely dispersed from May onwards. In the 2011 mating season, there was an influx of new males with seven males immigrating into the troop by August 2011.

2.4.3. STUDY FEMALES

All habituated adult females were selected as focal subjects (Altmann, 1974). One female in each troop was poorly habituated and rarely seen, and these were excluded from data collection. For the purpose of this study, a female was considered an adult if she had given birth or was classified as adult by size and copulation solicitations when the troops were first habituated. A description of the focal subjects is given in Table 2.2. A female was used as a baseline female if she was an adult and did not give birth during the 2010 birth season. Fig. 2.4 illustrates the age of the infants that was captured over the study duration. In many cases, the last couple months of pregnancy were captured in data collection, as depicted by the months preceding birth.

Table 2.2: Descriptions of focal subjects.

Troop	ID	Rank[1]	Parity[2]	Infant sex[3]	Infant D.O.B.[4]	Infant D.O.D.[5]	Female D.O.D.	Surviving infant from 2009?[6]
MOTHERS								
RST	Au	0.64	P	M	23-Nov-10	04-Jan-11	04-Jan-11	-
	Cl	0.63	M	U	29-Oct-10	23-Dec-10	2-Jan-11	na
	Dt	0.84	M	U	20-Sep-10	22-Sep-10	-	na
	El	0.67	M	M	25-Dec-10	-	-	na
	Gl	0.30	M	F	17-Dec-10	14-Apr-11	-	Y
	He	0.80	M	F	13-Nov-10	-	-	na
	Iz	0.93	M	M	21-Dec-10	-	-	Y
	Li	0.42	M	U	28-Oct-10	11-Dec-10	01-Feb-11	na
	Pr	0.90	P	M	24-Nov-10	-	-	-
	Te	0.61	M	F	27-Nov-10	-	-	Y
	Um	0.63	M	F	05-Nov-10	-	-	na
	Wi	0.75	M	F	24-Oct-10	-	-	na
	Xa	0.54	M	F	19-Nov-10	-	-	na
	Ye	0.45	P	F	20-Nov-10	-	-	-
RBM	Ae	1.00	M	U	31-Oct-10	23-Nov-10	23-Nov-10	Y
	Ds	0.54	M	M	04-Nov-10	07-Mar-11	07-Mar-10	Y
	Fa	0.99	M	F	06-Oct-10	-	-	na
	Gi	0.49	M	M	23-Nov-10	-	-	Y
	Ho	0.35	M	M	27-Dec-10	-	-	Y
	Lo	0.70	M	F	17-Oct-10	-	-	na
	Oc	0.20	M	F	25-Oct-10	04-Dec-10	-	N
	Pe	0.50	M	U	24-Nov-10	09-Dec-10	-	Y
	Sa	0.85	M	M	31-Oct-10	-	-	Y
	Sc	0.83	P	M	11-Oct-10	25-Nov-10	-	-
	Ts	0.69	M	F	03-Nov-10	-	-	Y
BASELINE								
RST	Fe	0.40		-	-	-	-	na
	Je	0.54		-	-	-	29-Dec-10	na
	Ki	0.33		-	-	-	-	na
	Me	1.00		-	-	-	-	Y
	Ni	0.62		-	-	-	-	na
	Ru	0.51		-	-	-	-	Y
RBM	Mi	0.59		-	-	-	-	Y
	Va	0.35		-	-	-	-	na

1. Rank by standardized David's score, 2= Multiparous/Primiparous, 3-M=male F=female, 4. D.O.B.= Date of Birth, 5. D.O.D. = Date of Death or Disappearance, 6. Y= Yes, N=No, na= not applicable (did not have an infant in the previous year).
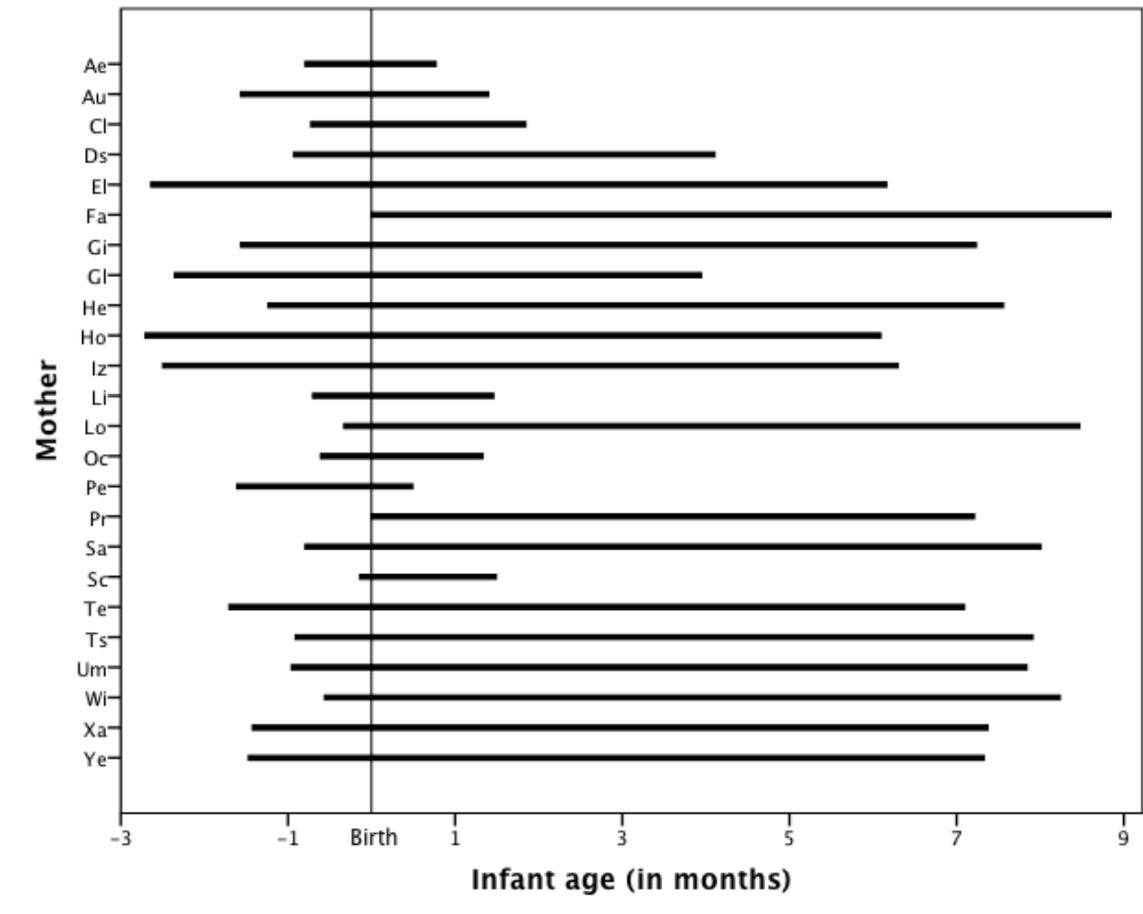
Figure 2.4: Infant age during data collection.

2.5. BEHAVIOURAL SAMPLING TECHNIQUES

Troops were followed for ten hours a day, either capturing the first ten hours starting at sunrise (starting between 04:30h-07:00h) or the last ten hours finishing at sunset (ending between 1700h-1900h). This sampling strategy was used due to marked variation in daylight hours between the seasons, with over four hours more daylight in the summer compared to winter. Behavioural data collection started October 2010 and ended in June 2011.

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2.5.1 FOCAL ANIMALS SAMPLES

The day was divided into four time periods, each two and a half to four hours in length

depending on the time of year. Since there are diurnal changes in female's activity

budgets (Baldellou & Adan, 1997; Harrison, 1985), each female subject was sampled at

least once per time block per month, often twice. Focal animal samples were 20 minutes

in length. If the focal subject went out of the observer's sight for more than five minutes,

the focal was stopped. A female was never focaled within three hours of her previous

focal sample. Table 2.3 shows the total focal times for the individual months.

Behavioural data were recorded on hand-held Recon and Janem devices using Pendragon

Forms©.

Table 2.3: Summary of focal data collected (in minutes per month) for pregnant females, mothers, and baseline females.

Month	Pregnant females	*n*	Mothers	*n*	Baseline females	*n*
Oct 10	3583	21	727	5	990	7
Nov 10	2397	11	3679	19	1353	6
Dec 10	511	4	2781	21	1125	7
Jan 11			3326	17	1342	7
Feb 11			3152	17	1286	7
Mar 11			3669	17	1473	7
Apr 11			1926	16	844	7
May 11			2952	15	1348	7
Jun 11			1794	15	829	7
	Pregnant		**Mothers**		**Baseline**	
Total (min)	6492		24007		10591	

Instantaneous point samples were taken at two minutes intervals recording:

i. The activity of the focal female (see Table 2.4). If the focal female was a mother or was holding an infant, the activity of the infant was also included (with the same categories as in Table 2.4 with the addition of nursing and resting ventral)

ii. The location of the focal female (Ground (<2m to a tree or shrub), Open (>2m to a tree or shrub), Shrub or Tree)

iii. If the focal female was a mother, the infant distance (nipple, ventral, within 1m, 2m, 5m, or >5m) was recorded and if the infant was in distress (vocal, squirm or tantrum)

iv. The neighbours within 5m of the focal female and infant (if applicable). The identity of the adults were noted with the distance (in contact, within 1m, 3m, or 5m) and the number of juveniles within 5m

Table 2.4: Activity categories for point samples.

Activity	Subdivision
Foraging	Specific food item
Moving	Walk/run/climb
Resting	Lay/sit/stand/autogroom
Social	Is grooming/ is being groomed, playing, agonistic interaction, copulating
Grooming infant	Mothers grooming their own infant

The following data were recorded continuously during the focal sample:

i.   Social interactions of the focal female and/or her infant (if applicable) with the

        identity of the partner (see Table 2.5)

ii.   Changes in distance between the mother and infant (nipple/ventral/contact/2m,

        5m, >5m), indicating the individual responsible for the transition if noticeable

iii.   Grooming bouts (durations) of the focal female with the identity of the partner

Table 2.5: Interactions between focal female and her infant or another individual
recorded continuously.

Activity	Description
Approach/leaves	To/by the mother within 2m
Aggression	Threats to/by the mother
Allomothering attempts	To/by the mother, with the following data recorded: - Distance of actor to guardian - Guardian activity (Foraging, Moving, Resting or Social) - Action toward infant (Reach, Contact, Groom, Take) - Guardian response (Guardian resist (Yes/No) - Infant resist (Yes/No) - Infant transferred (Yes/No)
Reject from nipple/ventral	Mother stops access to nipple or ventral through either: - Passive: obstructing the access to the nipple/ventral by pulling the nipple up or making a slight movement away from the infant - Active: pushing the infant away or being aggressive towards the infant if couldn't distinguish nipple contact from ventral, ventral was used
Tantrum	Infant response (shriek, jump, tactile) Mother response (ignore, turn back, eye threat, nips, push, allow ventral/nipple)
Sociosexual act	Initiator (Male, Female, Unknown) Female present (yes/no) Copulation act (grab, mount, copulate)

Ad libitum records were maintained on aggressive and sociosexual beahviour whenever they were witnessed using the same categories as in Table 2.5. Events such as predator calls and intertroop encounters (ITE's) were recorded with identity of the individuals involved and a GPS point was taken for the location. GPS points were taken every 30 minutes to monitor troop movement throughout the day.

2.6. NUTRITIONAL ANALYSES

Samples were taken of 28 plant parts from 12 species that make up > 80% of the vervets diet (Pasternak, Barrett and Henzi, unpublished data), and analyzed at the University of Free State to provide data on total crude protein (g RP/ kg DM) and total energy (MJ / kg DM) (Table 2.6). Ground level plants weren't identified to the species level; therefore, the average of the three ground plant species was used, which composed roughly 23% of the vervets diet. The raw protein value is potentially a conservative estimate, since it's possible the vervets were targeting *Cynodon incompletus* which has higher raw protein than the other two species. When the digging values were unknown (roughly 7% of the diet), the average was taken of the two species possibilities. Termites and ants were the most frequent insects eaten (with insects composing an average of 6% of the diet); therefore, the average value for the African termite was used (crude protein raw 204 g/ Kg, energy 14.91MJ/ kg) (Bukkens, 1997). Since the samples were only taken once, and some of the values are averages, the nutritional quality is a very rough estimate.

Table 2.6: Crude protein (in g RP per kilogram of dried mass) and total energy (in mJ per kilogram of dried mass) of plant values.

Sample		RP (g RP / kg DM)	Total energy (MJ/ kg DM)
Acacia karoo	Sap	15.7	13.25
	leaves	155.6	19.08
	pods	275.4	19.87
	flowers	166.0	18.84
	dry pods	280.9	18.91
Lycium cenaruium	berries	222.0	21.52
	flowers	306.3	18.83
Schinus molle	pods	97.0	20.29
Lycium cenaruium	flowers	240.7	17.61
Asparagus retrofractus	root	167.3	6.63
Grewia robusta	berries	79.7	18.38
	flowers	166.8	17.91
Carissa bispinosa	berries	69	23.04
Sceletium	leaves	307.5	13.02
Rhus lancea	berries	89.8	18.88
Rhus longispina	berries	170.5	16.96
Diospyros lyciodes	berries	83.0	19.42
	leaves	194.0	20.08
	flowers	167.5	19.03
Ground plants[a]			
Drosanthemom spp		226.0	12.85
Helictotrichon turgidulum		226.4	17.66
Cynodon incompletus and		323.7	18.37
Panicum maximum			
	Mean	258.7	16.29
Digging unknown[b]	Mean	224	12.27
Insects[c]		204	14.91

a. Ground plants weren't species classified during data collection. As a result, the mean from the possibilities was used. b. When digging was indistinguishable, the mean of the two most common possibilties (*Acacia karoo* dried pods and *Asparagus retrofractus* was used). c. the value for the African termite was used as an average for insect protein and energy (from Bukkens 1997)

The percentage of each of food item ingested while foraging per individual per month of infant life was then calculated. The average protein intake was determined by multiplying the percentage of each food item in the diet by its crude protein value over the total percentage of known food items.   The same procedure was used to calculate total energy intake.

2.7. DOMINANCE HIEARCHY

All observed agonistic interactions between adult females within both troops were recorded. If there was a clear winner and loser, it was noted on an interaction matrix with the "winner" assigned a "1" for the interaction and the "loser" assigned a "0". The sum values in the interaction matrix were used to calculate David scores, which is based on the unweighted and weighted sum of the number of wins and losses (David, 1987). By using the David score, defeating a low ranking animal is weighted less than defeating a high ranking one (De Vries, Stevens, & Vervaecke, 2006). The David score is preferred over other measures of dominance ranking such as the popular Clutton-Brock et al.'s index since it takes into consideration repeated interactions between individuals (Gammell, De Vries, Jennings, Carlin, & Hayden, 2003). Normalized David scores were calculated to factor in the maximum achievable David score within a group given its size (De Vries et al., 2006). Lastly, in order to pool the data from both troops, the normalized David scores within each troop were divided by the highest David score for that troop, giving standardized values with a range between zero and one.

2.8. DATA ANALYSIS

A minimum of one focal per time block per month (minimum of 80 minutes) was required in order to be included in analysis. This restriction was applied for either grouping by calendar month or month of infant age. Data were tested for normality using SPSS 19.0 ®. Unless otherwise stated data were not found to deviate from a normal distribution and parametric tests were used for analyses. When data did deviate, a transformation was applied in an attempt to achieve normality. If a transform could not be applied, an equivalent, non-parametric statistical test was used. All univariate analyses were conducted in SPSS 19.0®. Multivariate analyses were conducted in JMP 9 ® using the default values of the "Fit Model" platform with Subject ID as a random factor for analyses with repeated measures since it would otherwise violate the assumptions of simple regression models. Seasonal effects were incorporated into maternal time budget components using linear mixed modeling in RStudio Version 0.95®, with the add-on 'nlme' and 'MuMIn' packages. The specific analyses are described in each section.

CHAPTER THREE. INVESTIGATING ALTMANN'S MATERNAL TIME BUDGET MODEL

3.1. INTRODUCTION

Lactation is generally considered the most energetically expensive phase of reproduction in female mammals, with energy intake ranging from 66 to 188% of that taken in by non-lactating females (Glittleman & Thompson, 1988). Most female primates are faced with an additional challenge since they are "dual-career mothers in a complex ecological and social setting" (p. 6 Altmann 1980): caring for their infant while going about their daily activities, including maintaining their social affiliations. In order to address the compromises faced by females during lactation, Altmann (1980) developed a model of feeding time for baboon mothers. This predicted the extra feeding time that would be necessary for mothers to maintain their own body weight while also providing all the energy requirements of their growing infant. The percentage of a time that a mother needs to spend feeding (f_t) when her infant is at age t (in days) is given by:

$$f_t = Am^{.75} + \frac{A(i_o + t\Delta i)^{.75}}{E}$$

where $A=$ a constant that converts energy requirements into feeding time (by dividing feeding time immediately at birth by the mother and infant weight to the power of 0.75); $m=$ mother's body weight in kg; $i_o=$ infant weight (in kg) at birth (both infant and

mother's weight are scaled to the 0.75 power to estimate energetic requirements in accordance with Kleiber's law); Δi= change of infant weight per unit time (kg/day); E= net efficiency of lactation and of assimilation by the infant (estimated by Altmann (1980) to be 0.80).

As is usual in such cases, Altmann (1980) made several simplifying assumptions in the construction of the model:

i. Feeding efficiency is constant (i.e., the value of A is unaffected by changes in dietary quality).

ii. Infant growth rates remain constant over the first year of life. In addition, the energy an infant requires is used only to maintain its own weight, not to produce new tissue.

iii. A non-pregnant non-lactating female has the same energy requirements as a female in late pregnancy of the same weight.

iv. Infant and maternal activity levels remain constant and infant activity levels are the same as its mother's.

v. Socializing is considered to be "uncommitted" time from which extra feeding time can be drawn.

When Altmann (1980) tested the model against her own baboon data from Amboseli, she observed an increase in the amount of time feeding across the lactational period as the model predicted, although feeding time fell below the actual predicted values; in other words, the model provided a good qualitative fit, but a poor quantitative fit. Altmann (1980) concluded that mothers' probably weren't maintaining their own weight and that,

over time, infants also obtained some of their own food, and were not solely dependent on lactation. Bercovitch (1987) confirmed that lactating females do lose weight, in a study of olive baboons: he found that lactating females weighed 7% less than cycling females. In addition, the assumption that extra time spent feeding results in decreased time spent socializing may have been violated, although this wasn't tested directly. Using Altmann's Amboseli data, Dunbar et al. (2002) found that including precipitation improved the fit of the model, with more precipitation in the previous two months resulting in less time needing to feed, and concluded that maternal feeding time was a function of both infant demand and nutritional quality.

Altmann's model has subsequently been tested in several other baboon populations: gelada baboons (*Theropithecus gelada*) in the Simen Mountain National Park (Dunbar & Dunbar, 1988; Dunbar et al., 2002), olive baboons (*Papio cynocephalus anubis*) in Laikipia Kenya (Kenyatta, 1995), and chacma baboons (*Papio hamadryas ursinus)* at De Hoop Nature Reserve, South Africa (Barrett et al., 2006a) and the Drakensberg Mountains, South Africa (Lycett, Henzi, & Barrett, 1998). It has also been tested recently in a lesser ape species, the siamang (*Symphalangus syndactylus)* (Lappan, 2009).

When Dunbar and Dunbar (1988) tested the model, they found that, like Altmann's yellow baboons, gelada mothers increased feeding time during lactation, but unlike Altmann's study, gelada mothers' feeding times were above model predictions from months two to five of infant life. In addition, they found that gelada mothers used resting time for additional time spent feeding before giving up social time. Using the same

dataset, Dunbar et al. (2002), found that cumulative rainfall, temperature (^{o}C) and infant age were all significant factors influencing time a lactating female spent feeding in the gelada baboons. Lycett et al. (1998) also found that mothers' observed feeding time exceeded the model predictions in chacma baboons, to an even greater extent than gelada. Moreover, they observed that even non-lactating females' feeding times exceeded the model predictions, leading them to suggest that Drakensberg females are more adversely affected by infant demands than other baboon populations.

Testing the model on olive baboons, Kenyatta (1995) noted a positive relationship between infant age and mothers' feeding time, although, as with Altmann's original study, there was a poor quantitative fit with the data, with very little of the variance explained by either a linear or power relationship. In comparison to females without infants, Kenyatta (1995) also showed that mothers actually spent less time feeding in the second month of infant life and only increased feeding time above non-lactating females when the infant was five months of age and older. As a consequence, her mothers spent more, not less, time resting and socializing in the infant's earliest months of life. Kenyatta (1995) suggested that, in this population, mothers may have been employing a energy conservation strategy, and actively attempting to rest more in order to decrease their energy expenditure throughout the day.

Barrett et al. (2006a) followed on from Kenyatta's (1995) work, with a study on chacma baboons. They found that feeding time fell below model predictions across the entire lactational period, with no evidence of increased time feeding over infant age. Like

Kenyatta's study, mothers seemed to be actively increasing resting time as part of an energy sparing strategy. Barrett et al. (2006) also found, however, that mothers were significantly more vigilant during lactation compared to non-lacting females (and also compared to periods when they themselves were not lactating), and suggested that increased resting time could also serve to increase the amount of time spent vigilant. As predators were absent in this habitat, they concluded that high rates of infanticide (which are characteristic of chacma baboons populations) may have been responsible for the increased amount of time spent vigilant by mothers with vulnerable infants (Barrett et al., 2006a). Barrett et al. (2006) tested seasonal influences but found no significant effect of mean temperature or cumulative rainfall on maternal feeding time.

Barrett et al. (2006) also examined all previous baboon studies that tested Altmann's model in relation to environmental variables, and found a negative correlation between mean temperature and the degree to which observed data deviated from the model's prediction. Specifically, they showed that in habitats with a low mean annual temperature, maternal feedings times tended to sit above the line predicted by Altmann's model, whereas maternal feeding time fell below prediction in habitats with a higher mean annual temperature. They suggested populations with observed feeding times that fell above the predictions lived in lower quality habitats.

The main factors that influence habitat, and so nutritional quality, are temperature and precipitation: animals need to increase the amount of time spent feeding when nutritional quality is low (Dunbar et al., 2002). Annual rainfall is positively correlated to net

primary productivity in tropical savannah (Pandey & Singh, 1992) as well as grassland biomass in southern Africa (Deshmukh, 1984). Temperature has a less clear effect on productivity. Dunbar (1992a) found that grass cover and protein content have a negative quadratic relationship with temperature, indicating productivity is lowest at both low and high temperature extremes. When analyzing their gelada data, Dunbar et al. (2002) noted a significant positive relationship between temperature and amount time feeding, suggesting this was due to the negative effects high temperatures have on nutritional quality. Similarly, Sims et al. (2008) found that in non-drought environments gross primary productivity increased in a linear manner with temperature, but was best described by a bell-shape relationship in drought environments, with optimum productivity around 30°C. Low temperatures also have increased metabolic costs, due to increased energy needed to maintain internal body temperature (Kleiber, 1961; Tokura, Hara, Okada, Mekata, & Ohsawa, 1975). Populations in lower temperatures have been found to spend significantly more time feeding compared to populations in warmer temperatures in baboon populations (Dunbar, 1992b) and klipspringer populations (Dunbar, 1979). Iwamoto and Dunbar (1983) found that time spent feeding by gelada increased with ambient temperature even when controlling for nutrient quality, in the manner predicted by energetic demands of thermoregulation.

The variability of environments and nutrient quality has a large impact on reproductive strategies. In some of the aforementioned baboons populations, there is a birth peak, with a majority of conceptions occurring in the months following rain, when food resources are plentiful (Altmann, 1980; Dunbar, 1984; Lycett, Weingrill, & Henzi, 1999). Despite

certain birth peaks, the baboons are able to give birth throughout the year, which is the exception rather than a rule for cercopithecine primates (Lindburg, 1987). Lee (Lee, 1987; Lee & Hauser, 1998) found that, in her studies of the Amboseli vervet population, peak nutritional quality corresponded to peak lactation, suggesting that birth seasonality ensured mothers obtained sufficient nutrients when they were in the most reproductively stressed phase of reproduction. Given that vervets have potentially been selected to reproduce at times when they can obtain the highest quality diet at the point when they have the highest lactation demands, it becomes interesting to test whether they still increase the amount of time spent feeding as predicted by Altmann's model. Therefore, the objectives and predictions for this chapter are:

1. To test Altmann's maternal time budget model in a seasonally breeding old-world monkey, *Chlorocebus aethiops.*

2. To test the assumptions of the model by comparing activity budgets between mothers and non-pregnant, non-lactating females, and by examining activity budget trade-offs amongst mothers.

  - I predict lactating females will feed more than non-lactating females.
  - I predict extra time feeding will come from time resting, conserving social time as suggested by Dunbar and Dunbar (1988).

3. To determine the influential seasonal factors that predict the amount of time that lactating females spend foraging.

  - If peak nutrient quality corresponds with peak lactation, then I predict mothers may not be increasing the time they spend feeding; rather, dietary quality will be highest during that time. In addition, environmental

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variables (temperature and precipitation) should significantly factor into a maternal feeding time budget model.

3.2. METHODS

3.2.1. DATA COLLECTION

I collected behavioural data between October 2010 and June 2011 on two troops of vervet monkeys located in the Samara Game Reserve, Eastern Cape, South Africa. The troops consisted of 49 to 72 individuals, with the adults recognizable through individual markings. The troops were generally well habituated and could be followed from a distance of two to five meters. Detailed descriptions of the study area, study animals and behavioural observations are given in Chapter 2.

As with all vervet populations, births at Samara are seasonal, with all the births in the 2010 birth season occurring between September and December, following a similar pattern to those reported in Amboseli (Lee, 1984; Struhsaker, 1971). I conducted focal animal sampling (Altmann, 1974) on all but two females (who were poorly habituated), allowing for comparisons between lactating and non-lactating non-pregnant (baseline) females. Each sampling day was divided into four equal time periods (early morning, late morning, early afternoon and late afternoon) varying in length depending on the time of year. Focal samples were 20 minutes in length, though they were terminated if the focal animal was out of sight for more than five minutes. If mother and infant were

separated, I followed the mother. As a result, infant foraging time was recorded only as a

percentage of the time they spent within five meters of their mother. Data on female

activity budgets were collected via instantaneous scans collected every two minutes

throughout the focal, with female activity allocated to one of four mutually exclusive

categories: feeding, moving, resting and socializing, with an extra fifth category of

"grooming infant" for lactating females only. Social interactions between mother and

infant and between mothers and other group members were recorded continuously (see

Table 2.5).

Focal scan data were used to calculate the time allocated to each activity as a percentage

of overall activity for each sample female for each month of infant life. A minimum of

one focal sample per time period per month (i.e., a minimum of 80 minutes) was required

for a given female to be included in analyses. On average, females were sampled twice

per time block per month (average sampling per individual per month = 179 min ± sd

43min). Percentage data were used to compare observed data to the predictions of

Altmann's model. For all other analyses, data were converted to hours to account for

variation in day length (Barrett et al., 2006a), since day length in the winter months is

roughly 4.5 hours shorter than in the summer months.

3.2.2. PARAMETER VALUES FOR ALTMANN'S MODEL

The values used for vervets used to generate predicted feeding time from Altmann's

model are listed in Table 3.1.

Table 3.1: Values for maternal time budget model.

Symbol	Description	Value	Reference
i_o	Vervet neotal weight	0.430 kg	*Lee (1991)*
Δi	Change in infant weight	0.003 kg/day or 0.005 kg/day	*Lee (1987) Seier (1986)*
M	Maternal weight	3.142 kg	*Fuller, Mitchell, Barrett and Henzi unpublished data**
fp	Percent of time feeding before giving birth	34.95%	*This thesis*
$A = \dfrac{fp}{(m + i_o)^{.75}}$	Coefficient of energy ingestion during lactation	13.45	*This thesis*

* average of 9 females across the two troops that were darted and weighed as part of another study at Samara in September 2010

3.2.3. ENVIRONMENTAL VARIABLES

Average daily temperature (^{o}C) and total precipitation (mm) per day throughout the study was available from the South African Weather Bureau station in the town of Graaff-Reinet, located approximately 50km from the study site. These data were used to calculate average monthly temperature and cumulative rainfall for the two months preceding the study month (to be comparable with Dunbar *et al.* 2002 and Barrett *et al.* 2006).

3.2.4. NUTRITIONAL ANALYSES

The procedure for nutritional analyses is described in Chapter 2, section 2.6.

3.2.5. STATISTICAL ANALYSES

Data were tested for normality using SPSS 19.0 ®.   Unless otherwise stated data were

not found to deviate from a normal distribution and parametric tests were used for

analyses.   When data did deviate, a transformation was applied in an attempt to achieve

normality. If a transform could not be applied, an equivalent, non-parametric statistical

test was used. All univariate analyses were conducted in SPSS 19.0®. Multivariate

analyses were conducted in JMP 9 ® using the default values of the "Fit Model" platform

with Subject ID as a random factor for analyses with repeated measures since it would

otherwise violate the assumptions of simple regression models. Seasonal effects were

incorporated into maternal time budget components using linear mixed modeling in

RStudio Version 0.95 ®, with the add-on 'nlme' and 'MuMIn' packages. The specific

analyses are described in each section.

3.3. RESULTS

3.3.1. TROOP COMPARISONS

Lactating females activity budgets for the two troops are shown in Figure 3.1. In order to determine if troop data could be pooled, standard least squares regression with restricted maximum likelihood (REML) method was used. The percent of time mothers spent foraging was listed as the dependent variable, subject I.D. as a random factor and infant age (in months), troop and the interaction between troop and infant age were entered as model effects. There was a significant main effect of both month ($F=68.41$, $p<0.0001$), and troop ($F=5.92$, $p=0.029$) but no significant interaction between infant age and troop ($F=2.29$, $p=0.13$). Due to the differences in troops, data were analyzed separately when examining percentage of maternal feeding time over infant age (pooled data is presented in Appendix A).
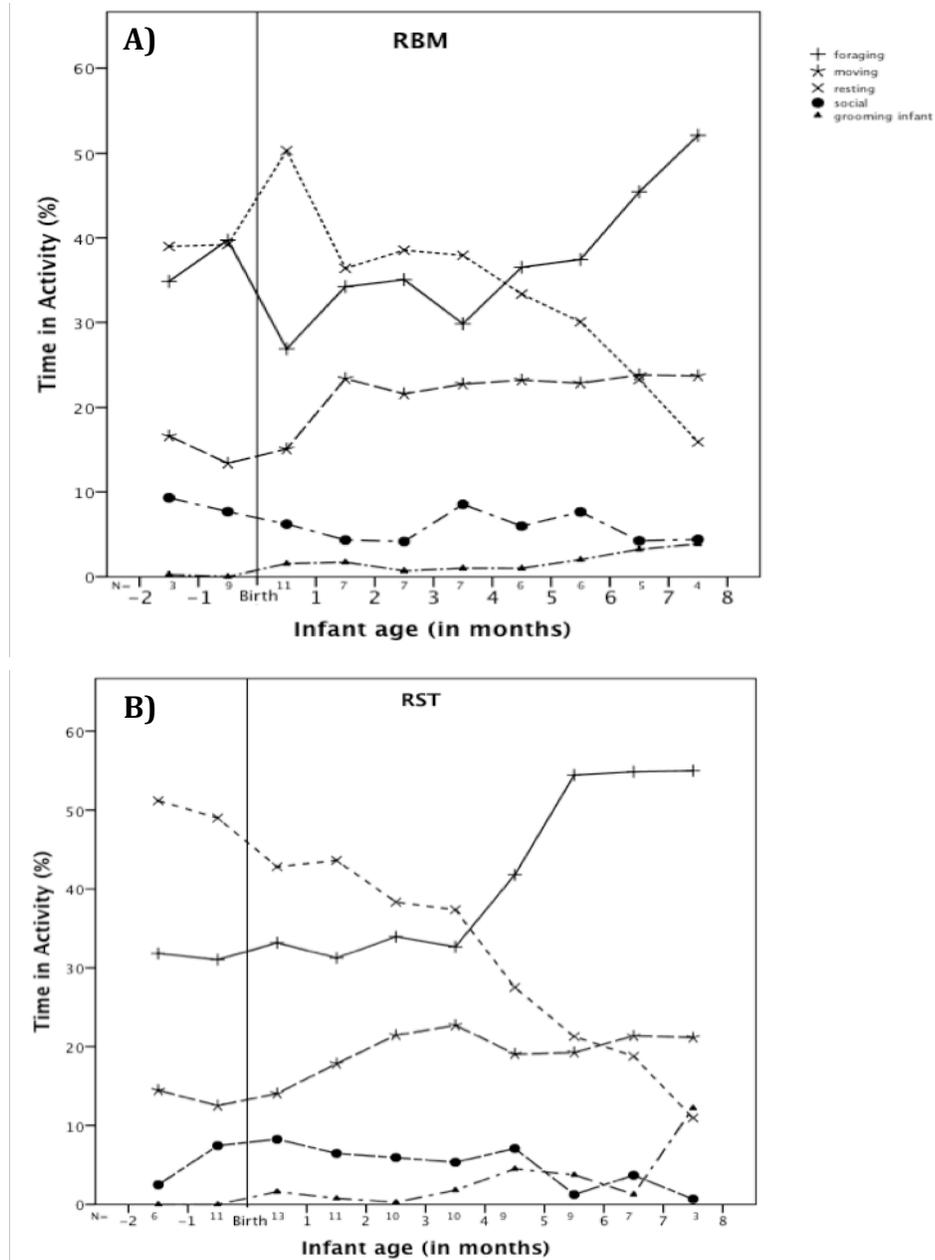
Figure 3.1: Mean activity budget of mothers over infant age (in months) for A) RBM and B) RST. Sample sizes are listed below the x-axis.

The same procedures (standard least squares regression with REML method) were used

to determine if baseline female data could be pooled. The time (in hours) females spent

in one of the four activities (foraging, moving, resting, and social) was listed as the

dependent variable, subject I.D. as a random factor and calendar month, troop and the

interaction between troop and calendar months were entered as model effects. The main

effects and interactions for each of the activities are presented in Table 3.2.

Table 3.2: Standard least squares regression of activity (in hours) over calendar months
by troop with female I.D. as a random effect.

		Df	F-ratio	p-value
Foraging	Month	8	2.94	0.012*
	Troop	1	0.08	0.778
	Month X Troop	8	0.25	0.979
Moving	Month	8	5.41	<0.001*
	Troop	1	2.49	0.123
	Month X Troop	8	3.04	0.010*
Resting	Month	8	5.62	<0.001*
	Troop	1	0.15	0.705
	Month X Troop	8	1.03	0.432
Social	Month	8	0.85	0.563
	Troop	1	0.14	0.713
	Month X Troop	8	2.36	0.035*

*$p<0.05$

Due to the significant difference between troops and months in time moving and social,

baseline data on females could not be pooled across troops for comparison to lactating

females (see Appendix A for pooled data). Since there were only two baseline females in

RBM, activity budget comparisons of lactating to baseline females were performed on

RST only (see Figure 3.2 for activity budget of RST baseline females). Differences in rank between mothers and baseline females in RST were tested using independent t-tests for each calendar month and were not significant (largest difference was in May, t=1.127, p=0.282).
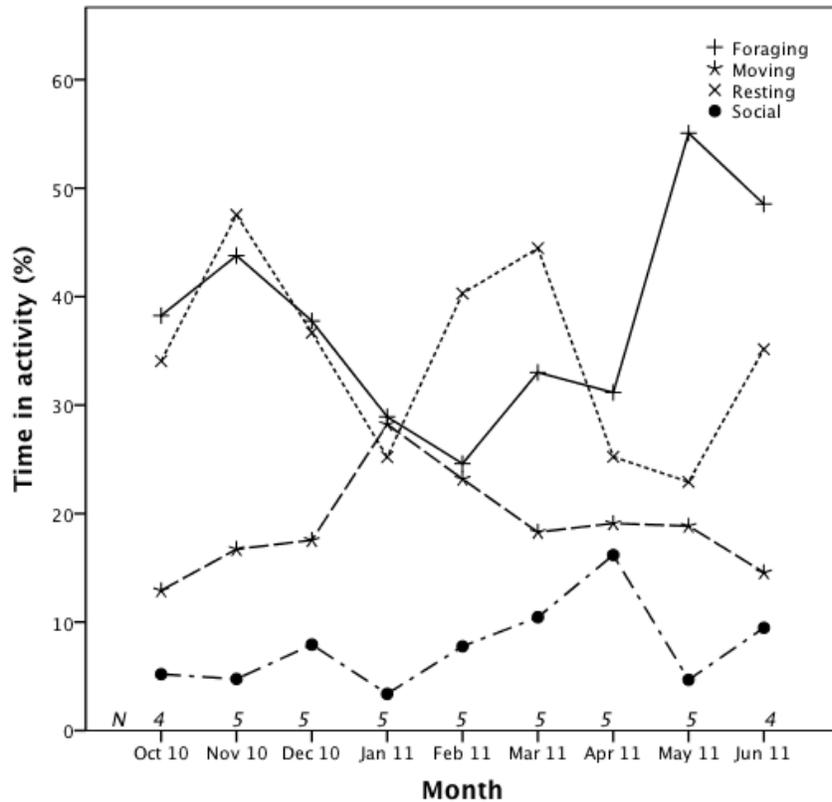
Figure 3.2: Activity budget of the RST baseline females for the duration of the study.

3.3.2. TESTING ALTMANN'S MODEL

Standard Least Squares regression with REML for each troop was used to assess the relationship between maternal feeding time and infant age, with Mother I.D. entered as a random effect. There was a statistically significant relationship between infant age and

percent of time spent foraging (RBM: t=4.65, p<0.0001, df=1, adjusted R^2= 0.4190; RST: t=7.00, p<0.0001, df=1, adjusted R^2= 0.3826), which is given by the equations:

$f_t = 25.85 + 2.64i_{age}$ RBM; $f_t = 26.46 + 3.95i_{age}$ RST.

Given the significant relationship between infant age and maternal feeding time, maternal feeding time was compared to Altmann's predicted model for both troops (Figure 3.3). Altmann's predicted feeding times are represented by the dotted lines. As depicted by the graph, percentage of feeding time does increase over time, although observed and predicted levels are significantly different until month four of infant life, as indicated by the confidence intervals, and the mean feeding time does not reach that predicted until month five for RST and month seven for RBM. Overall, then, there was a good qualitative fit between observed and predicted values, i.e., the overall shape of both graphs conformed to prediction, despite observed values generally falling below those predicted (correlation of mean monthly values and predicted RBM: Δi=0.003kg/day: r=0.881, p=0.005; Δi= 0.005kg/day: r=0.870, p=0.005; N=8; RST: Δi=0.003kg/day: r=0.912, p=0.002; Δi= 0.005kg/day: r=0.912, p=0.002).
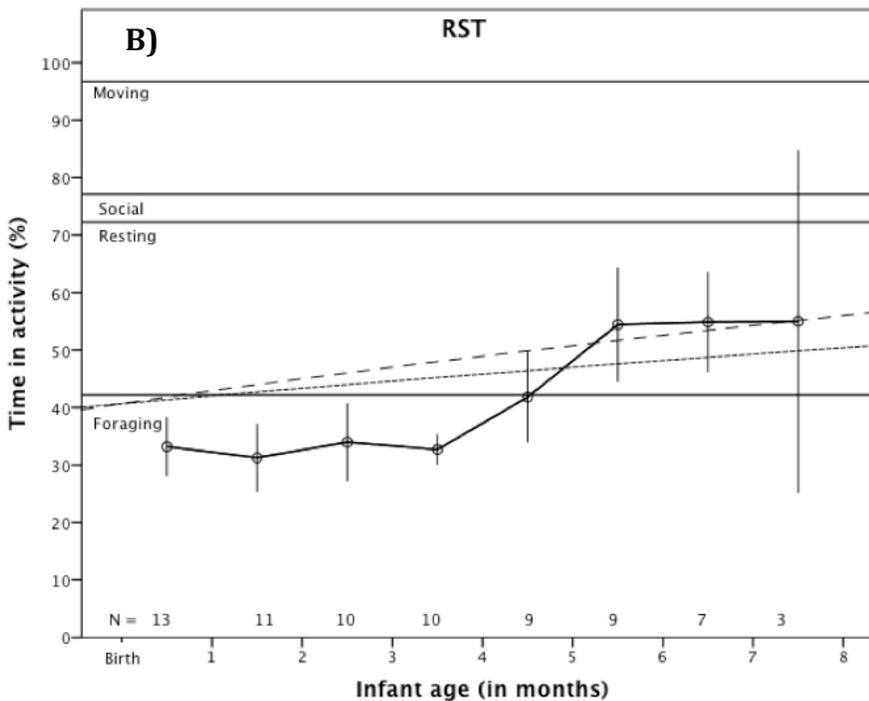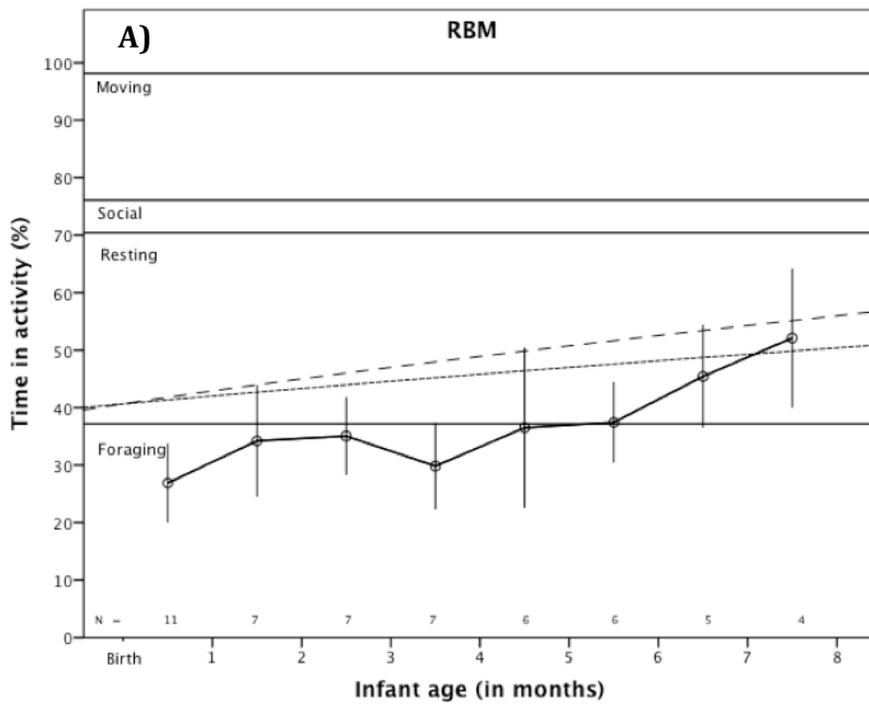
Figure 3.3: Altmann's predicted model with Δi=0.003 kg/day (thin dotted line) or Δi=0.005kg/day (thick dotted line) compared to observed values (solid line) for each troop, A) RBM and B) RST. The horizontal lines represent the mean time budgets of the mothers throughout the study months. Error bars represent 95% confidence intervals.

Maternal feeding time across infant age was then compared to baseline feeding time values for RST to control for any possible variations in feeding time due to seasonal effects, following Barrett et al. (2006). This was to control for differences in birth timing across the breeding season (since there was 72 days difference between the first and last born infants, see Table 2.2) that could mean that mothers and infants were exposed to different environmental conditions at the various infant ages. The mean feeding time for mothers (adjusted to daylight hours) relative to non-lactating baseline females for RST is illustrated in Figure 3.4. Maternal feeding time was significantly below baseline values at birth (t=-2.904, df=12, p=0.013), and then increased above baseline following the second month of life, although the difference was only significant during the infant's fourth month of life (t=5.755, df=9, p<0.001). This trend of foraging less in the first month and then foraging more in the later months is even more pronounced when the troop data are pooled (see Appendix A). The large variation in feeding time in Month 7 is due the low sample size, since only three mothers had their infant early enough in the birth season to capture the first eight months of infant life.
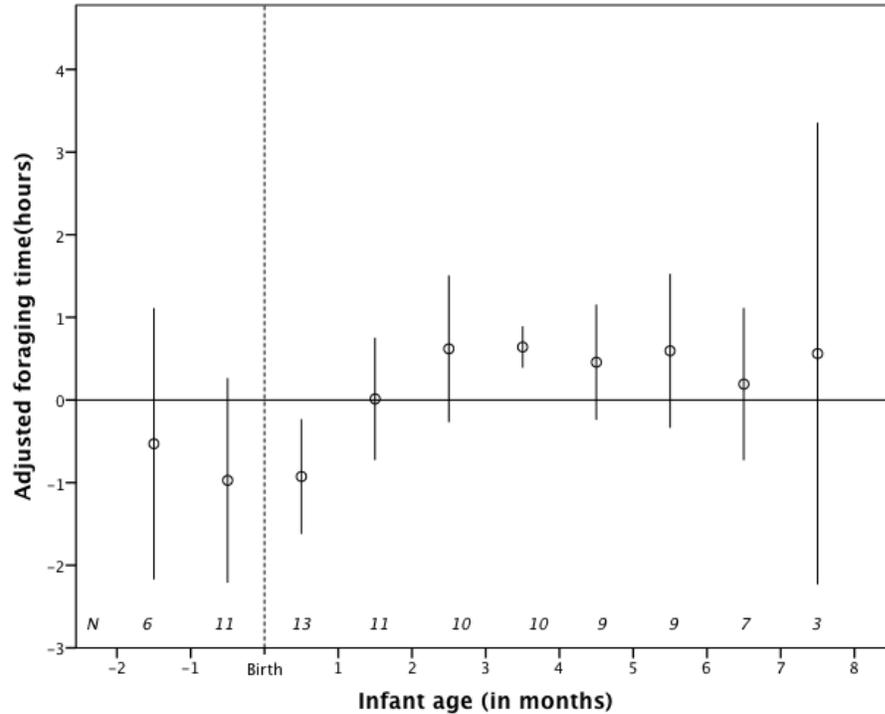
Figure 3.4: Mean maternal feeding time relative to baseline females (in hours) by infant age in RST. Sample size is noted above the x-axis.

3.3.3. EXAMINING ALTMANN'S ASSUMPTIONS

3.3.3.1. Infant provides some of own food

Similar to previous studies, I found that maternal feeding time did not fit the model predictions directly, which suggests one or more of Altmann's assumptions has been violated. Altmann (1980) suggested one of the violations in her baboon population was that infants began obtaining some of their own food (Altmann, 1980). I therefore looked at the first eight months of infant life, comparable to the length of Altmann's (1980) study. The assumption that infants are solely reliant on their mother for nutrition over the

duration investigated is violated by the vervets, and to an even greater extent compared to the Amboseli baboons, as baboons become independent later than vervets (Altmann 1980). The percent of time individual infants spent foraging while within 5m of their mother is depicted in Figure 3.5.
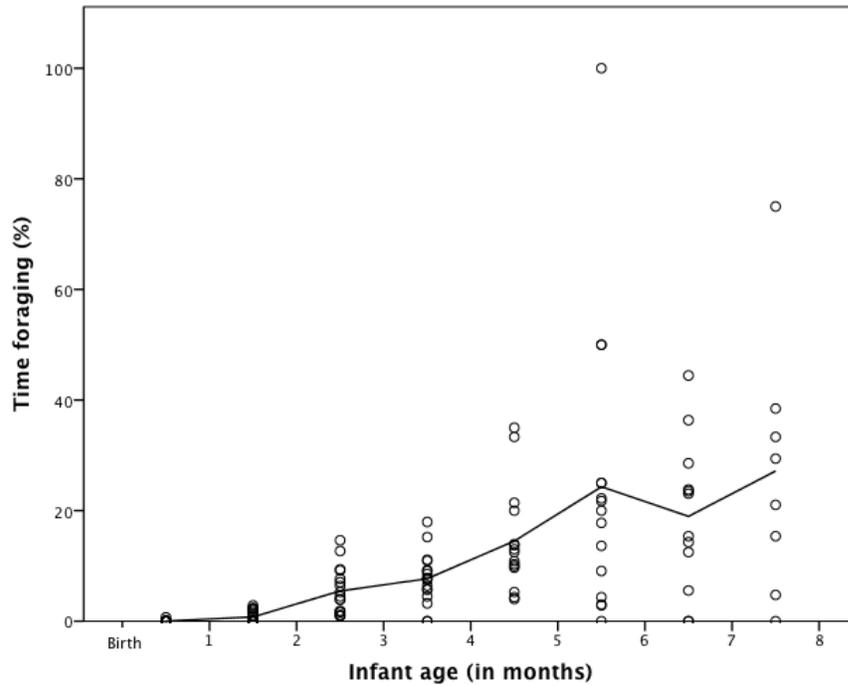
Figure 3.5: Time (%) infants foraging while within 5m of their mother for their first eight months.

Most infants begin foraging independently at the age of two months, and this increases steadily as the infants get older. In combination with Figure 4.1 (Chapter Four, which shows infant ventral/nipple contact rates with their mother remain level and below 10% from month five onwards), this suggests infants are relatively independent from a nutritional point of view from month five onwards. As a result, the slope of the predicted line for Altmann's model should become less steep as infants begin supplementing their

own diet. The large variation in the later months is due to the skewed sampling since the

infants are within 5m of their mother only roughly 25% of the time.

3.3.3.2. Activity remains constant

One of Altmann's (1980) assumptions was that activity of the mother and infant were the

same and remained constant over the course of lactation. Altmann recognized the

limitations of this assumption, stating that infant activity level was most likely lower than

the mother for the first couple of months and then increased with age. My study supports

this: infants were not very active in their first month, spending an average of 88.20%

(sd=11.35%) resting on their mother's ventrum (see Chapter 4). Altmann (1980) also

noted a general trend in her study population of mothers moving less in the first week of

infant life. The mean amount of time (adjusted daylight hours) that mothers spent

moving relative to baseline females for RST is depicted in Figure 3.6. Mothers spent

significantly less time than baseline females in RST moving in month 0 (t=-2.937, df=12,

p=0.012) and month 1 (t=-3.540, df=10, p=0.005), although they spent significantly more

time moving in month 6 (t=3.288, df=6, p=0.017).
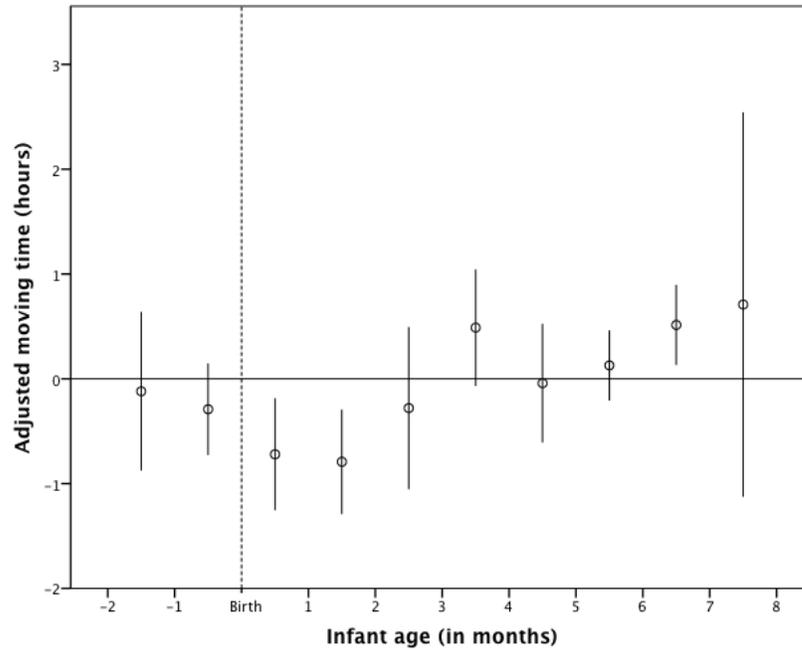
Figure 3.6: Mean maternal moving time relative to baseline females (in hours) by infant age. Error bars represent 95% confidence intervals.

3.3.3.3. Social time is sacrificed

Altmann (1980) assumed that additional time spent foraging was at the expense of social time. The assumption was confirmed in chacma baboons (Barrett et al. 2006), although Kenyatta (1995) and Dunbar &Dunbar (1988) found that resting time was sacrificed before, or in addition to, social time. I investigated whether any similar trade-offs could be seen in vervet mothers using standard least squares regression with REML. Hours spent foraging was entered as the independent variable and hours of moving, resting or social time were entered as dependent variables, with mother I.D. as a random factor. Pregnancy data were not included. The regression graphs are shown in Figure 3.7.
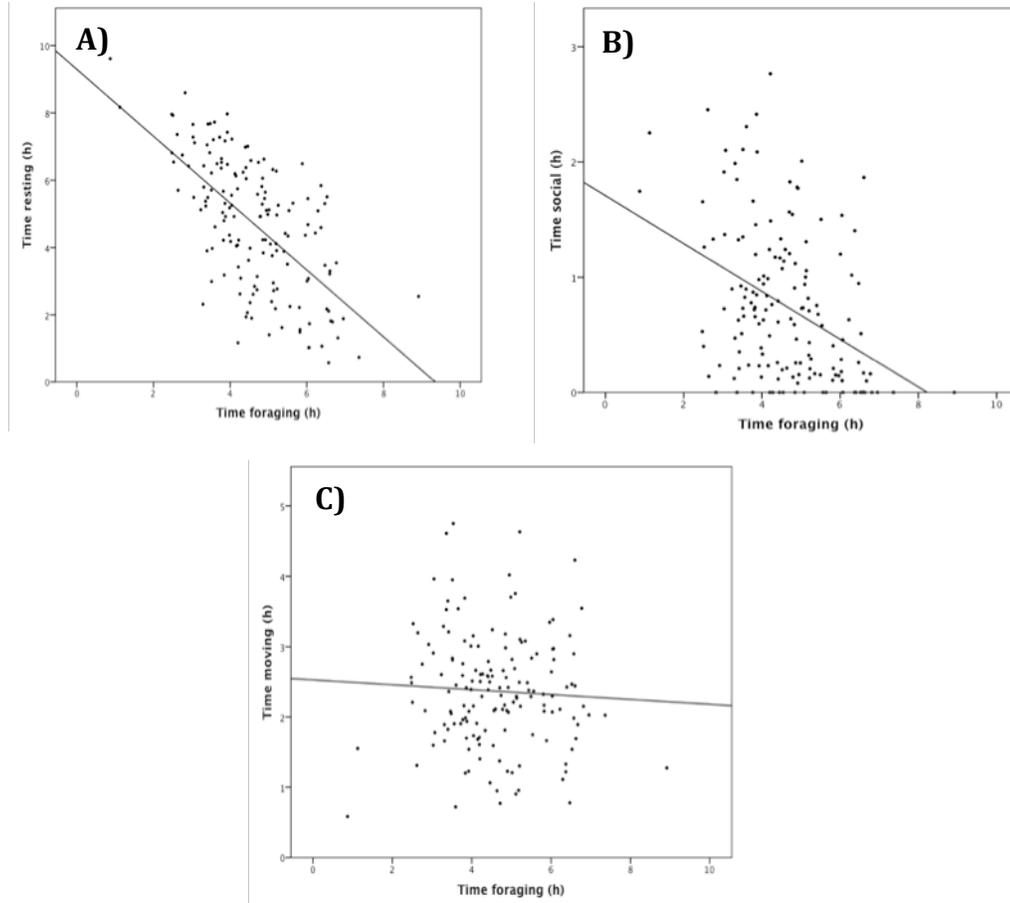
Figure 3.7: Regression between maternal feeding time (in hours) for A) resting B) social and C) moving (bottom). Each point represents the mean for individual mothers for each month of infant life.

There was no relationship between time spent foraging and time spent moving (Table 3.3), but both resting and socializing were negatively related to feeding time, indicating that the vervets traded-off these activities against feeding time. Resting time appears to be drawn on at a faster rate than social time, as indicated by the steeper slope. This is not surprising considering there is more time available to draw from resting, which makes up 15-55% of the time budget (see Figure 3.1) compared to time spent socializing, which comprises only 5-10% of the total time budget.

Table 3.3: Regression equation values of time spent foraging using standard least squares (REML) in relation to time spent moving, resting and socializing.

Activity	β	Intercept	t ratio	p	Adj. R^2
Moving	-0.042	2.68	-0.69	0.49	0.11
Resting	-1.03	9.14	-8.93	<0.001	0.29
Social	-0.23	1.80	-5.25	<0.001	0.11

In order to examine how time spent resting and socializing changed over infant age while controlling for seasonal influences, maternal time was compared to baseline values for the same time period (Figure 3.8). Only values for RST were used. Mothers spent significantly more time than baseline females resting in the last month of pregnancy (t=2.274, df=12, p=0.046) and tended to rest more in the infant's first month (t=2.166, df=12, p=0.051), compared to later months when they tended to rest less (month 3: t=-2.145, df=9, p=0.060; month 4: t=-2.461, df=8, p=0.039). Mothers spent significantly more time socializing directly after birth (t=2.262, df=12, p=0.043) and then significantly less time in months three (t=-6.396, df=9, p<0.001), five (t=-3.775, df=8, p=0.005) and seven (t=-6.638, df=2, p=0.022). Time spent socializing was more variable than time resting across females.
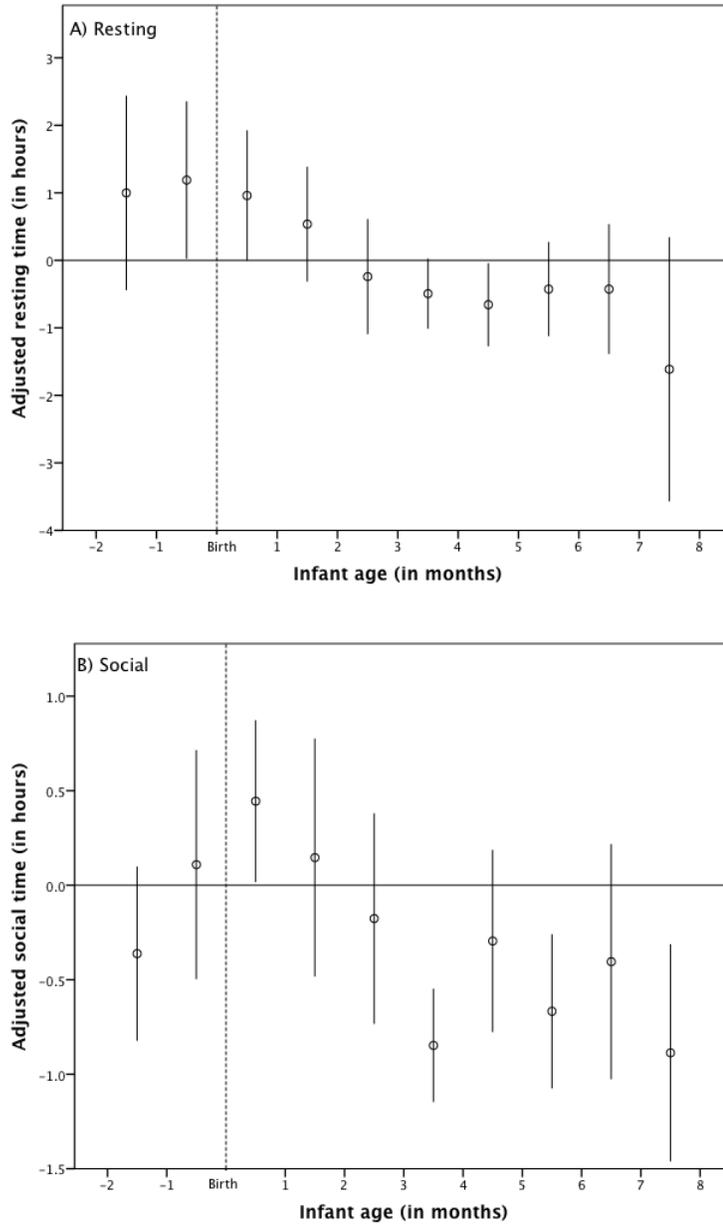
Figure 3.8: Mean maternal time A) resting and B) social relative to baseline females (in hours) by infant months. Error bars represent 95% confidence intervals.

As mothers with new infants often attract the attention of other group members, there are

often differences in the amount of grooming given and the amount received by mothers

versus non-mothers (Kenyatta 1995, Altmann 1980). This is particularly pronounced in

vervet monkeys, which allow other individuals to hold their infants and 'allomother'

them, often following a grooming session (Lancaster, 1971). This relationship was

examined by comparing grooming times between mothers and baseline females (Figure

3.9). Only data for RST were used, although similar results were obtained with the

pooled data (see Appendix A). The data were taken from focal samples that were

extended until a grooming bout finished, and total time grooming was calculated. Due to

a slight skew in opposite directions for differences in amount of grooming in some of the

months, the non-parametric equivalent of the paired t-test was used, the Wilcoxon signed

rank test.
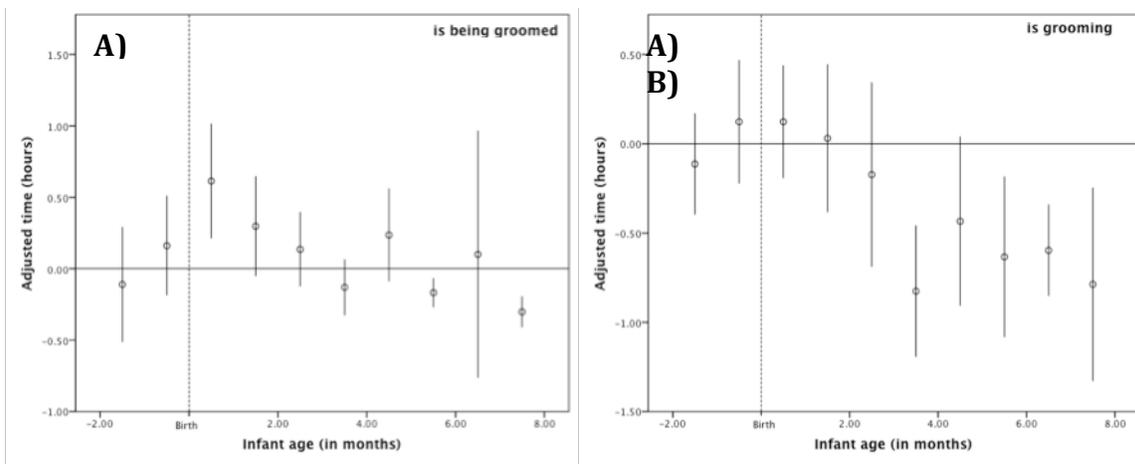
Figure 3.9: Mean maternal time A) being groomed (on the left) and B) is grooming (on
the right) relative to baseline females (in hours) by infant months. Error bars represent
95% confidence intervals.

Mothers were groomed significantly above baseline levels in the first month of infant life

(N=13, z=3.110, p=0.002) and significantly less in month five (N=9, z=-2.547, p=0.011).

The large variation in month six is due to one female who was groomed for 25% of the

time observed. Mothers groomed others significantly less in month three ($N=10$, $z=$-2.803, $p=0.005$), five ($N=9$, $z=-2.668$, $p=0.008$) and six ($N=7$, $z=-2.366$, $p=0.018$).

Standard least squares regression with REML was used to determine whether there was an effect of rank on the amount of time a mother spent grooming or being groomed (in hours). In order to normalize the data, an inverse transformation was applied. Mother I.D. was entered as a random effect and the standardized David Score and infant age (as a factor) were entered as independent variables. All mothers were used (for both RST and RBM), with troop entered as a factor to control for any troop differences. Infant age had a significant effect on the amount of time a mother was groomed ($F=2.25$, $df=7$, $p=0.036$) but there was no effect of rank ($F=0.078$, $df=1$, $p=0.78$) or troop ($F=0.067$, $df=1$, $p=0.80$). Infant age had no effect on the amount of time that mothers groomed others ($F=0.45$, $df=7$, $p=0.87$) and nor did maternal rank ($F=0.92$, $df=1$, $p=0.35$) or troop ($F=0.19$, $df=1$, $p=0.67$).

3.3.3.4. Maternal condition remains constant

Altmann's (1980) model also assumes that mothers maintain their body weight over the course of lactation. Another possibility, however, is that they draw on fat reserves over the course of lactation and so lose body condition. Only one mother with a surviving offspring was weighed before and after the birth season so it was not possible to test directly whether mothers' body weight decreased during lactation. However, previous studies have found that wild vervets in areas of high habitat quality have shorter average

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interbirth intervals (approximately 12 months) compared to lower quality habitats (approximately 18 months) (Lee 1987), and it is therefore possible to assess this relationship indirectly, by assuming that greater losses of weight and body condition will require longer recovery times and thus a delay to next conception (i.e. a longer inter-birth interval).

Mean birth rate was calculated by summing the number of infants born during each birth season since 2008 and dividing by the additive number of fecund females in the troop during each birth season. For example, in RBM there were 31 infants born between summer 2008 and spring 2012, out of a possible 51 fecund females over the fours years, giving an average of 0.607 infant born per female each year (interbirth interval of 19.8 months). In RST, there were 41 infants born over the four birth seasons, out of a possible 80 fecund female years, giving an average of 0.5125 infants born per female each year (interbirth interval of 23.4 months). Therefore, it appears females give birth roughly once every other year (the numbers are most likely underestimated as it includes infants that did not survive to six months). With only four years of data, this result must be considered with some caution but, given that most females only seem to conceive and give birth once every two years, it seems likely that females either lose weight and condition during lactation or that that the weaning process takes longer, so that such females fail to conceive during the breeding season immediately following the birth of their infants.

3.3.4. NUTRITIONAL QUALITY

3.3.4.1. Energy and protein intake

Another assumption of the model is that feeding efficiency remains constant across lactation. However, a reduction in nutrient quality can lead to longer feeding times (eg. Dunbar et al. 2002). In order to explore how nutrient quality changed across the year, energy and protein in the diet were calculated for baseline females in RST across the calendar months of the study in Figure 3.10 (see Chapter 2, section 2.7 for calculations). Dunbar et al. (2002) found a significant positive correlation between biomass and rainfall in the previous two months. Therefore, whether the relationship is the same as in the Dunbar et al. (2002) study was qualitatively explored in Figure 3.10 by comparing monthly precipitation to energy and protein in the diet. In addition, the validity of the estimated nutritional measures is increased if the energy and protein follow the levels predicted by precipitation (ie. higher protein and energy in the diet in the month or two following higher levels of precipitation).
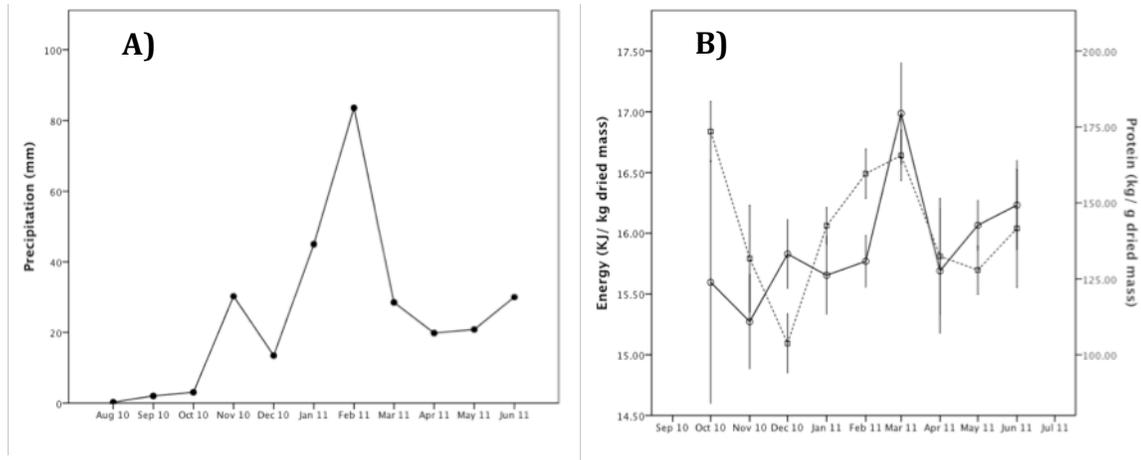
Figure 3.10: A) Total monthly precipitation (in mm) and B) Mean energy (KJ) per kg dried mass (represented by circles and solid lines) and crude protein (Kg) per g dried mass (square and dotted line) (±1 S.E) across calendar months of non-lactating females.

As illustrated in Figure 3.10, energy and protein in the diet roughly follow the pattern of precipitation. The highest rainfall occurred in February, which was followed by the highest protein and energy in the diet in March. Nutrient levels in general increased after rainfall. The only exception is in the first study month (October), where baseline females had high levels of protein in the diet, and a large variance of energy, as indicated by the large standard error bars. In October, vegetation was limited and females spent a large portion (up to 50%) of their diet eating dried acacia pods, which are high in protein. In addition, sample size was smallest in October (four non-lactating females), which would result in larger standard errors. However, in general, the nutrient quality of the diet seems to approximate environmental conditions, with the highest levels occurring following the rain in February.

The mean energy (MJ/ kg dried mass) and mean raw protein (g/ kg dried mass) in the diet were examined for each mother over the last two months of pregnancy and the first eight

months of infant life. Standard least squares regression with REML was used to determine whether there was a significant difference in mean energy and mean protein in the diet (as separate dependent variables) across infant age (as a factor) between the troops. Mother I.D. was entered as a random effect to control for repeated measures of individuals. There was a significant effect of infant month ($F=6.1221$ $df=9$, $p=<0.0001$), but no significant effect of troop I.D. ($F=0.053$, $df=1$, $p=0.82$) on average energy in the diet. There was a significant main effect of infant month ($F=34.16$, $df=9$, $p<0.0001$) on average protein in diet, and a significant effect of troop ($F=4.74$, $df=1$, $p=0.043$). Due to the differences in troops in protein intake, data were separated by troop for both protein and energy, with the mean energy intake of the troops presented in Figure 3.11 and the mean protein intake presented in Figure 3.12. The pooled data are presented in Appendix A. Average energy intake steadily increased from pregnancy as the infant got older, whereas protein intake showed greater fluctuations, but tended to decrease at birth and increase as the infants got older.
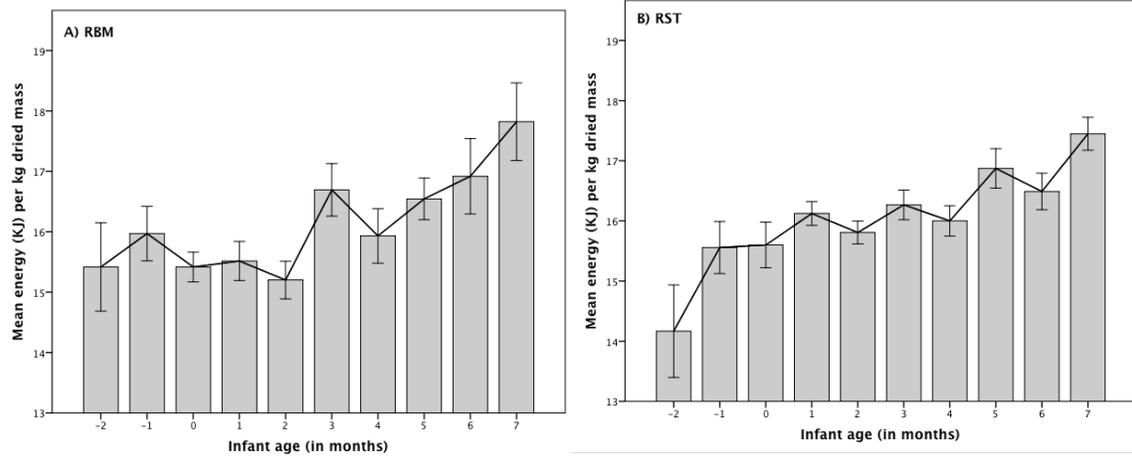
Figure 3.11: Mean total energy (MJ) per dried mass (kg) over infant age for A) RBM and B) RST. Error bars represent ± 1 standard error.
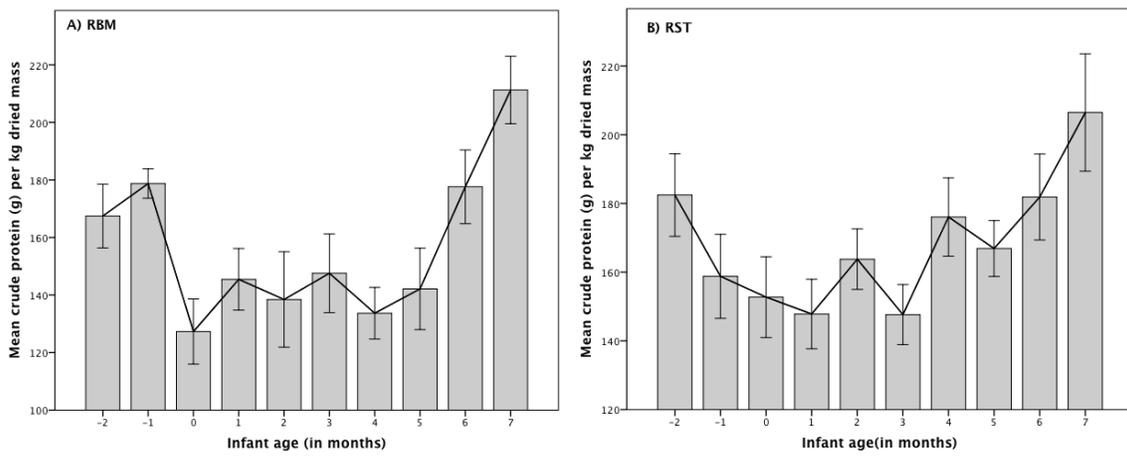
Figure 3.12: Mean crude protein (in g) per dried mass (kg) over months of infant age for A) RBM and B) RST. Error bars represent ± 1 standard error.

Standard least squares regression with REML was used to determine whether there was a significant difference in mean energy and mean protein in the diet (as separate dependent variables) across infant age (as continuous) separated by troop. Only values from parturition to month seven were used. Mother I.D. was entered as a random effect to control for repeated measures of individuals. Infant age had a significant effect on energy intake for RBM (β=0.30, t=4.70 p<0.0001) and RST (β=0.18, t=3.70, p=0.0004). Infant

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age had a significant effect on protein intake for RBM (β=7.72, t=3.54, p=0.0009) and a significant effect for RST (β=5.34, t=2.96, p=0.0042). As the infant gets older, protein and energy intake in the maternal diet significantly increases.

Average energy and protein in the maternal diet were compared to baseline female diet for RST females only (see Figure 3.13), using paired t-tests. Mean energy in the diet was consistent with baselines and did not differ significantly at any point across the period covered by the sample. Mean protein in diet was above baseline levels for the last two months of pregnancy and most of the first eight months of infant life (although this was only significant two months before birth: t=3.238, df=5, p=0.023; month five: t=3.564, df=8, p=0.007; and month six: t=3.708, df=6, p=0.010). These trends are comparable to the grouped data (presented in Appendix A).
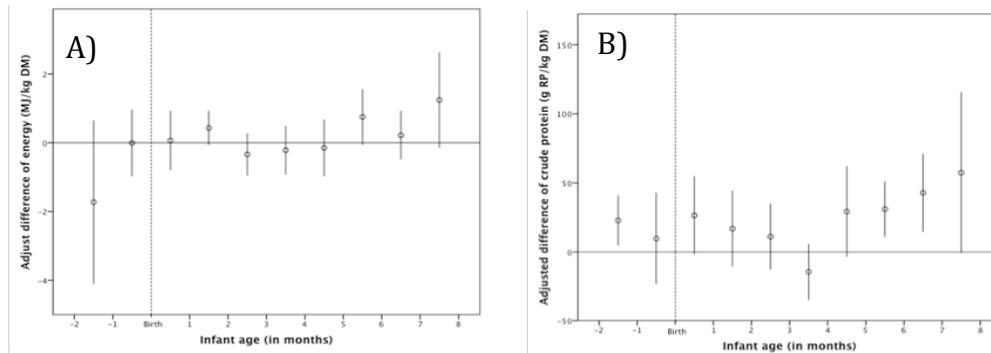
Figure 3.13: A) Mean energy (MJ) per dried mass and B) mean crude protein (g) per dried mass (kg) of maternal diet relative to baseline females over age of infant months.

3.3.4.2. Seasonal factors

Nutritional quality and primary productivity can vary across the seasons. Temperature and precipitation can be used as indices of nutrient quality, which are important variables to include in any feeding time model (eg. Dunbar et al. 2002). A full factorial linear mixed effect model (lme) was run on the percentage of time that mothers spent foraging from birth to eight months of infant age. Mother I.D. was entered as a random effect with the independent variables infant age (in months), cumulative precipitation (mm) for the two preceding months, and average temperature (^{o}C). All the independent variables were centered using the grand mean in order to reduce multicollinearity between the factors and the interactions (Tabachnick & Fidell 2006). All possible models were tested, but the respective main effects were retained when entering interaction terms. I considered candidate models to be the best set of models predicted by the data if they differed by two or less (ΔAICc) to the best model predictor (Burnham & Anderson 2002). A random intercept and random slope for infant month were entered into the models. For the AICc based model selection, models were fitted with Maximum Likelihood (ML), which is necessary when comparing models of different fixed effects (Burnham & Anderson 2002). Models were fitted with Restricted Maximum-Likelihood (REML) to obtain unbiased parameter estimates. The full model factors for maternal time spent foraging are listed in Table 3.4.

Table 3.4: Linear mixed model analysis (REML method) for the factors infant age (in months), precipitation (mm) and temperature (°C) and their interactions influencing the percentage of maternal time spent foraging.

	Slope (β)	St. Error	t	p
Infant age	0.54	1.08	0.50	0.62
Precipitation	-0.032	0.039	-0.81	0.42
Temperature	-1.97	0.42	-4.66	<0.001*
Infant age * Precipitation	-0.050	0.02	-2.47	0.015*
Infant age * Temperature	0.34	0.19	1.77	0.080
Precipitation * Temperature	-0.005	0.010	-0.54	0.59
Infant age * Precipitation * Temperature	-0.00077	0.0050	-0.16	0.88
Intercept	*41.85*	*2.05*	*20.39*	*<0.001**

*$p<0.05$

In the global model, temperature had a significant negative effect and the interaction effect of infant age and precipitation also had a significant negative effect on maternal time spent feeding. The negative effect of temperature on feeding suggests thermoregulatory costs and/or poor nutrient quality require mothers to forage longer when it is colder.

In order to determine the fewest parameters that best predict maternal feeding time, all the possible models of the three factors and interactions were run (infant age, temperature and precipitation) using linear mixed effect models and the ML method. The highest ranking models with ΔAICc < 2 are reported in Table 3.5. As the table indicates, in all highest ranking models, temperature has a significant effect on maternal feeding time highlighting the importance of including it in maternal feeding time models. Infant age

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and precipitation had a significant effect in two of the highest ranking models, and infant

age factored into all the models.

Table 3.5: Highest ranked models according to the ΔAICc < 2 explaining percent of maternal time spent foraging using linear mixed effect models with mother ID as a random factor. Explanatory variables included in the model are marked by an X, with significant predictors indicated by X*.

Explanatory variable	Rank			
	1	2	3	4
Infant age (in months)	X	X	X	X
Precipitation (mm)	X		X	X
Temperature (^{o}C)	X*	X*	X*	X*
Infant month * Precipitation	X*		X	X*
Infant month * Temperature	X			X
Precipitation * Temperature				X
ΔAICc	0.00	1.27	1.49	1.70

Dunbar et al. (2009) have highlighted the importance of time as an ecological constraint.

The limitation of time is particularly pronounced in winter months, when daylight hours

are restricted. Therefore, the amount of time spent feeding (in hours) for mothers was

examined in a full factorial model with infant age, precipitation and temperature, to tease

out changes in percentage time budgets that are occurring as a result of changes in

daylight hours.

The same procedures were used to look at any seasonal effects of on maternal feeding

time in hours rather than percentage, with the global model presented in Table 3.6. The

only significant factor on maternal foraging time (in hours) was a negative effect

temperature and a very small effect (in terms of slope) of the interaction of infant age and

precipitation.

Table 3.6: Linear mixed model analysis (REML method) for the factors infant age (in months), precipitation (mm) and temperature ($^{\circ}$C) and their interactions influencing the amount of hours a mother spent foraging.

	Slope (β)	St. Error	t	p
Infant age	-0.03897	0.1309	-0.2977	0.767
Precipitation	-0.003883	0.00498	-0.7796	0.4376
Temperature	-0.1497	0.0492	-3.043	0.0030*
Infant age * Precipitation	-0.005363	0.002441	-2.197	0.0305*
Infant age * Temperature	0.03269	0.02351	1.391	0.1676
Temperature * Precipitation	-0.001158	0.001253	-0.9242	0.3578
Infant age * Precipitation * Temperature	0.000015	0.0006118	0.0237	0.9811
Intercept	*5.007*	*0.2518*	*19.89*	*<0.001**

* $p<0.05$

In order to determine the fewest parameters that best predict hours of maternal feeding,

all the possible models of the three factors were run with their interactions (infant age,

temperature and precipitation) using linear mixed effect models and the ML method.

The highest ranking models with ΔAICc < 2 are reported in Table 3.7. As the table

indicates, in all the highest ranking models, temperature has a significant effect.

Precipitation factored into the second best ranked model, and infant age didn't factor into

any of the top models. Infant age and precipitation had a significant negative interaction

effect in only the top model.

Table 3.7: Highest ranked models according to the ΔAICc < 2 explaining hours of maternal time spent foraging using linear mixed effect models with mother ID as a random factor. Explanatory variables included in the model are marked by an X, with significant predictors indicated by X*.

Explanatory variable	Rank	
	1	2
Infant age (in months)		
Precipitation (mm)		X
Temperature (^{o}C)	X*	X*
ΔAICc	0.00	0.59

When time spent feeding is controlled for day length by examining hours spent foraging, infant age no longer factors into any of the best fit models. In the global model, the slope of infant month is very close to zero, and is sometimes negative, indicating the influence of infant age on percentage of time spent foraging reflects the correlation between shorter day lengths and infant age, rather than the effect of infant age per se. Temperature has a significant negative effect on time spent feeding in the global model and the high ranked models, for feeding in percentage and hours. The negative relationship could be either due to thermoregulatory demands increasing the time that needs to be spent feeding, or the negative effect cold temperatures have on nutrient quality.

3.4. DISCUSSION

3.4.1. ALTMANN'S MODEL

The objective of this chapter was to test Altmann's maternal foraging time budget model on the Samara vervets. In general, maternal foraging time was found to increase in the manner predicted; however, it fell below the predicted level of feeding time until the infant's sixth or seventh month of life. As this is when the infant is mostly foraging independently, this violates one of the model's assumptions. Nutrient quality tended to increase throughout lactation, violating another assumption. Furthermore, the increase in time spent foraging is best explained by decreasing temperatures and decreasing daylight hours, rather than the increasing demands of a growing infant. Therefore, I suggest vervet monkeys do not conform to Altmann's model, and utilize other strategies to cope with the costs of lactation as assessed by exploring the violations of Altmann's model.

3.4.2. IN COMPARISON TO BABOONS

Altmann's model was developed for her particular study population of yellow baboons. However, there are several differences between baboons and vervets, which could limit the generality of the maternal time budget model. Two of the most important differences

are the rates of development between vervet and baboon infants and the seasonal breeding pattern of vervets.

3.4.2.1. Infant development

According to the Appendix in Lee et al.'s (1991) study, neonatal weights of vervets are roughly 14% of the maternal mass, compared to baboons which are around 7% and gelada which are around 3-4%. That is, relative to their mother's mass, vervets are considerably heavier than baboons and gelada infants. Vervet infants grow proportionally faster and are roughly 30% of their adult weight at 6 months in vervets, compared to 18 months in baboons and gelada (Lee et al., 1991). In addition, while most primates are weaned at roughly four times their neonatal weight, vervets seems to fall below this and are weaned at roughly three times their neonatal weight (Lee et al., 1991), most likely due to their relatively larger proportional infant birth weight. As a result, vervet infants are nutritionally dependent on their mothers for a much shorter time period than in baboons and geladas.

Vervets begin feeding independently during their second month of life (Figure 3.5), although they are heavily reliant on their mother for nutrition until about their fifth or sixth month, at which point they could potentially survive their mother's death (Cheney, Lee, & Seyfarth, 1981, see Chapter Four for infant contact rates over time). Mothers aren't just a source of nourishment to their infants; they also provide a source of protection from aggression by other troop members and predators, as well as a grooming

partner for removing ectoparasites, meaning nutritional independence doesn't mean full independence. In Altmann's (1980) study at Amboseli, infants didn't start independently foraging until their third or fourth month, and could more readily do so if the right weaning foods were available in their fifth and sixth month. Baboon infants were, however, still heavily reliant on their mother's milk until eight to twelve months of age, and could potentially survive their mother's death only at 1 year of age (Altmann 1980). Similarly, gelada infants begin to feed for themselves at roughly four months of age, which corresponds with a gradual decline in time spent feeding by the mothers, although foraging time remained high until the infants were nine months old, and infants were nursing at a negligible level (Dunbar & Dunbar, 1988). Given these differences in infant development, it is clear that strategies that are optimal for baboons may not be so for vervets and vice versa. For example, Harrison (1983) suggested that, in green monkeys, lactating females may minimize energy expenditure immediately following parturition because infants are solely dependent on their mother's milk for such a short period of time, and given birth seasonality, any maternal weight loss can be recouped easily following the rains which happen a month or two after infant birth. Harrison (1983) suggested the monkeys were using a high-cost, high yield/low-cost, low-yield strategy of increasing time spent feeding when food was more available, and resting more and feeding less when food was less available and energy demands are higher (i.e. during lactation).

3.4.2.2. Seasonality

The situation is further complicated in vervet populations since vervets are seasonal breeders, where the infants are typically born within a three-month time window (see Table 2.2 for my study, Butynski, 1988; Rowell & Richards, 1979). In my study population, the birth season takes place in mid- to late spring (October to December), with most infants becoming nutritionally independent in the fall (March to May). Therefore, the maternal feeding time budget reflects not only the nutritional demands of the infant but also the changing environmental conditions to which the mother is exposed. As a result, infant age, number of daylight hours and temperature are inevitably confounded with one another (i.e., there is a negative correlation with daylight hours for infants born late in the birth season, close to the summer equinox, a bell-shaped relationship for the first six months for infants born early in the birth season. Temperature has a bell shaped relationship with infant age: positively correlated with infant age for the first few months, with highest temperatures in January and February, and decreasing temperatures as the infant gets more independent. Temperature and daylight hours are in turn positively correlated). In addition, mothers are exposed to more similar environments of nutritional quality and periods of productivity during lactation than non-seasonal breeders.

3.4.3. NUTRITIONAL QUALITY

One of the assumptions of the model is that *A,* the coefficient of energy ingestion, remains constant. Dunbar and Dunbar (1988) suggests the increases in feeding time above those predicted by Altmann's model for their gelada population was due to changes in the value of *A* as infants got older. As all but two infants were born within a one-month period, most of the lactating females were exposed to the same environmental conditions at each infant age. Therefore, changes in nutrient quality across calendar months would reflect changes in maternal foraging time, with mothers needing to forage more when food quality and/or quantity decreased. Dunbar and Dunbar (1988) suggested that the value of *A* increased as the infants got older since nutritional quality decreased, causing females to spend more time foraging. In a study of langurs, a decrease in time spent foraging corresponded proportionally with an increase in the mean energy ingested (Koenig, Borries, Chalise, & Winkler, 1997).

When examining nutrient content, I found that both protein and energy in the diet significantly increased as the infants got older. This could explain why mothers might show feeding times lower than those predicted by Altmann's model: rather than spending more time foraging, females may have been able to meet their nutritional demands by targeting higher quality items which had become available in the environment. In order to confirm that such changes in food abundance and availability were influencing maternal feeding times in this way, phenology of plant data would be needed.

Surprisingly, during my study, nutritional quality was highest when time spent foraging

increased to the level predicted by Altmann's model (approximately infant month sixth).

This suggests mothers were both feeding more *and* obtaining more nutrients in the

infant's fifth and sixth month. The increase in foraging time along with the increase in

nutritional intake may reflect increased nutritional stress, perhaps due to reduced daylight

hours and lower temperatures (eg. Hill et al., 2003). Lactating females also responded by

increasing the protein in their diet above baseline levels during this period. Changing

dietary items in response to lactation has been found in other populations. For example,

Muruthi et al. (1991) in their Amboseli baboon study population found no difference in

protein intake between pregnant or lactating and cycling females, but in addition to the

extra time spent feeding, pregnant or lactating females also had a higher energy intakes

and rates of ingestion. Similarly, pregnant and lactating females chimpanzees have been

noted to have a higher percentage of fruit in their diet than cycling females (Murray,

Lonsdorf, Eberly, & Pusey, 2009).

3.4.4. BEYOND ALTMANN'S MODEL

The observed relationship at Samara, where there is an increase in nutrient quality as

vervets infant gets older and require more energy, may reflect natural selection pressures

on birth seasonality. In my study year, nutritional quality in the diet was highest in

March (Figure 3.10). This is comparable to Lee's study (1987), which found highest

nutrient quality in February (although she found high levels for December and January

and sharp decrease after February, in contrast to this study where quality declined

gradually). In Lee's (1987) study, nutritional quality was measured as the ratio of protein to calories available from the average mouthful of each food type, compared to this study which measured protein in kg and energy in KJ, both per g of dried mass. Therefore, Lee's study emphasized protein intake, as well as considering wet mass (since a greater wet mass would mean there would be less per mouthful). Given this, Lee's results and mine can really only be compared qualitatively rather than quantitatively. Lee (1987) suggested that high nutrient quality corresponded to peak lactation, whereas my study indicates a gradual increase in the energy and protein targets of the diet in lactating females, with the peak of dietary quality occurring when lactation demands are beginning to decrease and infants are beginning to become independent.

There is also some potential for some experimental error associated with my nutrition values, as several of the food targets were estimations (for example, using an average of three species values for ground plants): slight differences in food targets could have been missed. In addition, no distinction was made between young and mature leaves and, given that young leaves have higher nutrient content, lower fibre and a greater digestibility than mature leaves, they tend to be preferred over mature leaves (McKey, Gartlan, Waterman, & Choo, 1981). Furthermore, the plants were only sampled once for nutritional analyzes, and protein content changes with both rainfall and temperature (Dunbar, 1992a). Therefore, in futures studies, I would try to identify food plants at the species level, discriminate between young and mature leaves and collect plant samples monthly. However, given the close qualitative fit between precipitation and nutrient quality (Figure 3.10), nutritional quality as measured here seems to provide a reliable, if

rough, estimate, if higher nutrient items are more available following rainfall. This must still be treated cautiously, however, since Lee and Hauser (1998) found that, at Amboseli, while grass cover was highly correlated with precipitation, production cycles of trees and shrubs was uncorrelated with precipitation, and was therefore a poor predictor of overall diet. Grass cover did influence (although non-significantly) the percentage of time feeding, however, with groups that had high percent of grass cover spending less time feeding (Lee & Hauser, 1998).

Another difference between Samara and the Amboseli studies is rainfall distribution. Amboseli is characterized by two rainy periods, one between November and December, and the other between March and April (Lee & Hauser, 1998), with most births occurring in November and December (Lee, 1987). At my study site, the peak in precipitation was between January and February, with most births occurring between October and December. In order to not draw conclusions of life history characteristics based one study period, I looked at the precipitation at the study over a period of twelve years (from 1998 to 2010), in comparison to my study year (2010-2011) and the percent of total births born in the calendar months since 2008 (total of 63 births) (see Figure 3.14).
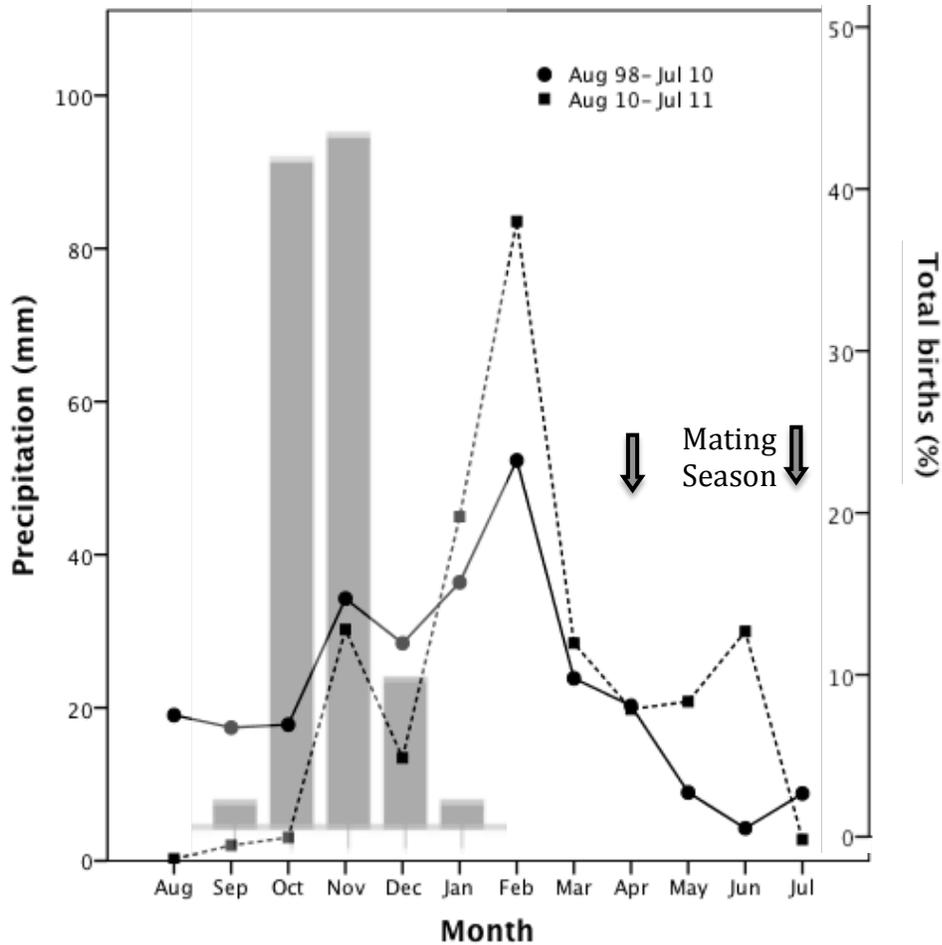
Figure 3.14: Average precipitation for August 1998 to July 2010 (circles and solid line) compared to the duration of my study from August 2010 until July 2011 (squares and dashed line). Grey bars are the percent of total births for each calendar month (total of 63 births collected for 2008-2010 birth seasons). Arrows indicate approximately the start and end of the mating season (from Freeman, 2012).

Figure 3.14 illustrates that based on the average precipitation, the area is characterized by

a dry season from April to October, and rainy season from November to March with a

peak in February. Precipitation during my study year was lower than average for August

to December, but was higher than average for January to June. As a result, peak

nutritional quality in my study year may have been delayed and then extended due to a

longer rain season than average, and cannot be generalized to typical conditions.

Nonetheless, with peak precipitation in February, primary production is likely the highest

on average between March and April, when infants are becoming independent and just before mating season, since rainfall in the previous two months positively correlates with plant biomass (Dunbar et al., 2002).

In spite of a similar birth season to the Amboseli vervets, timing of food quality appears to be different. In Amboseli, highest nutritional quality corresponds to peak lactation, which Lee (1987) proposed as occurring when infants were around one to two months of age, suggesting this benefits the mother when nutritional demands are highest. At my study site, nutritional quality gradually increased over the course of the females' lactational period and was highest when the infants are actually becoming more independent and just before mating, suggesting it parallels the increased demands of a growing infant and may assist females regain condition following peak lactation. In green monkeys in Senegal (Harrison, 1983) as well as a troop of vervet monkeys in South Africa (Baldellou & Adan, 1997), infant births occurred a couple of months before the rainy season, which would again suggest peak food abundance toward the end of lactation, when infants are becoming independent and a month or two before the mating season begins.

An ultimate explanation for the timing of reproductive events has been explained in terms of capital versus income breeding animals. The terms were first applied to clutch size in birds and later expanded to general life history theory (for a review, see Brockman & van Schaik, 2005). Income breeders use energy acquired during the reproductive period, whereas capital breeders store energy prior to the energetically expensive reproductive

period, with both points representing the extremes of a continuum (Stearns, 1989). More recently, Brockman and van Schaik (2005) divided income breeders into two categories: strict income breeders and relaxed income breeders. Strict income breeders have a very narrow conception window, and respond strongly to exogenous rather than endogenous cues, such as changes in photoperiod rather than reaching an internal threshold condition in order to conceive, and as a result remain seasonally breeding in captivity (Brockman & van Schaik, 2005). Relaxed income breeders fall in between income and capital breeders, and respond to a combination of endogenous and exogenous cues, and may increase their conception window in captivity as a result of consistent food abundance (Brockman & van Schaik, 2005). Vervets were classified as relaxed income breeders based on physiology (due to lessening of seasonality in captivity), and the likelihood of aborting if the female is food sensitive (meaning the rate of aborting/reabsorbing a fetus is increased if there is a scarcity of food), but placed with the strict income breeders based on Lee's (1987) nutritional data, since it implies there is no effect of condition to conceive (Brockman & van Schaik, 2005). My data suggests they should potentially be placed within the relaxed income breeding category for nutrition as well, since higher food quality at the end of lactation suggests females may be re-gaining condition before mating season.

3.4.5. TEMPERATURE

When examining the percentage of time spent feeding, temperature had a significant effect in the global model, and was included in all the highest ranking models as a

significant effect on feeding time. Infant age factored into all the models and infant age and precipitation had a significant interaction effect in two of the candidate models. The inclusion of infant age in the candidate models was better understood when examining hours spent foraging. Infant age had a small non-significant negative effect on time spend foraging in hours, indicating the influence of infant age on time spent foraging when analyzed as a percentage was due to the correlation of decreasing daylight and infant age. When looking at the candidate models of time spent foraging in hours, it is clear temperature is the main explanatory variable.

Low temperatures increase feeding requirements either through thermoregulatory costs or decline in nutrient quality (Dunbar, 1992b). Given the non-significant effect that precipitation had in the global and candidate models, it suggests the increase in foraging time is due to thermoregulatory costs rather than lowered food availability. When examining the effect of day length on time budgets, Hill et al. (2003) noted an increase in hours foraging in the cold winter months, pointing out the possibility of increased thermoregulatory requirements. In a study of provisioned barbary macaques, feeding time (in hours) was also higher in the in the winter compared to summer (Fa, 1986). Higher cortisol levels in a troop of free ranging baboons marked the stress of colder temperatures and shorter day length (Weingrill, Gray, Barrett, & Henzi, 2004). Therefore, when examining the foraging percentage data, the increase to the line predicted by Altmann's model is a reflection of the decreasing daylight hours and decreasing temperatures which require the mothers to forage more overall, rather than a reflection of a response to increased infant demand. This is also reflected in non-lactating

females foraging at a comparable level to mothers at infant month six and seven, when the percentage reaches Altmann's predicted model. Precipitation appears not to play a large role, although it does factor into the second highest ranked model, which indicates that while it may be important for the timing of reproductive events, it does not significantly influence foraging time.

Dunbar et al. (2002) noted a seasonal birth peak in the gelada study population and in lactating females found a significant negative effect of precipitation and a positive effect of temperature on time spent feeding, as well as infant age in lactating females. Due to the positive effect temperature had on time spent feeding, Dunbar et al. (2002) suggested it influenced maternal foraging time due to the negative effect of high temperatures on nutrient quality, rather than thermoregulatory costs of low temperatures. When Dunbar et al. (2002) tested Altmann's baboon data, they found inclusion of rainfall but not temperature provided the best fit equation. Part of the differences of temperature factoring into maternal feeding time budgets in vervets and not baboons could be that vervets are smaller, and therefore have a larger surface area to volume ratio and may be more severely affected by colder temperature. In addition, minimum temperatures in the winter at Samara are potentially up to 5°C colder than at Amboseli (compare Figure 2.3 in this thesis to Figure 1 in Altmann, Alberts, Altmann, & Roy, 2002).

3.4.6. IN COMPARISON TO NON-LACTATING FEMALES

All members of the troop are exposed to the same seasonal influences, but in order to determine how mothers specifically are structuring their time budgets in response to their infants' needs, the time budgets of mothers needs to be discussed in relation to non-lactating females.

3.4.6.1. Pregnancy

In Altmann's (1980) model, pregnant females were assumed to be comparable to non-lactating females. The costs of gestation are much lower than lactation costs, but are still higher than cycling costs (Glittleman & Thompson, 1988). In this study, I was able to compare the last two months of pregnancy to non-pregnant non-lactating females. In the last month of pregnancy, mothers tended to forage and moves less (although these values were not significant) and rested significantly more than non-pregnant females. This suggests females in their last month of pregnancy may be slightly readjusting their activity time budgets. Comparably, wild female chimpanzees move significantly less during pregnancy compared to cycling and lactating females (Murray et al., 2009).

3.4.6.2. Month zero

In the infant's first month, the mother is resting and socializing more and moving and feeding less. This is when the infant is spending most of its time in ventral contact (88%,

see Chapter four). Thus the mothers may be recovering from parturition and/or employing an energy-sparing strategy by increasing their time spent in less energetically costly activities. Part of the increased time spent in 'energy-sparing' activities is due to the social attention from other females attracted to newborn infants (Lancaster, 1971), as indicated by the higher rates of grooming received by lactating females following parturition (similar to: Altmann, 1980; Henzi & Barrett, 2002; Kenyatta, 1995; Seyfarth, 1980; Struhsaker, 1971).

The tendency of engaging in less energetically costly activities was also found in baboons by Kenyatta (1995) and Barrett et al. (2006a), where lactating females tended to rest more and feed less than non-lactating females in the infants first few months. Barrett et al. (2006a) found it wasn't sufficient to offset the costs of lactation and females were still losing weight. In addition, lactating females had higher vigilance rates in the months following the birth of their infant, an activity that is incompatible with foraging (Barrett et al., 2006a). Although vervets are not exposed to same infanticide risks as baboons, lactating females may have been increasing their time resting to be vigilant of predators. Predation risk may be high, as nine infants died/disappeared between birth and eight weeks of age.

3.4.6.3. Month one to five

In month one, lactating females differ from non-lactating females only by spending less time moving. Because infants are still dependent on their mother for nutrition at that

time, it is more efficient for mothers to carry their infants rather than have the infants move independently (Altmann & Samuels, 1992). Carrying an infant still incurs an addition costs (roughly 5%: Altmann & Samuels, 1992), therefore mothers are saving energetic expenditure by moving less.

By month two, their infant is gaining independence (Chapter four) and moving more. Even though infants begin supplementing their diet at this point, they are still heavily reliant on their mother for nutrition, and their increased activity levels potentially result in a greater energetic demand of the mother. Lactating females respond by spending more time foraging than non-lactating females from months two to five (although it is only significant in month four in the RST only data).

When lactating females were foraging more, they were also spending less time resting and socializing than non-lactating females. The trade-offs of less time socializing and resting for time spent foraging was confirmed by a significant negative relationship between the activities. Mothers appear to be trading off first resting than social time. This is consistent with Dunbar and Dunbar's (1988) study, which found mothers tried to conserve social time as much as possible, and in contrast to Barrett et al.'s study (2006a) which found mothers conserved resting time as much as possible (presumably due to the importance of maintaining high rates of vigilance while resting). Comparably to my study, in rhesus macaques, extra feeding time came at the expense of resting and social time (Seth & Seth, 1986). The vervets in my study have more resting time to give up than social time compared to baboon and gelada populations (Table 3.8).

Table 3.8: Approximate average percent of time budget spent resting and socializing.

Resting (%)	Social (%)	Species	Location	Reference
30	25	*Theropithecus gelada*	Simen Mountains National Park, Ethiopia	Dunbar and Dunbar 1988
10	12	*Papio hamadryas ursinus*	DeHoop Nature Reserve, South Africa	Barret et al. 2006
18	18	*Papio cynocephalus*	Amboseli, Kenya	Altmann 1980
40	13	*Macaca mulatta*	India	Seth and Seth 1986
35	7	*Chlorocebus aethiops*	Samara Game Reserve, South Africa	This study

Dunbar and Dunbar (1988) found that when mothers exhausted available resting time, they drew on social time. When they did draw on social time, they maintained their primary partners. Given the low percent of time spent socializing in the vervets in my population (5-10% of the time), it would be interesting to see how decreased social time influences individual relationships.

3.4.6.4. Month six and seven

The infant is mainly independent at month six and seven, foraging on its own, although still nursing roughly 5% percent of time (Chapter four). Lactating females are foraging at baseline rates during those months. Looking at Figure 3.3, it seems as though lactating females reach a maximum threshold for time spent foraging at 55%. Possibly further increases would cut into too much resting time, and would result in greater energy expenditure. Instead of foraging more, during this time lactating females appear to be targeting higher protein items than baseline females. Therefore, lactating females are

obtaining more protein whilst spending the same amount of time feeding, potentially due to either an incurred deficit from peak lactation, or because of the continued low levels of nursing. Lactating females are moving more in months six, perhaps as a result of targeting more specific dietary items. Lactating females are also spending less time resting and socializing, which was only significant for socializing in month seven. This could be due to the increased time mothers spent grooming their infants, which on average was less than five percent of the time until month six and seven when it increases up to ten percent of the time. Mothers seemed to frequently groom their infants after rejecting or removing them from nursing, and rejection rates were highest in months six and seven (Chapter Four).

3.4.7. IN SUMMARY:

- Altmann's model is not a good predictor for maternal feeding time while the infant is dependent on the mother

- Nutritional quality in the diet seems to increase as the infant gets older, with the highest quality and foraging time when the infant is six and seven months and is mostly independent

- In the first month after parturition, mothers may be using an "energy sparing strategy" of resting and socializing more and feeding and moving less

- Lactating females spend more time feeding and less time resting and socializing in infant months two to five compared to non-lactating females. Increased

foraging time seemed to be drawn mainly from time resting, although social time

was used to a smaller extent.

- Temperature is the most important variable explaining maternal feeding time (and

  presumably baseline feeding time). Due to the high nutrient quality, it is

  suggested temperature influences feeding due to the negative effects of

  thermoregulatory costs. In addition, the importance of considering daylight hours

  as a limiting factor is highlighted.

CHAPTER FOUR. MATERNAL INVESTMENT

4.1. INTRODUCTION

In order to maximize inclusive fitness, females need to produce as many surviving offspring as possible over the course of their reproductive lives. This inevitably requires a trade-off between investment in current versus future offspring (Trivers, 1972): females must invest sufficiently in offspring to ensure their survival, while at the same time retain the capacity to invest in future offspring. An example of how continued investment in the current offspring delays reproduction in future offspring is lactational anoestrus. A number of studies have shown a positive relationship between length of interbirth interval and infant suckling frequencies (eg. vervets: (Lee, 1987), gorillas (Stewart, 1988), rhesus macaques (Gomendio, 1989)). The goal of this chapter is to examine individual differences in maternal investment and infant independence.

4.1.1. LENGTH OF INVESTMENT

One of the most influential factors on the length of investment in offspring is food availability. By comparing captive and/or food provided troops with wild troops, a few trends emerge on the influence of food supplements on reproductive parameters, indicating the effect of environment on reproductive success. Most notably, captive/food provisioned troop females tend to give birth earlier, have lower inter-birth intervals and higher infant growth rates (Lee & Bowman, 1995; Lee et al., 1991). Lee et al. (1991)

noted that infant weaning weight was roughly the same between food enhanced and food restricted groups, despite slower infant growth rates, due to a longer lactation period in the food restricted groups. In a study of red deer hinds, Loudon et al. (1983) demonstrated that hinds in lower nutrient quality environment produce lower milk yields, and as a result, the infants of hind in lower quality environment grow slower and suckle more frequently, which extends lactation anoestrous. Hauser and Fairbanks (1988) found that in conditions in the free-ranging Amboseli vervets, the decrease in the rate of contact was faster in a swamp environment (which is high in nutrient quality) compared to a dry woodland environment (which is poor in nutrient quality), with more rejections occurring in the swamp environment.

4.1.2. TRIVERS AND WILLARD AND LOCAL RESOURCE COMPETITION MODEL

Trivers and Willard (1973) suggested natural selection may favour differential investment based on infant sex in poor conditions compared to good conditions, which has been attributed to potential differences in investment between the sexes for mothers of different ranks. Specifically, the Trivers-Willard hypothesis predicts that females in good condition will invest more in the sex that has the greater variability in reproductive success, and would benefit from increased investment (which is often sons), whereas females in poor condition will invest more in offspring that have stable reproductive success (usually daughters) (see Chapter 1, Trivers & Willard, 1973). In social groups with dominance hierarchies, condition is often equated to rank, since high-ranking animals have priority of access to feeding sites, and this has been associated with

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significant differences in diet (and therefore condition) and reproductive success (eg. vervet monkeys: Harcourt, 1989; Whitten, 1983), (for a review, see Harcourt, 1989).

The local resource competition model, first proposed by Clark (1978) and later expanded by Silk (1983), suggests that, because females compete for resources in societies with female philopatry, females will try to limit the production of daughters by other females. Therefore, low -ranking females who are unable to protect their daughters from aggression from other females are expected to have a male-biased sex ratio (Silk, 1983). In addition, and as a direct result of aggression by other group members, investment in females is predicted to be higher than investment in sons.

Studies examining maternal investment based on rank and infant sex have produced mixed results. Gomendio (1990) tested the time spent in nipple contact in relation to both the offspring sex and maternal dominance rank in captive rhesus macaques. Daughters of low-ranking mothers had higher rates of nipple contact (Gomendio 1990). At first glance, this seems to support the Trivers- Willard hypothesis since low-ranking females seem to be investing more in daughters. However, Gomendio (1990) suggested the difference could be due to daughters of low-ranking females spending more time in contact to avoid aggression by other group members, which relates to Silk's resource competition hypothesis. In vervets, Lee (1984) found that dominant mothers were less rejecting towards sons and more rejecting towards daughters than were low-ranking mothers, which could suggest greater investment in sons by higher ranking females, supporting the Trivers-Willard hypothesis. In a study of captive Japanese macaques,

high- ranking females spent more time in contact and carried male infants for longer than females, although no differences were observed in sex for low-ranking females (Schino, Cozzolino, & Troisi, 1999). The higher male investment in high-ranking females supports the Trivers-Willard hypothesis. In spider monkeys, which show male philopatry, high-ranking females had a male biased sex-ratio, and invested more in their sons (as measured by longer interbirth interval after having a son and longer time carrying the son), though there was no difference in investment in daughters between low and high rank (McFarland Symington, 1987). Because males in this species remain in the natal troop, this potentially supports both Trivers and Willards hypothesis and the local resource competition model. The effect of infant sex and maternal rank/condition in investment levels is so far inconsistent, with neither hypothesis favoured over the other (Brown, 2001).

4.1.3. WEANING CONFLICT

4.1.3.1. Trivers

Trivers (1974) extended Hamilton's (1964) theory of kin selection and suggested that parents and offspring should disagree on both the amount and duration of parental investment. This parent-offspring conflict stems from fact that all offspring share an average of 50% of the their genes with their mother, and an average of 25-50% of genes with current/future siblings, but 100% of their genes with themselves. As a result, the point at which the costs of continued investment in current offspring outweigh the

benefits is reached earlier in mothers than it is in offspring. Mothers are therefore

selected to halt investment at a stage when infants have been selected to continue to elicit

more. Trivers (1974) suggests this is why "weaning conflict", often in the form of infant

tantrums, occurs. However, Trivers' theory of conflict between parents and offspring is

not, in fact, well supported by behavioural data (Bateson, 1994). For example, Barrett

and Henzi (2000) found infant chacma baboons did not display tantrum behaviour if they

were foraging independently when weaning foods were readily available. Two of the

infants that did display tantrum behaviour were foraging when weaning foods were not

sustained, and as a result, mothers invested more, not less, in their offspring (Barrett &

Henzi, 2000). Bateson (1994) instead suggested that weaning was a dynamic process

with mothers and infants monitoring each other's condition closely and responding

appropriately. Therefore, rather than mothers and offspring disagreeing on the amount of

investment, they converge on the optimum amount that the offspring should receive and

there is no conflict.

4.1.3.2. Timing hypothesis

Altmann (1980) and Dunbar (1988) suggest that at least some conflict between mothers

and infants arises over the timing of access to the nipple, rather than conflict between

parents and infants being about the amount of investment. In most primates, infants are

carried on the caretaker's ventral surface (which is the exclusive form of infant carrying

in vervet monkeys), and can incur costs by interfering with maternal maintenance

activities, particularly as the infant gets larger. Therefore, it has been suggested that

mother-infant conflict occurs more over the timing of access to the nipple rather than amount of nipple access time, referred to as the timing hypothesis (Altmann 1980, Dunbar 1988).

In support of the timing hypothesis, numerous studies have that time in ventral contact decreases more rapidly during feeding and moving activities than resting and socializing (Atmann 1980, Barrett et al. 1995, Kenyatta 1995). These results also correspond to greater rejections of infant contact when the mother is foraging compared to when resting (Altmann 1980, Barrett et al. 1995). In siamangs, Lappen (2009) found that males and females spent more time feeding when the infant was not in ventral contact than when the infant was clinging ventrally. Green (1995) tested the timing hypothesis in vervet infants up to three months old. Time in both nipple and ventral contact decreased more while the mother was foraging compared to moving and resting, but time the infant spent in ventral contact while the mother was socializing was lower than the other activities and was relatively level for the first six weeks, when it began decreasing (Green 1995). This is in contrast to gelada, which tended to have higher levels of infant contact time while the mother was socializing compared to when the mother was foraging or moving (Barrett, Dunbar, & Dunbar, 1995). A possible explanation for the difference in vervets could be the existence of allomothering in vervets, particularly when the mother is relaxed during a grooming session (Lancaster, 1971).

4.1.4. ALLOMOTHERING

Infant caretaking by individuals other than the mother could be another factor influencing maternal investment. Mitani and Watts (1997) demonstrated higher postnatal growth and lower interbirth intervals in species that exhibited allocaretaking compared to only maternal caretaking species. The amount of caretaking by others varies by species. In some species, aggression and assault are typical and others exhibit protective caretaking (Hrdy, 1976). Infant caretaking by others in vervet monkeys is typically characterized by relaxed and friendly contacts, with the highest rates of contact occurring in the infant's first month and equal rates of approaches for the first three months of an infant's life (Lee, 1983). Given the large troop sizes my study groups (see Chapter 2), there are potentially more allocartakers available, which may influence infant independence compared to other vervet study troops.

4.1.5. OBJECTIVES AND PREDICTIONS

The objectives of this chapter are to explore the factors influencing infant independence, specifically to:

1. Determine the rate of decrease of infant proximity over infant age and the effect of maternal rank and infant sex.

- According to the Trivers-Willard hypothesis, investment will be greater for daughters of low-ranking females and greater for sons of low-ranking mothers

- Local resource competition hypothesis predicts investment will be highest for daughters

2. Determine the role the infant and mother play in establishing/breaking contact.

3. Qualitatively compare investment, as measured by time in ventral contact and interbirth interval, in relation to other vervet populations.

4. Examine the rate of decrease of maternal investment based on maternal maintenance activities.

- According to the timing hypothesis, time in ventral contact should decrease more rapidly in the activities in which the presence of the infant is a hindrance.

- According to the investment hypothesis, time in ventral contact should decrease in a manner independent of maternal activity.

5. Explore the frequency of allomothering and its influence on maternal time budgets.

4.2. METHODS

4.2.1. DATA COLLECTION

I collected behavioural data between October 2010 and June 2011 on two troops of vervet monkeys located on Samara Game Reserve, in the Eastern Cape, South Africa. The troops consisted of 49 to 72 individuals, with the adults recognizable through individual markings. The troops were generally well habituated and could be followed from a distance of two to five meters. Behavioural data for twenty-four mother-infant pairs was captured for the first month of infant life. The number of full data pairs decreased thereafter due to deaths/ disappearance and timing of the births; consequently, data was collected up to seven months of data on fifteen mother-infant pairs and eight months of data for seven pairs. Detailed descriptions of the study area, study animals and behavioural observations collected are in Chapter 2.

I conducted focal animal sampling on mother-infant pairs (Altmann 1974). Focal samples were 20 minutes in length, though they were terminated if the focal animal was out of sight for more than five minutes. If the mother and infant were separated, I followed the mother. Data on female activity budgets were collected via instantaneous scans collected every two minutes throughout the focal, with female activity allocated to one of four mutually exclusive categories: feeding, moving, resting and socializing, with an extra fifth category of "grooming infant" for lactating females only. Average infant grooming was less than five percent of the activity budget for most months and was therefore not included in analyses.

Interactions between mother and infant were recorded continuously, including distance to the mother (on the nipple/ventrum, in contact, 1m, 5m, >5m), along with the initiator of the individual who made or broke contact if it was noticeable. When analyzing contact transitions by the mother compared to the infant, only occasions in which it was clear who made/broke contact were used, producing an underestimate of the rate of contact transitions. The rate of making contact is per hour of observation, whereas the rate of breaking contact is calculated over time in contact (in order to account for decreased time spent in contact as infants get older). For investigation of changes of infant distance over time, I used the continuous data. Maternal activity was collected at the two-minute instantaneous scans. Ventral contact is used as a measure of maternal investment, since it represents opportunity to suckle as well as carrying costs.

Interactions between the focal mother and other individuals were recorded continuously (see Table 2.5), including all attempts to contact the infant. The behaviour of the monkey initiating infant contact and the behaviour of the monkey guarding the infant were recorded, as well as if the infant was successfully transferred (defined as no longer in contact with its guardian). As infants were not followed individually, the rate of allomothering excludes any episodes that occurred while the infant were separated from its mother by a distance greater than 5m or while the infant was in another individual's care (it was too challenging to record all the allomothering attempts once another individual had possession of the infant while recording mother activity). As a result, it is a conservative estimate of allomothering rates. The data were non-normally distributed;

however, the mean is presented rather than the median as the latter for allomothering in month four was zero and would not have been represented. A successful allomothering attempt was scored when the individual as able to remove the infant from its guardian's care. When examining the effect of maternal rank and infant sex on allomothering attempts/success, only data from the infant's first month were used, since it was normally distributed and would not be skewed by the low rates occurring in the later months.

4.2.2. STATISTICAL ANALYSES

A minimum of one focal sample per time period per month (i.e., a minimum of 80 minutes) was required for a given female to be included in analyses. On average, females were sampled twice per time block per month (average sampling per individual per month = 179 min ± sd 43min).

Data were tested for normality using SPSS 19.0 ®. Unless otherwise stated data were not found to deviate from a normal distribution and parametric tests were used for analyses. When data did deviate, a transformation was applied in an attempt to achieve normality. If a transform could not be applied, an equivalent, non-parametric statistical test was used. All univariate analyses were conducted in SPSS ®. Multivariate analyses were conducted in JMP 9 ® using the default values of the "Fit Model" platform with Subject ID as a random factor for analyses with repeated measures since it would others violate the assumptions of simple regression models. The specific analyses are described in each section.

4.3. RESULTS

4.3.1. INFANT CONTACT

4.3.1.1. All contact rates

In order to determine if there was a difference between troops in the percentage of time that infants spent in ventral contact across infant age (in months), a standard least squares regression was run with troop and infant month as independent variables, percent of time in ventral contact as the dependent variable and mother ID as a random effect to take into account repeated observations. Neither troop i.d. ($F=1.48$, $p=0.25$) nor the interaction of infant age and troop ($F=0.26$, $p=0.61$) had a significant effect on time spent in ventral contact; therefore, troops were pooled for analyses.

A standard least squares regression with mother I.D. as a random effect was conducted to determine the relationship between infant age (in months) and time (%) spent on/ close to the mother (nipple/ventral, contact, within 1m, within 5m). A significant negative relationship was found between infant age over the first eight months and percentage of time spent in ventral contact. The other distances over the eight months were roughly parallel, meaning infant contact and proximity decreased in a similar manner to time in ventral contact (Table 4.1).

Table 4.1: Standard least square regression (REML) of percent of time infants are within different distances (nipple/ventral, contact, 1m, 5) of their mother (with Mother ID as a random effect).

	β	Intercept	t	P	R^2adj
Nipple/Ventral	-13.16	78.49*	-23.05	<0.001	0.81
Contact	-13.00	80.92*	-20.25	<0.001	0.76
1m	-14.35	98.37*	-25.02	<0.001	0.83
5m	-14.14	106.28*	-24.69	<0.001	0.80

*$p<0.001$

The relationship between infant age and distance to the mother decreases sharply until the fifth month and then appears to level out (Figure 4.1). In order to test this, data were divided into two categories – months zero to four and months five to seven – and analyzed separately. Infant age had a highly significant effect on infant distance from the mother for the first five months (t=-27.65, $p<0.001$), with a steeper slope (β=-19.69) and more of the variance explained ($R^2adj = 0.91$) than if all eight months were included in the analysis. There was no significant effect of infant age on distance across months five to seven (β=-0.41, t=-0.46, p=0.65, $R^2adj = -0.49$).
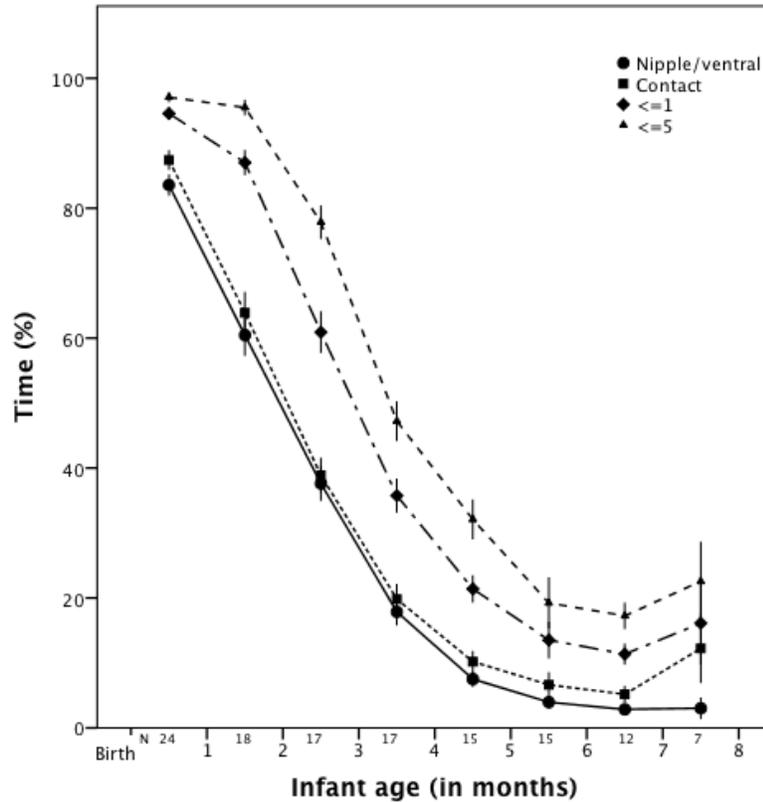
Figure 4.1: Time (%) over infant age (in months) the infant is either in nipple/ventral, contact, within 1m or within 5m of their mother. Sample size is listed below the x-axis. Error bars represent ± 1 S.E.

4.3.2. LENGTH OF INVESTMENT

Infant ventral contact decreased rapidly and in a linear fashion until the infant's fifth month, when it stabilized around 5%. In order to compare how ventral contact compares to other sites, ventral contact for my study site was plotted on the same graph as for Amboseli vervets in Figure 4.2, where the dry woodland was poor in nutrient quality and the swamp environment high in nutrient quality (Amboseli data presented in: Hauser & Fairbanks, 1988).
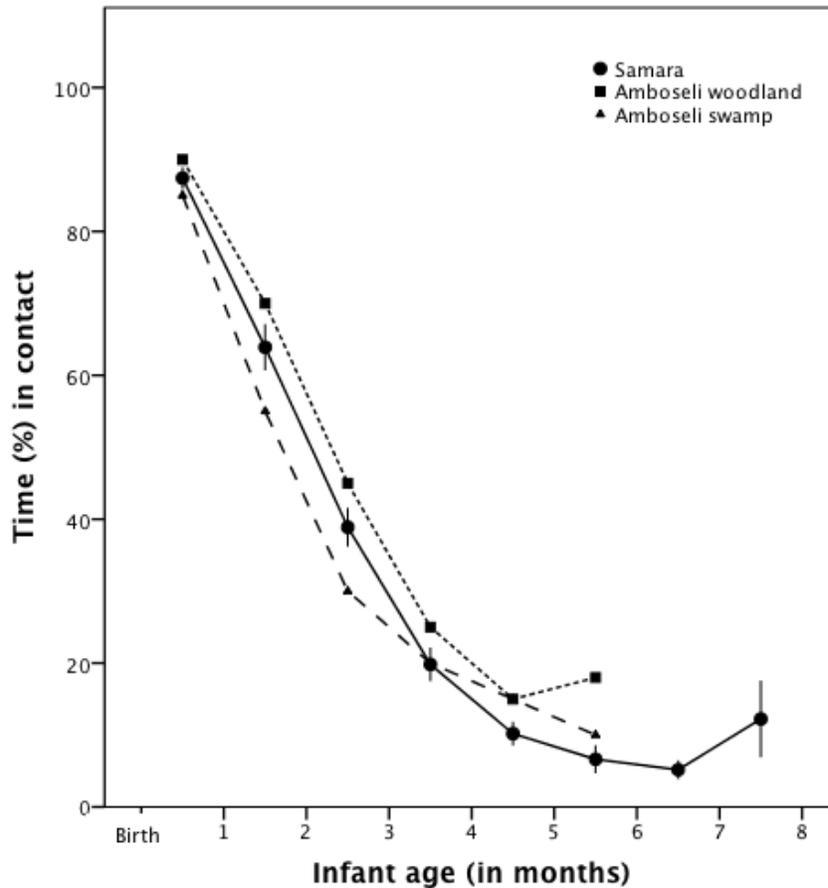
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Figure 4.2: Mean time (%) in contact for this study (Samara, circles and solid line) ± 1 SE, compared to Amboseli vervets (dry woodland, square and short dashed line; swamp, triangle and long dashed line).

As Figure 4.2 illustrates, the rate of decrease of contact is similar between the sites. I estimated the Amboseli data from Figure 1 in Hauser and Fairbanks' (1988) paper, and am therefore unable to do statistical comparisons. The Samara data lies below the Amboseli woodland and above the swamp for the first few months, but is probably within the margin of error and is unlikely to be statistically significantly different (except perhaps for month five, with infants at Amboseli woodland spending more than 10% of time in contact compared to infants at Samara). Despite the similarities in time in contact, vervets at Samara seem to have longer inter-birth intervals (see Table 4.2). In

Table 4.2, Group A is equivalent to the dry woodland in Figure 4.2 and Groups B and C the swamp environment.

Table 4.2: Infant survival, interbirth interval and site characteristics for vervets in two troops at Samara and three troops at Amboseli.

Site/ Troop	Probability of survival to 1yr (%)	Inter-birth interval overall	Inter-birth interval (surviving infants)[a]	Food quality	Troop size	*Reference*
Samara – RBM	67[b]	19.8	22.3[c]	Low[d]	49	*This thesis*
Samara- RST	65[b]	23.4	35.2[c]	Low[d]	72	*This thesis*
Amboseli- Group A	41	17.1	18.1	Low	18	*Lee 1984, 1987*
Amboseli- Group B	61	13.7	14.1	Medium	12	*Lee 1987, 1987*
Amboseli- Group C	42	13.5	13.6	High	21	*Lee 1984, 1987*

a- Surviving infants were classified as infants who survived to one year old.
b- Based on only two years of data, where the infants were individually recognized and kept track of for the year (since there are so few years, the total rather than the annual mean is presented out of 21 births for RBM and 23 for RST)
c- Calculated the same way as overall interbirth interval reported in section 3.3.3.4, but only for the two years where infant survival was monitored, and only counted infants that survived
d- Group A had territory in dry woodland, compared to Groups B and C, which were in swamp. Therefore, Samara's troops would most likely have similar food quality to Group A.

By comparing between the two environments, a few patterns are clear. First, lower nutrient quality seems to be have longer inter-birth intervals. In addition, when nutrient quality is low, troop size also seems to correspond to longer inter-birth intervals. Lastly, higher infant survivorship also corresponds to longer interbirth intervals.

4.3.3. INFANT SEX AND MATERNAL RANK

4.3.3.1. Ventral contact

Standard least squares regression was run to examine the effects of infant sex and maternal rank on the percentage of time spent in ventral contact. Percentage of time in ventral contact was the dependent variable, mother I.D. was included as a random effect and a full factorial mode was run with infant age (continuous), sex of infant (male or female) and maternal rank (continuous using standardized normalized David's score). The main effects and interaction effects are reported in Table 4.3.

Table 4.3: Main effects and interaction effects of infant age, maternal rank and infant sex on percent of time in ventral contact.

	β	Std. eror	t-ratio	p
Infant age	-13.94	0.63	-22.09	<0.001*
Infant sex	0.020	1.06	0.02	0.99
Maternal rank	1.92	6.27	0.31	0.76
Infant age * infant sex	-0.92	0.63	-1.46	0.15
Infant age * mother rank	3.17	3.55	0.89	0.37
Maternal rank * infant sex	17.57	6.27	2.80	0.013*
Infant age * infant sex *Maternal rank	-7.28	3.55	-2.05	0.043*
Intercept	76.72	4.58	16.75	<0.001*

R^2 adj= 0.84, *p<0.05

This confirmed that infant age had a significant negative effect on time in ventral contact (Figure 4.1). Infant sex had no significant main effect on time spent in ventral contact and there was no interaction with infant age (Figure 4.3). Maternal rank had no significant main effect on time spent in ventral contact, and there was no interaction with infant age. There was, however, a significant interaction between infant sex and maternal rank on time spent in ventral contact, with a negative relationship between rank and time spent in ventral contact with daughters and no relationship between rank and time in ventral contact for sons (see Figure 4.4): daughters of low-ranking mothers spent more time in ventral contact than daughters of higher ranking mothers.
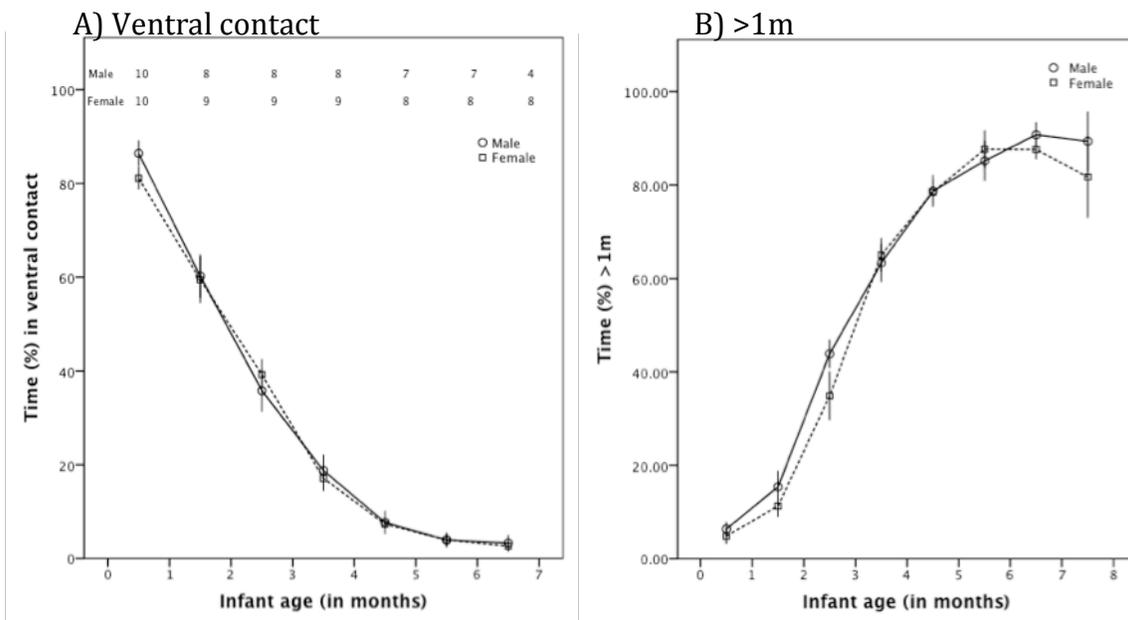
Figure 4.3: Time (%) in A) ventral contact or B) within 1m (right) over infant age for males (circles, solid line) and female (square, dashed line) infants. Samples sizes are noted on the upper left-hand portion of the graph. Error bars represent ± 1 S.E.
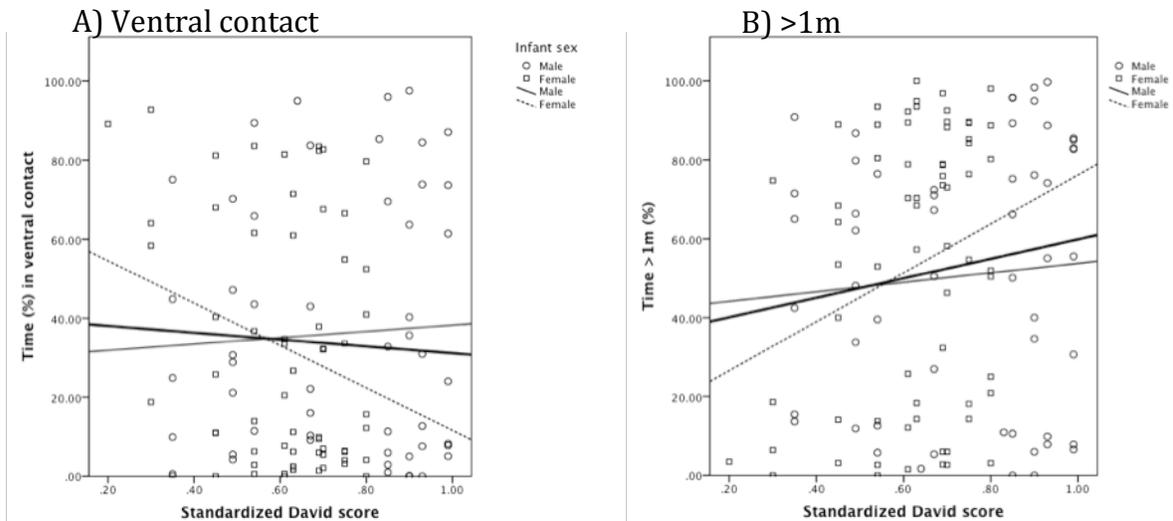
Figure 4.4: Time (%) in ventral contact and greater than 1m for all infant ages over mother rank (where 1.00 equals highest rank) for males (circles and solid line) and females (squares and dashed line). Thick solid line is time in ventral contact for both sexes combined over standardized David score.

A significant interaction of infant age, maternal rank and infant sex on time in ventral contact indicates that the rate of decrease in ventral contact is different between the sexes based on rank. This is illustrated in Figure 4.5, where sons of high-ranking mothers had a shallower rate of decrease than sons of lower ranking mothers, and daughters of high-ranking mothers having an initial higher rate of decrease than low-ranking daughters. The analyses was conducted with rank as a continuous variable, but for graphical convenience, data were divided into three categories of low (normalized standardized David score 0.2-0.63), middle (0.64-0.79) and high (0.80-1.00) ranking mothers, with the categories assigned to ensure there were at least one surviving individual in each category for each sex.
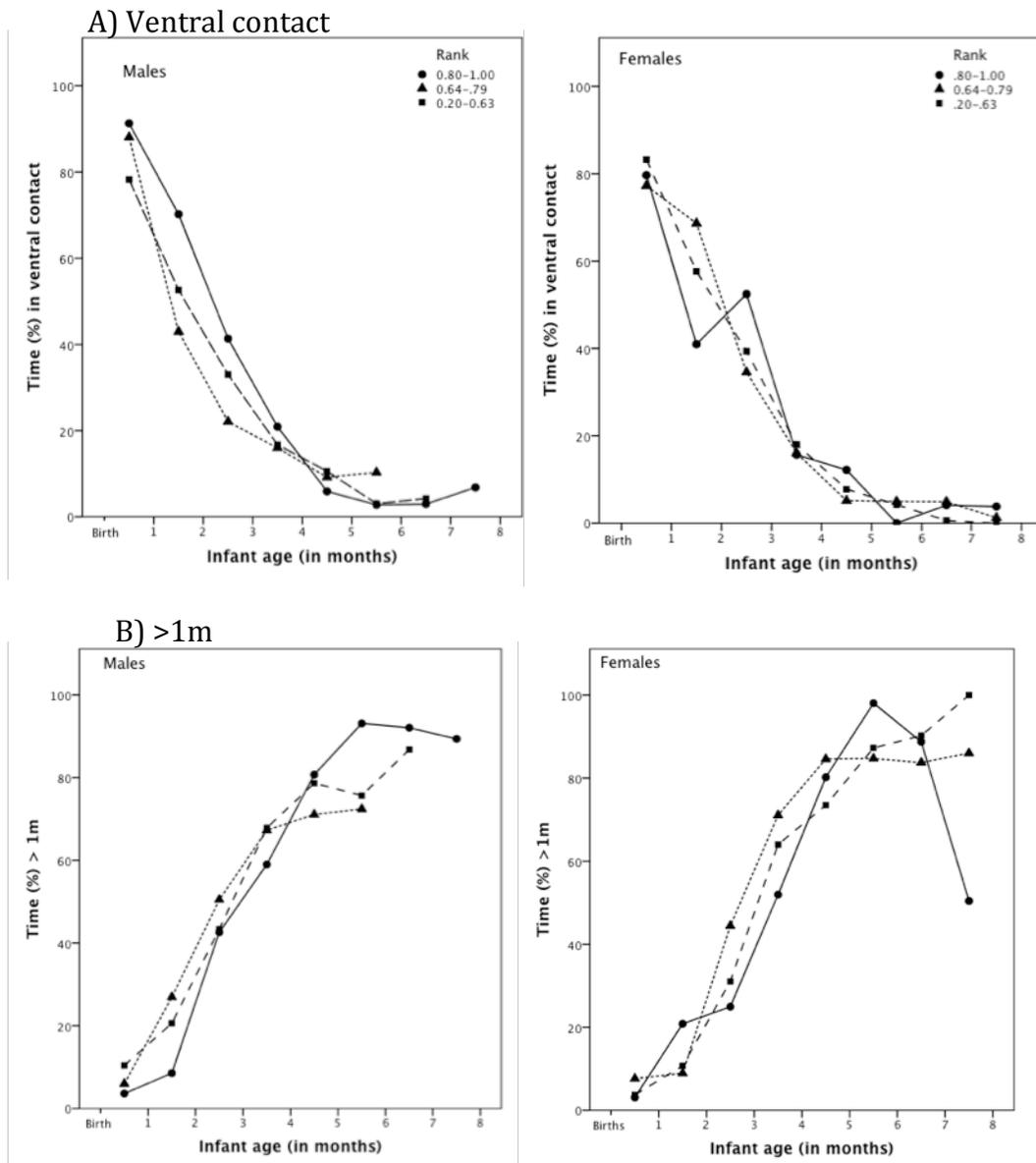
A) Ventral contact

B) >1m

Figure 4.5: Mean time (%) in ventral contact ((A)top) or greater than 1m ((B) bottom) over infant age and mother rank (as indicated by standardized David score where 1.00 is the highest rank) and infant sex. Solid line is for high rank, small dashed line for middle rank and long dashed line low rank.

Independent t-tests were run between the sexes on the ranks to compare mean rank

between the mothers of sons and daughters. The mother of daughters had a mean rank of

0.61 (±0.23) and the mother of sons 0.69 (±0.20).   There were no significant differences in maternal rank based on infant sex (t=-0.861, df=18, p=0.401).

4.3.3.2. Infant in proximity (>1m)

In order to explore if there was a difference in infant independence between rank and sex, the rate of decrease of when the infant was further than one meter from its mother was explored using a standard least squares regression. Percentage of time infant was greater than one meter distance was entered as the dependent variable, mother ID was included as a random effect and a full factorial model was run with infant age (continuous), sex of infant (male or female) and maternal rank (continuous using standardized normalized David's score).   The main effects and interaction effects are reported in Table 4.4.

Table 4.4: Main effects and interaction effects of infant age, maternal rank and infant sex on percent of time infant and mother are in proximity (<1m).

	β	Std. eror	*t-ratio*	*p*
Infant age	15.65	0.61	25.47	<0.001*
Infant sex	0.93	1.13	0.82	0.43
Mother rank	6.36	6.62	0.96	0.35
Infant age * infant sex	-0.057	0.61	-0.09	0.93
Infant age * mother rank	2.27	3.48	0.65	0.52
Mother rank * infant sex	-11.00	6.62	-1.66	0.11
Infant age * infant sex *mother rank	3.12	3.48	0.90	0.37
Intercept	-4.40	4.77	-0.92	<0..3662

*p<0.05, R^2 adj= 0.87

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In comparison to time in ventral contact, there was only a significant effect of infant age on time spent in proximity. This indicates the sex and rank differences only influenced time in ventral contact, with the same amount of time spent within 1m of their mothers. Time infants were greater than one meter to their mothers is contrasted to time in ventral contact in Figure 4.3 – Figure 4.5.

4.3.4. SPATIAL TRANSITIONS

Infant independence is characterized by a decreased rate of reliance by the infant on its mother. The rate of transitions of contact (average of the number of transitions per individual over focaled time in hours) was calculated for each infant month (Figure 4.6). The figure illustrates both the rate of making contact and breaking contact by the mother infant pair and by others (allomothers). The rate of transition by mothers and infants is quite low in the first month, presumably because the infants spend most of the time on the mother's ventral surface. Transitions are quite high for the following three months, and decline in the infant's fifth month indicating increased infant independence. Contact transitions due to others occur at much lower frequency than those by the mother-infant pair, and fall quickly after the first month.
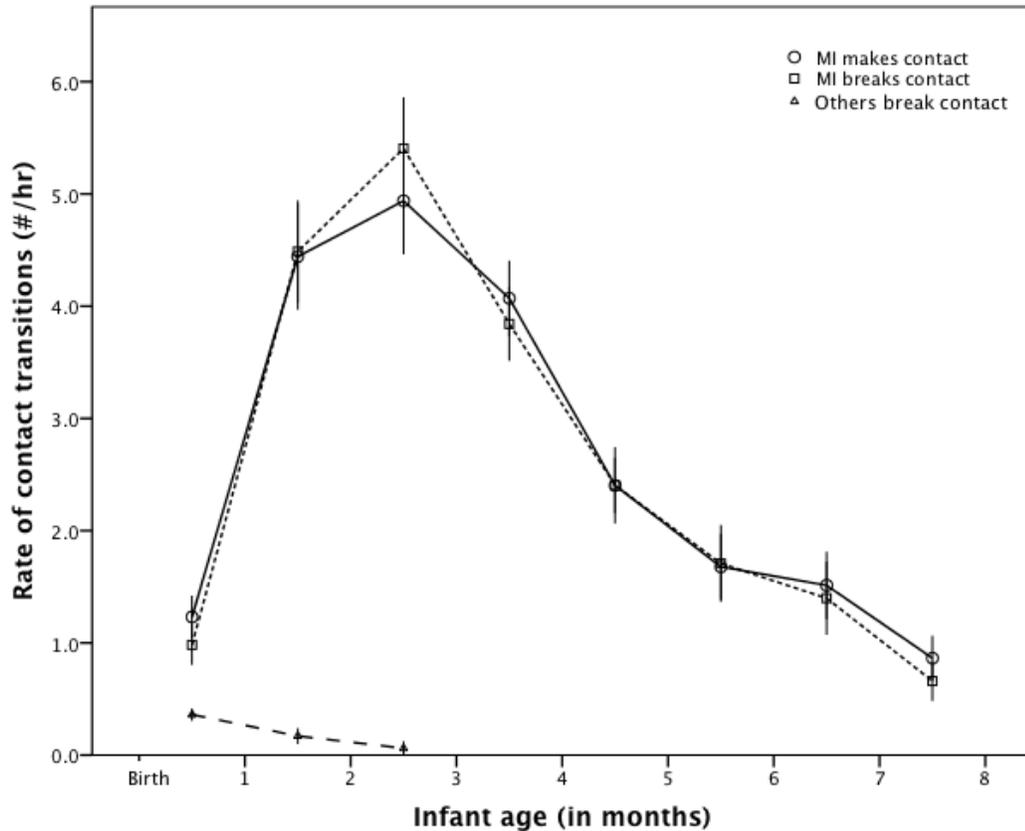
Figure 4.6: Mean rate of contact transitions (number per hour observed) by the mother-infant pair (MI) or others over infant age. Mother-infant making contact is illustrated by the solid line and circle and breaking contact by the square and short dashed line. Others breaking contact is illustrated by the triangle and long dashed line. Error bars represent ± 1 S.E.

Both mother and infants are involved in the infant becoming more independent. Figure

4.7 illustrates the rate of making contact (Figure 4.7a) and breaking contact (Figure 4.7b)

by both the mother and the infant.
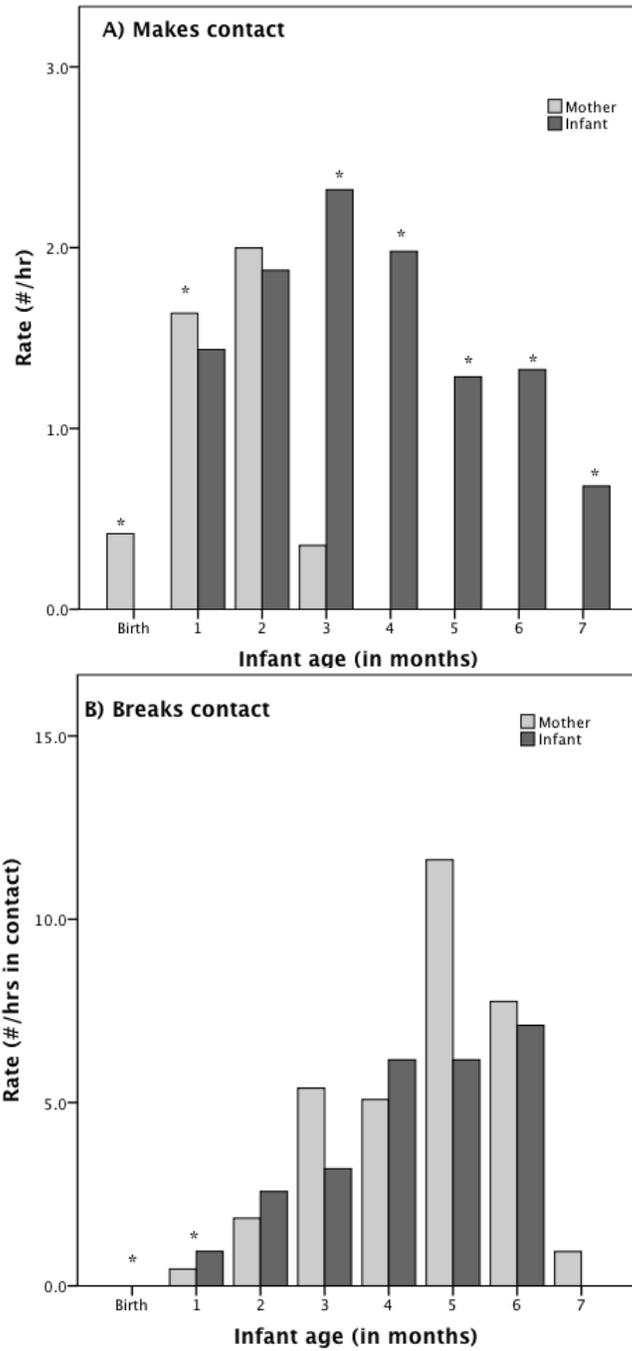
Figure 4.7: A) Median number of times either the mother (light grey) or the infant (dark grey) made contact over focaled time (in hours).   B) Median number of times the mother or the infant broke contact over time in contact (in hours). * $p<0.05$.

Due to slight skew, repeated non-parametric tests were used at each month of infant age (Wilcoxon paired tests). In the first two months of life, the mother made contact more than the infant (Month 0: $N=24$, $z=-3.506$, $p<0.001$; Month 1: $N=18$, $z=18$, $p=0.023$). Rate of contact was equivalent between mother and infant for the third month ($N=17$, $z=0.220$, $p=0.826$). For the remaining months, the infant initiated significantly more contact than the mother (Month 3-7: $7<N>17$, $2.023 < z > 3.296$, $p<0.05$). The infant broke contact significantly more than its mother in the first two months (Month 0: $N=24$, $z=2.934$, $p=0.003$; Month 1: $N=18$, $z=2.481$, $p=0.013$). For the remaining months, no significant differences were found between mothers and infants ($N= 6-17$, $p>0.05$). These results highlight the dynamic nature of mother infant interactions, with both highly involved in breaking contact and the mother initiating contact more in the first few months and infant more in the later months.

4.3.5. MATERNAL ACTIVITY AND INFANT CONTACT POSITION

4.3.5.1. Ventral contact and maternal activity

The time an infant spends in ventral contact when the mother is engaged in each maintenance activity is illustrated in Figure 4.8. Time in ventral contact decreases quickly when the mother is foraging, and also when she is moving. Time spent ventral while the mother is resting also decreases rapidly in the first few months and then levels out during the infant's fifth month of life. Time spent in ventral contact while the mother is socializing shows a more noisy pattern, although it does increase sharply from month

one to three when time in ventral contact while foraging and moving show a rapid

decline.   Contact during both resting and social time appear to level out at higher rates in

the infant's fifth month than moving and foraging time (in the infant's fifth month:

Foraging *M*=0.15% *sd*=0.61; Moving *M*=0 *sd*=0; Resting *M*=11.27% *sd*=11.77; Social

M=14.41%, *sd*=32.09; *N*=15).
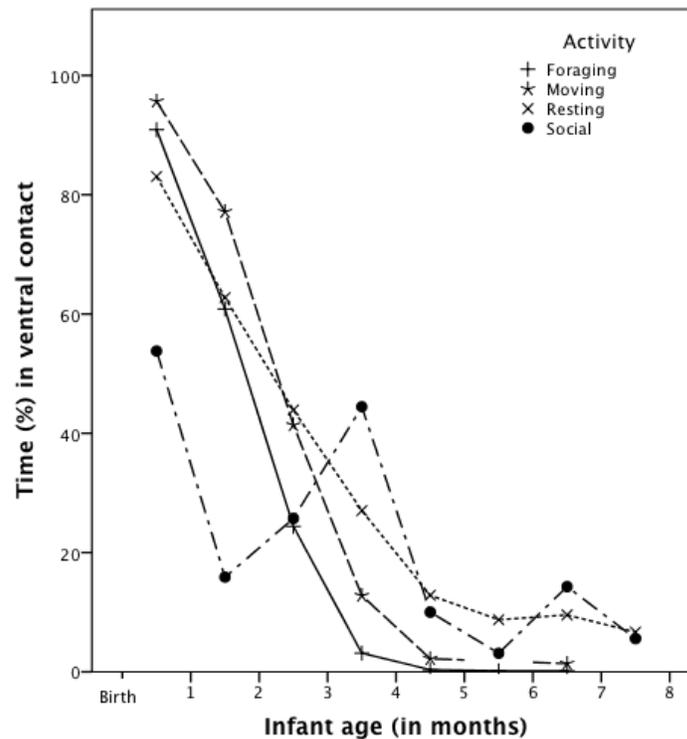
Figure 4.8: Median time the infant is in ventral contact over infant age while the mother
was engaged in maintenance activities.

Due to a lack of normality in the data, the percentage of time spent in ventral contact for

each infant during the mother's activities were compared for each month separately using

a Friedman test and followed up with pairwise comparisons using a Wilcoxon's test with

a Bonferroni correction (Table 4.5).

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Table 4.5: Percent of time infant was in ventral contact compared across mother maintenance activities in each month of infant age.

		df,N^a	χ^2	z	p
Month 0-1		3, 24	32.44		<0.001
	Social-Foraging			3.24	0.007
	Social-Moving			5.31	<0.001
	Resting-Moving			3.81	0.001
Month 1-2		3, 17	20.24		<0.001
	Social-Resting			2.92	0.021
	Social-Moving			4.38	<0.001
Month 2-3		3, 16	14.02		0.003
	Foraging-Moving			-2.88	0.024
	Foraging-Resting			-3.012	0.016
Month 3-4		3, 16	27.56		<0.001
	Foraging-Social			-4.45	<0.001
	Foraging-Resting			-4.517	<0.001
Month 4-5		3, 13	20.78		<0.001
	Foraging-Resting			-3.80	0.001
	Moving-Resting			-1.462	0.023
Month 5-6		3, 10	17.34		0.001
	Moving-Resting			-2.944	0.019
	Foraging-Resting			-2.771	0.034
Month 6-7	*No pair-wise significance*	3, 8	10.89		0.012
Month 7-8	*No pair-wise significance*	3, 3	3.00		0.392

a- *N* varies either due to death/disappearance or for cases in which there was no recorded social time for the month, it was excluded from analyses.

In the first month of life, time spent in ventral contact was lower when the mother was socializing compared to when she was foraging and moving, and they spent more time in ventral contact when the mother was moving compared to when she was resting. By the fourth month of life, time in ventral contact while moving was equivalent to the time

spent in contact while foraging and, in the fifth month, time in ventral contact was lower

when moving than resting, indicating the infants initially showed high levels of ventral

contact when travelling, but this decreased as infants became more independent. By the

third month, the infant was spending less time in ventral contact when the mother was

foraging than when she was resting, which was the case for the next three months,

indicating that time in ventral contact time decreased more rapidly while the mother was

foraging compared to when she was resting. By the infant's seventh month, there was no

significant pair-wise differences in ventral contact, which could be a result of a lower

sample size, or the total low percentage of time the infants were in ventral contact overall

(m=2.85%, sd=3.10, N=12).

In order to examine the differences in degree of association with activity and infant

month (non-parametric equivalent of slope), Kendall-Tau B was used to examine the

percent of time in ventral contact and infant month for each individual for each maternal

maintenance activity (foraging, moving, resting, and social). Only individuals who had a

full set of data for the first six months were included in the analysis (N=15), with the

individual coefficients reported in Appendix B. The coefficients were compared between

activities using Friedman's rank test, with follow-up pair-wise Wilcoxon test with

Bonferroni correction if the Friedman was significant. A significant difference was found

between associations of ventral contact and infant age between activities (N=15, df=3,

χ^2=31.51, p<0.001) and posthoc comparisons revealed a significant difference between

coefficients for socializing with all other activities (p<0.05), indicating that infant age

was a significant factor in the variability of time in ventral contact for all activities other than time spent social.

Green (1995) suggested that the unexpectedly low percentage of time the infant is in ventral contact while the mother is socializing for vervets up to twelve weeks of age could potentially be due allomothering, or an artifact of the short sampling duration. In order to further explore this, ventral contact while the infant was within one meter of its mother was explored. If mothers allowed infants to be handled by others while they were socializing, time within one meter should show a similar parallel decrease to all other activities (assuming the infant remained near or with the individual performing the grooming). As Figure 4.9 depicts, time within 1m decreases in a parallel manner to time the infant spends in ventral contact for foraging, moving and resting activities. The most noticeable difference was when the mother was socializing, time in proximity decreased in a more parallel manner over infant age, indicating the infant was most likely being held by the monkey interacting with the mother or a nearby individual, a relationship which is further explored in section 4.3.6. This suggests the noisier nature of the socializing data that Green (1995) and I found is not an artifact of the low rates of time spent socializing; rather, it is an indication of allomothering activity.
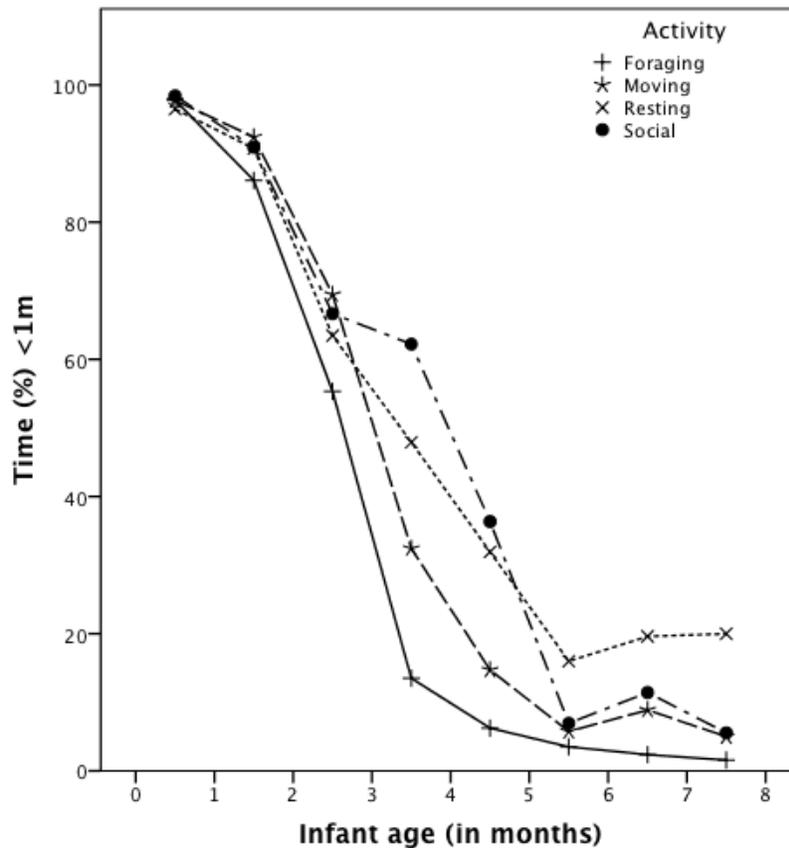
Figure 4.9: Median time the infant is within 1m of their mother while the mother was engaged in one of the maintenance activities.

The percent of time within 1m for each infant during the mother's activities was compared each month using Friedman test and followed up with pairwise comparisons using a Wilcoxon's test with a Bonferroni correction if the Friedman was significant (Table 4.6). Contrary to time in ventral contact, there was no significant difference of infant time within 1m between activities for the first couple of months. Mothers tended to be less in proximity to their infant when foraging in the later months compared to when engaged in other maintenance activities.

Table 4.6: Percent of time infant was within 1m of their mother compared across mother maintenance activities in each month of infant age.

		df,N^a	χ^2	z	P
Month 0-1	*No significant pair-wise comparisons*	3, 24	6.832		0.077
Month 1-2	*No significant pair-wise comparisons*	3, 17	4.988		0.173
Month 2-3		3, 16	9.868		0.020
	Foraging-Resting			-2.944	0.019
Month 3-4		3,17	34.527		<0.001
	Foraging-Moving			-3.055	0.013
	Foraging-Resting			-4.450	<0.001
	Foraging-Social			-5.513	<0.001
Month 4-5		3, 14	20.143		<0.001
	Foraging-Social			-3.220	0.008
	Foraging-Resting			-4.245	<0.001
Month 5-6	*No significant pair-wise comparisons*	3, 9	7.670		0.053
Month 6-7	*No significant pair-wise comparisons*	3, 8	6.973		0.073
Month 7-8		3, 3	2.077		0.557

a- *N* varies either due to death/disappearance or for cases in which there was no recorded social time for the month, it was excluded from analyses.

4.3.5.2. Infant rejections and activity

The rate of rejections per maternal activity was examined to test whether rejections were related to maternal activity (see Figure 4.10). As activity was recorded at two minute intervals and rejections recorded continuously (see section 4.2), the recorded activity of the mother before the rejection at the interval is presented (Figure 4.10a), as well as the

activity of the mother at the interval following rejection (Figure 4.10b). Due to the low

percentage of time spent in social and grooming infant activities (<10%), it was grouped

with time spent resting under 'Inactive/Groom' category. Data is non-normally

distributed; however, the mean rather than the median is presented since the median is

often zero (which indicates the low rates of occurrences recorded, and as a result, is

biased by low sample size).
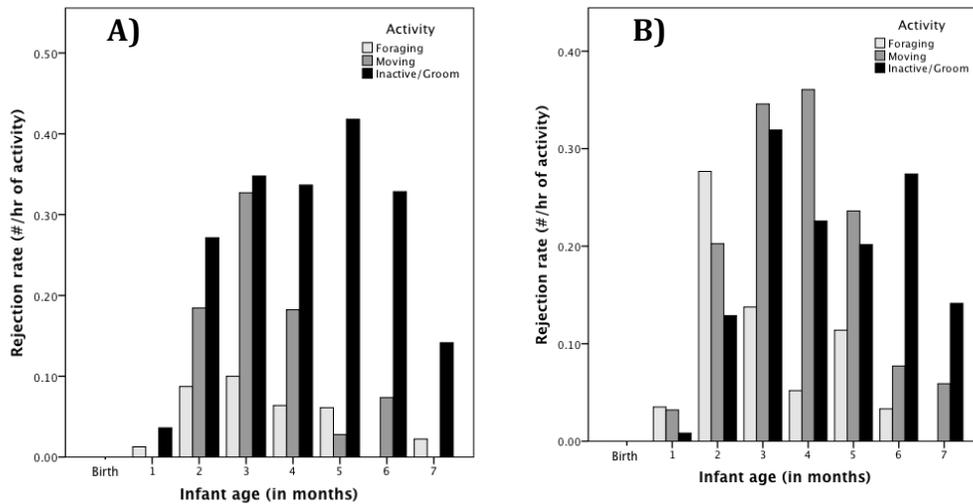
Figure 4.10: Rate of rejection (#/hr of activity) for maternal maintenance activities
foraging, moving, and inactive/groom (which combines resting, social and grooming
infant) from birth to month seven. A) Maternal activity before rejection, B) maternal
activity following rejection

Overall rejection rates were highest in month three. Rejection rates while the mother was

foraging and moving before rejection were highest in month three and tended to decrease

thereafter, whereas rejection rates while the mother was resting before rejection was

highest in month five. Related samples Friedman's tests were used to detect a difference

in rejection rates between activities for each month (with each month analyzed

individually). If a significant difference was detected, paired Wilcoxon tests with

Bonferonni correction were applied. When examining the activity at the interval before rejection, a significant difference was detected in rejection rates for month two ($z=6.00$, $df=2$, $p=0.05$; no pairwise differences), month three ($z=7.00$, $df=2$, $p=0.030$; no pairwise differences), month four ($z=15.073$, $df=2$, $p=0.001$; with significant differences between foraging and inactive ($z=1.10$, $p=0.008$) and moving and inactive ($z=-0.900$, $p=0.041$)), month five ($z=9.742$, $df=2$, $p=0.008$; no pairwise comparisons), month six ($z=8.375$, $df=2$, $p=0.015$; no pairwise comparisons). Therefore, there was an overall difference between rejection rates, but there were not sufficient occurrences to detect pair-wise differences (though from the graph, rejection rates tended to be highest while mothers were resting and lowest while foraging).

When examining rejection rates using the interval activity following rejection, a significant difference was detected in rejection rates for month three ($z=6.218$, $df=2$, $p=0.045$) and there were no significant differences between activities detected in any of the other months. These results indicate that, while mothers may reject infants more often while resting, their activity following rejection changes, with the mother engaging more equally in foraging, moving and resting/grooming. Since mothers tended to rest more before rejecting their infant, this indicates mothers are sometimes changing their activity from resting to moving and foraging after rejecting their infant.

4.3.6. ALLOMOTHERING

4.3.6.1. Allomothering attempts

The average rate of allomothering attempts (number per hour) while the focal mother was within 5m of her infant or was in possession of her infant is shown in Figure 4.11 for both total rate and rate while the infant was in ventral contact. The highest number of attempts occurred in the infant's first month of life, and there were no attempts beyond the infant's fourth month (and very few in the fourth month, as indicated by a median of zero). It also shows that that allomothering attempts are more common in the early months, but that overall success rates do not vary much over time. Success rates are much lower, however, when the infant is in contact, particularly after the first month.
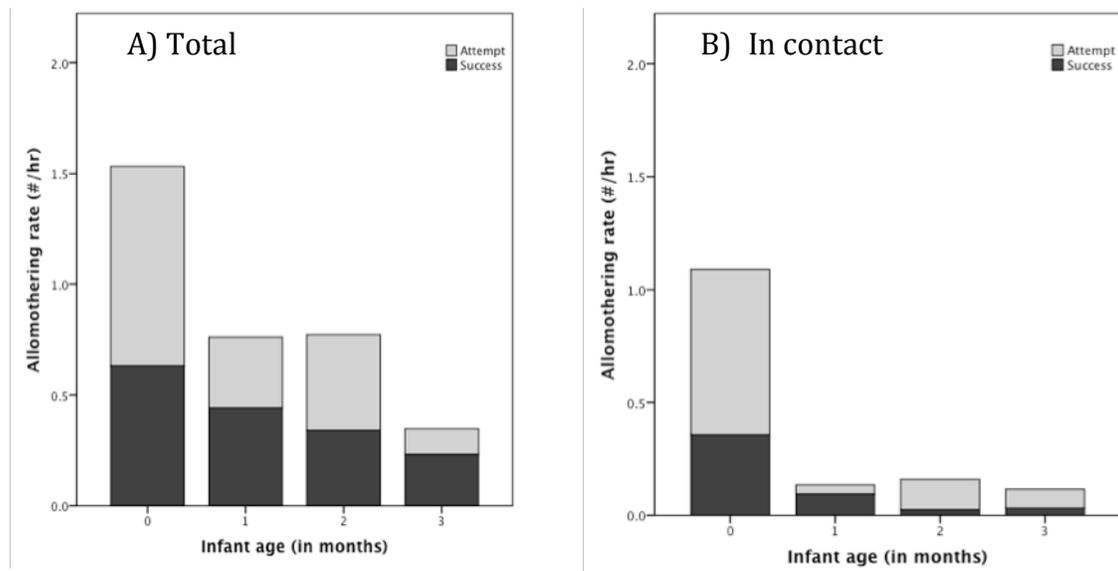
Figure 4.11: The mean rate of allomothering attempts and rate of allomothering success of focal female infant's while the infant was a) within 5m of its mother and b) in contact with the mother.

Figure 4.12 shows the percentage of attempts and success for allomothering when the

infant is in contact with its mother (as opposed to out of contact). As the figure

indicates, roughly two thirds of the allomothering attempts occurred while the infant was

in ventral contact for the first month, but in the later months, most of the allomothering

occurred while the infant was out of ventral contact. This could in part be because the

infant spends less time in ventral contact as it gets older. Successful allomothering times

ranged from as little as a few seconds to as long as a few hours.
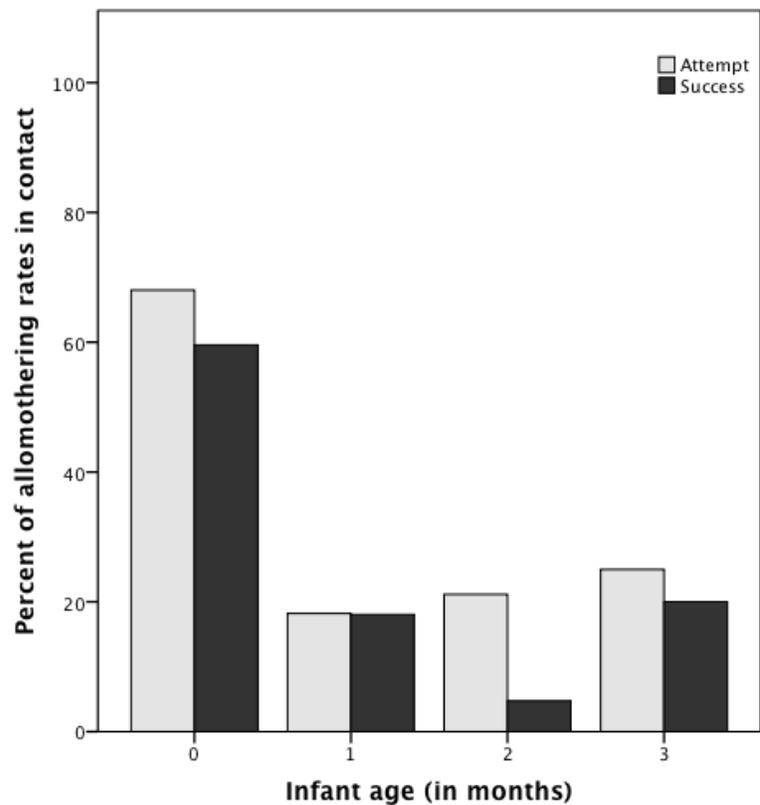
Figure 4.12: Percent of allomothering attempt and success rates that occurred while the
infant was in contact with its mother.

Table 4.7 indicates the association between ventral contact and allomothering attempts. (while the mother was in sight), with each month analyzed separately. As indicated, a significant association with ventral contact was found only in the infant's first month for allomothering success and in the infant's second month for attempts. As remarked before, this only reflects allomothering rates while the mother was within 5m. These results indicate that allomothering has a significant association with time spent in ventral contact for the first two months of infant life (in other words, individuals who had higher allomothering rates spent less time in ventral contact). Due to the correlational nature of the analysis, it does not indicate the direction of the causation; as a result, potentially individuals who were out of ventral contact more were more likely to be allomothered, or higher rates of allomothering significantly decreased time spent in ventral contact.

Table 4.7: Association (Kendall Tau-B) between ventral contact and rate of allomothering attempts while the mother was within 5m.

	Attempts		Success	
	τ	P	τ	p
Month 0	-.236	0.11	-3.62	0.015*
Month 1	-.496	0.006*	-.244	0.18
Month 2	-.105	0.56	-.153	0.43
Month 3	-0.29	0.88	-.256	0.32

*$p<0.05$

Infant contact was generally friendly, with juveniles often hugging the infant to their chest. Lee (1983) remarked that, in captive studies, there are occasional threats and aggression directed toward the infant, which she did not notice with the vervets in the

wild in Amboseli. In most cases, contacts at my study site were of a friendly nature

(though the infants were occasionally tugged and wrenched from the grasp of the

caretaker). One exception was the dominant female in RBM, who was seen on a couple

occasions nipping the infant she was caretaking, and on one occasion she pushed an

infant off her, which then fell from a tree over 5m to the ground (the infant was

uninjured). Another exception was when an infant jumped on an adult resident male, and

the male turned around and grabbed the infant's neck in his jaws, killing the infant (see

Chapter 2, section 2.2.3).

4.3.6.2. Infant sex and mother's rank on allomothering rates

A standard least squares regression was run to determine the effect of maternal rank and

infant sex on attempts and success of allomothering rates in the infant's first month, when

the infant was within 5m of its mother. Infant sex had a significant main effect on

allomothering rates, ($F(1,16)=6.02$, $p=0.026$), where daughters received more attempts

than sons (see Table 4.8). Neither maternal rank, $F(1,16)=0.99$, $p=0.34$, nor the

interaction of maternal rank and infant sex, $F(1,16)=0.92$, $p=0.35$, had a significant effect

on allomothering attempts. A similar pattern occurs for allomothering success rates,

though since the effect of infant sex is only marginally significant ($F(1,16)=4.45$,

$p=0.051$), I am unable to conclude whether daughters were successfully removed from

their mothers more often than sons. Again, neither maternal rank, $F(1,16)=0.26$, $p=0.62$,

nor the interaction of maternal rank and infant sex, $F(1,16)=0.22$, $p=0.64$ had a

significant effect on allomothering success rates.

Table 4.8: Means (number/ hour) and standard deviations of allomothering attempt and success rates by infant sex, while the mother was within 5m, in the infant's first month.

	Males	Females
Attempt rate	1.07 ± 062	1.94 ± 1.05
Success rate	0.39 ± 0.53	0.97 ± 0.48

4.3.6.3. Allomothering attempts by the mother

Of the observed allomothering attempts during focal samples, 55% were by juveniles and the other 45% by adult females. It is possible juveniles were more likely to attempt allomothering when the mother was out of sight (data not captured). Mothers were also interested in other females' infants and if mothers allomothered other infants at an equivalent rate to which they received allomothering assistance, there would no longer be a benefit. The rate of allomothering by mothers throughout pregnancy and infant life is depicted in Figure 4.13.
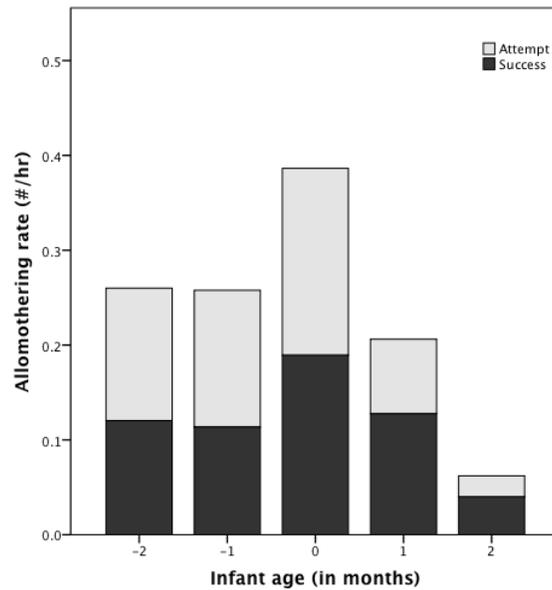
Figure. 4.13: Mean allomothering rates per hours observed of pregnant and lactating focal females.

Allomothering by mothers was highest right after her own infant was born, and declined thereafter. Mothers still attempted and succeeded in allomothering over the course of lactation, but at lower rates than the allomothering she received (Figure 4.14). Mothers would often the hold an infant briefly and then it let go, although on a couple of rare occasions mothers were recorded walking with their own infant and another infant clinging on her ventral surface. As vervets are seasonal breeders, part of the decline in rates of allomothering could be due to a reduction in the number of newborn (and therefore "attractive") infants, because as their own infant gets older, so do the infants born around the same time.
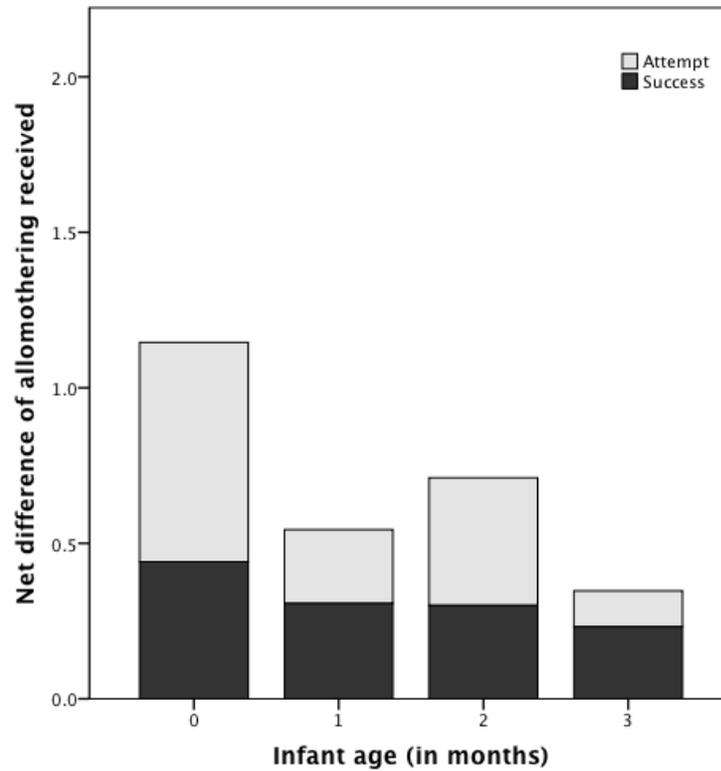
Figure. 4.14: Mean allomothering rate received by mothers when the infant was within 5m minus allomothering rates performed by the mother.

4.3.6.4. Activity budgets while infant is off ventral contact

In order to explore the potential benefits of allomothering, mothers' activity budgets when the infant was not in ventral contact was compared to the mothers' budgets when the infant was in ventral contact, as illustrated in Figure 4.15. Only the first three months in which allomothering occurred in the majority of infants were examined.
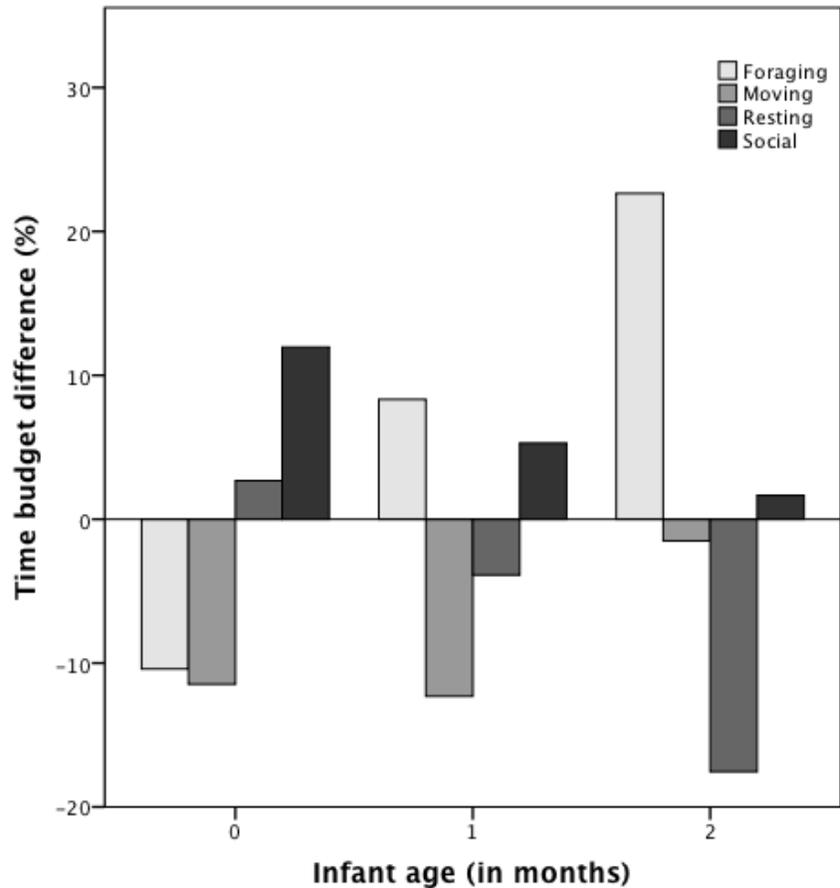
Figure 4.15: Median difference (%) of time budget for when the infant is not in ventral contact compared to when the infant is in ventral contact for the infant's first three months.

To determine the differences in activity budgets, paired Wilcoxon rank tests were used for each activity within each month. In the infant's first and second month, mothers were moving significantly less (Month 0: $N=24$, $z=-4.257$, $p<0.001$; Month 1: $N=18$, $z=-3.245$, $p<0.001$) and socialized more (Month 0: $N=24$, $z=3.686$, $p<0.001$; Month 1: $N=18$, $z=3.148$, $p=0.002$) when the infant was not in ventral contact. By the infant's third month, mothers were foraging significantly more ($N=17$. $z=3.053$, $p=0.002$) and resting significantly less ($N=17$, $z=-2.959$, $p=0.0003$) when the infant was not in ventral contact. This illustrates that when allomothering is highest, the time when the infant is not in

ventral contact corresponds to increased time spent socializing by the mother. By the time the infant is a little more independent, the difference in ventral contact could be a reflection of timing between the mother and the infant, which was explored in section 4.3.5.

4.4. DISCUSSION

4.4.1. OVERVIEW

My results indicate that maternal investment is influenced by a variety of factors. Both mother and infant are involved in the transition to independence. Length of interbirth interval is increased in low quality environments, by large troop sizes, and by a higher probability of infant survivorship. Infant ventral contact seems to be contingent on maternal behaviour, with infants spending more time in contact while the mother is resting than moving and feeding. Daughters of low-ranking females tended to spend more time in ventral contact than daughters of high-ranking females, and sons of any rank spent equal amount of time in contact. This could be because low-ranking females were protecting their daughters from others, as female infants were targeted for allomothering more often. Allomothering occurred most often in the infant's first month and declined until month four when very little allomothering occurred.

4.4.2. LENGTH OF INVESTMENT

The length of lactational anovulation can be a major determinant in reproductive rates (Lee & Bowman, 1995). Even though the decline in ventral contact between mother and infants at Samara and Amobseli sites is similar (Figure 4.2), there could be differences in number of suckling bouts, which has been noted to differ between reconceivers and non-conceivers, where females that reconceived had infants with low suckling rates (Lee & Bowman, 1995).

Consistent with Lee's (1987) and Hauser and Fairbanks (1988) findings within the Amboseli population, the Samara troop also reflects troops in lower nutrient quality having longer inter-birth intervals. As suggested by Hauser and Fairbanks (1988), poor food quality may act as a constraint on the females, restricting them to an inter-birth interval of two years, unless conditions are favourable (for example, a longer rainy season extending food abundance).

Within the low quality environment, troop size appears to be related to greater interbirth interval (Table 4.2). Altmann and Alberts (2003) noted interbirth interval is shorter when group size is small, where an increase of 10 adult females in the group was associated with a 2.5 month increase in interbirth intervals. The authors stated that low-ranking females bear a disproportionate cost of living in larger groups, reaching menarche later and having longer interbirth intervals (Altmann & Alberts, 2003). Low-ranking females

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may have longer interbirth intervals due to having a higher likelihood of miscarriages or still births, potentially due to the effects of social stress (K. Kavanagh et al., 2011).

Females whose offspring survive are more likely to skip the following birth season than females whose offspring don't survive (Cheney et al., 1988).   In my study, most infant deaths occurred within the first eight weeks (9/11), compared to Cheney et al. (1988) who found infant mortality peaks at four months and eight to nine months. The infants were only closely monitored the infants until most of them were seven to eight months old, so it's possible I didn't capture some infant deaths occurring after month seven. Nonetheless, infant mortality risk seems to be highest at Samara within the first two months following parturition. Given a female would have to conceive when her infant is between five to seven months old to have an offspring each birth year, it's not surprising that infant survival has a stronger influence on increasing interbirth interval at Samara than at Amboseli, since earlier infant mortality causes the female to resume cycling in time for the mating season. Infant mortality causes were for the most part unknown. Three infants disappeared at the same time as their mothers (perhaps due to predation since there was no noticeable change in condition), one was premature, one was killed by a resident male and in the remaining five the cause is unknown.

4.4.3. TRIVERS-WILLARD VS LOCAL RESOURCE COMPETITION

No difference was found in time spent in ventral contact across infant age between the infant sexes. Most primate studies do not find such a sex difference, potentially due to

the equal rates of growth between males and female infants while they are reliant on their mother's milk (eg. Altmann & Alberts, 1987). In captive vervets, no sexual dimorphism in weight is apparent until the infant is roughly 39 months old (Seier, 1986). However, in the Amboseli vervets, Lee (1984) did find an effect of sex, with females decreasing contact earlier than males. Alternatively, Lee (1984) only had four females in her sample, and the results could have been skewed by low sample size. Rank alone had no effect on time in ventral contact.

A significant interaction of sex and rank was found and maintained across infant months. By looking at figure 4.3, it appears daughters of low ranking females spend more time in ventral contact than daughters of high ranking females, with sons of any rank falling in between. Similarly, Lee (1984) noted that, in the Amboseli vervets, high ranking females were more rejecting towards daughters and less rejecting towards sons than low ranking females. Gomendio (1995) noted in her study of captive macaques that daughters of low ranking females attempted to make nipple contact more frequently than other infants, and in combination with low ranking mothers being less rejecting, spent a greater proportion of time in nipple contact than other infants. Daughters of lower ranking females received more aggression than other individuals, suggesting the daughters were seeking nipple contact for protection (Gomendio, 1995). Similarly, in my study, daughters of low ranking females may have been targeted for aggression. While infant handling contact was generally friendly, a more detailed recording of infant handling by allomothers is needed. In addition, low-ranking females typically are not able to control access to their infants like high-ranking females. As female infants were targeted for allomothering

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more than male infants, and low-ranking females cannot necessarily control access in the way that high-ranking females can, low-ranking mothers may provide more ventral contact as protection to a daughter as a result. Even though Silk (1983) originally proposed greater investment overall in daughters, this pattern may be indicative of the local resource hypothesis, rather than the Trivers- Willard hypothesis, as there is no difference in male investment across ranks (although aggression directed towards daughters would need to be quantified to conclude this).

A rank related-sex difference in investment or birth-sex ratio would be expected only if reproductive success was influenced by rank. Some studies have found support for differences in reproductive success based on rank, and corresponding investment in the direction predicted (i.e. if higher ranking females had higher reproductive success, then investment should be biased towards daughters). For example, in free-ranging baboons in Amboseli, daughters of high ranking females reach menarche earlier than daughters of low-ranking females, giving them roughly a 7% adult life span advantage in offspring production (Altmann, 1988). In the same population, high-ranking females were more likely to invest more in daughters and low-ranking females to invest more in sons (Altmann, 1988). In Kenyatta's (1995) troop of baboons, high-ranking females showed a trend toward experiencing shorter inter-birth intervals. Daughters of high-ranking females spent more time on the nipple than daughters of low ranking females, and sons of low-ranking females spent more time on the nipple than their daughters (Kenyatta, 1995).

Other studies have found no correlation with female rank and age at first reproduction, interbirth interval, infant survival or female lifespan (eg. vervets Cheney et al., 1988), meaning even in female philopatric societies where daughters typically inherit their mother's rank, there may not be a reproductive benefit to females born in higher ranks. For example, at Amboseli, predation rates are high and even females that breed for a number of years are not guaranteed to leave a surviving offspring (Cheney et al., 1981; Cheney et al., 1988). This is in stark contrast to provisioned troops, or troops with low predation, when selection may influence investment based on infant sex and rank to a greater extent than when mortality is high and random. Infant mortality at Samara is lower, than at Amboseli so it is possible there are different selection pressures that favour differential investment of offspring.

The measure of investment explored in this study was time in ventral contact. However, this is an indirect measure of maternal investment, and direct measures should include techniques like radio-labeled isotopes to measure the amount of milk transferred (Brown, 2001). Alternatively, many studies have used length of inter-birth interval as an indicator of investment (since a longer inter-birth interval decreases investment potential in other offspring). With just one birth season with infant sex known, I am unable to examine the differential interbirth interval between the sexes. In addition, other types of investment extending past the post-natal phase need to be furthered explored. For example, Fairbanks and McGuire (1985) noticed a difference in proximity of offspring ages one to three years old, with daughters spending more time in proximity and more time being groomed by the mother than sons, and high ranking daughters spending more time in

proximity than low ranking daughters. Lastly, whether the difference in early investment extends in adulthood has to be determined (Brown, 2001).

The best way to distinguish between the Trivers-Willard hypothesis and the resource competition hypothesis is to compare birth sex ratios between the ranks. However, with only one birth season, I am unable to draw any conclusions, although sons and daughters had mothers of equivalent rank distributions. In other vervet troops, no rank related sex biases have been found (Cheney et al., 1988). Primate studies have found contrasting results, with Brown (2001) reviewing the many studies that demonstrate a male-biased sex ratio in high ranking females, others a female biased sex ratio in high ranking females and still others with no difference. In the end, Brown (2001) drew the conclusion that the most parsimonious explanation is accepting the null hypothesis of no consistent sex-biased birth ratios.

4.4.4. TIMING

In support of the timing hypothesis, infant ventral contact decreased in a disproportionate manner between maternal activities. Across infant age, maternal activity decreased fastest in time spent moving and foraging, with slower rates of decrease in time spent resting and social. A significant association was found between infant age and percentage of time spent in ventral contact for foraging, resting and moving. The pattern in relation to social time was noisier, and this was best explained by examining time spent within 1m, where infant proximity when the mother was engaged in social activities

paralleled that of other activities.   In combination with allomothering rates being highest during first three months, this suggests the initial low rates of time in ventral contact while socializing may be due to allomothering. Sharp decreases in ventral contact while foraging and moving seemed be compensated for by increases in time in ventral contact while socializing. These results suggest infant ventral contact is contingent on maternal behaviour.

These results parallel those in Green's (1995) study, which examined the first twelve weeks of an infant's life. She found no significant association between infant age and time in ventral contact for the majority of the infants, whereas I found a strong association for the first five months of infant life. In addition, Green (1995) noted that ventral contact time decreased most rapidly with time spent foraging, and the decease of ventral contact while the mother was moving was less step. My results support this finding, with significantly lower ventral contact while the mother was foraging compared to resting at month two (the median time would be ~ 10 weeks), and ventral contact during moving not significantly different until month four (~18 weeks). In fact, in the first month, time in ventral contact while moving was significantly higher than while resting. This could reflect the difference in energy requirements needed to transport an infant. While the infant is solely reliant on mother's milk, it is more energy efficient for her to carry her infant than to have it move independently (Altmann & Samuels, 1992). By the time ventral contact while moving is significantly different from when resting, infants have begun foraging independently (Figure 3.5). My results also add that infant ventral contact is contingent on mother's behaviour until infant months six and seven,

when no significant differences were found, corresponding to when ventral contact

stabilizes and is no longer correlated with infant age.

The results are similar to those reported in gelada by Barrett et al. (1995) and Kenyatta

(1995) in baboons, although the rate of decrease in gelada and baboons was shallower

than that seen in the Samara vervets. This could be due to the relative size difference of

the infants and the extent to which they would interfere with the mother's maintenance

activities. As discussed in Chapter Three, vervets obtain 30% of their adult weight by six

months, compared to 18 months in baboons and gelada (Lee et al., 1991). Therefore, the

infants are likely to pose a greater inconvenience when carried ventrally earlier in vervets

than in gelada. The decrease in contact while the mother is foraging follows closely the

rate observed by Johnson (1986) in the more comparable sized rhesus monkeys, with

contact rates at about 30% while the mother is foraging at week 10 (average of month

three).

The timing hypothesis also predicts that mother-infant conflict occurs in relation to the

timing of investment (i.e., nursing) rather than the amount of nursing received.

Therefore, the rate of rejection while the mother was engaged in maintenance activities

was explored. If mothers are rejecting their infants when interference with activities is

highest, then the highest rejection rates are expected while the mother is foraging and

moving. For example, Barrett et al. (1995) found a majority of the rejections in their

gelada population occurred during feeding, as did Johnson (1986) in his study of rhesus

macaques. Rejection rates recorded in this study were fairly low; this could be a result of

low sampling time per individual or because I only recorded rejections that were clearly performed by the mother (and not ties of both mother and infant involved), the results could be too conservative. As a result, I can only highlight trends rather than conclude anything decisively.

Rejection rates were different between activities when using the activity recorded before the rejection, with a trend of more rejections occurring while resting, followed by moving and lastly foraging. Similarly, Chism (1986) found in captive patas monkeys, most rejections occurred while the mother was resting or socializing, with very few rejections occurring while the mother was foraging. This is opposite to what is predicted under the timing hypothesis. However, when using the activity after rejection, rejection rates were almost equal amongst activities. This indicates that more rejections tend to occur while resting but the mother sometimes changes activities immediately following infant rejection. While still not supporting the timing hypothesis, it is indicative of maternal activity influencing infant ventral contact, or infant ventral contact influencing maternal activity. In the Amboseli vervets, Green (1995) found rejections during maternal moving was significantly higher than foraging and resting, and suggested mothers were rejecting their infants and going off to forage, as indicated by the steeper slope of ventral contact while foraging.

In my study population, by the time there is a significant difference between ventral contact when resting and foraging, infants are only in ventral contact less than 40% of the time (at month two). It therefore seems possible that perhaps mothers are not 'training'

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their infants to nurse while resting and social; rather, the mothers may utilize the time

infants are not in ventral contact to forage, which has been suggested to be a benefit of

allomothering in vervets (Hrdy, 1976). Alternatively, the easy access of a nipple while

the mother is resting or socializing may afford the infant the opportunity to nurse, which

given that by month three the infant is initiating more contact than the mother, is worth

exploring. An indication of this may be that time spent within 1m of the mother is

significantly lower for foraging compared to most other activities, meaning mothers are

either more likely to forage when their infants are not in proximity, or infants are less

likely to maintain proximity while their mothers are foraging. A better understanding can

be achieved by examining the activity of the mother when ventral contact is made. If

infants begin nursing more while the mother is resting/grooming, it would not be

unexpected that rejection rates are highest for those activities as well. While my results

in regards to rejection rates do not support the timing hypothesis, no conclusions can be

drawn due to the low rates recorded and resulting sample size bias.

4.4.5. ALLOMOTHERING

The pattern of allomothering found at Samara parallels results found in other studies,

with the highest rates occurring in the first month, and decreasing thereafter, with very

little rates from the third month on. (eg. captivity C. Johnson, Koerner, Estrin, & Duoos,

1980; wild Lee, 1983). The majority of attempts were by juveniles and sub-adult females

(55%), although adult females still participated in allomothering attempts almost half the

time (45%). The rate of allomothering by adult females is higher than that reported for

other studies (eg. Lancaster, 1971). As previously mentioned, it may be that juvenile females were more likely to attempt allomothering when the infant was not in sight of its mother (for example, with another allomothering), or perhaps juveniles/sub adults held onto the infants longer once they had them, as was found by Lancaster (1971).

Rank had no significant effect on allomothering rates, in contrast to studies of captive vervets (Fairbanks, 1990) and wild vervets (Lee, 1983). One of the differences may be that infants born in captivity spend almost four times longer in the care of individuals other than the mother within the first couple of months compared to infants born in the wild (Hauser & Fairbanks, 1988). In Lee's (1983) study, a significant difference in rank was only found once first born infants were removed, since they were allomothered more often. The rate of contacts made per hour are very similar to those obtained by Lee (1983) in the Amboseli vervets (median of roughly 1.5 contacts per hour in the first months and 0.5 contacts/hr for the following two months).

Frequently when juveniles and adult females would hold an infant that was not their own, they would inspect the genitals, with nuzzling of the infant's genitals a common behaviour of allocaregivers (Lancaster, 1971). The results do indicate a sex preference for allomotheirng, with females targeted and taken more than males. This may relate to the resource competition hypothesis, and perhaps females were handled more roughly than males. Alternatively, perhaps a bias exists for preferring female infants due to their potential as coalition partners in the future. Yet another explanation could be that males were more active than females, and less likely to be taken. Detailed interactions of infant

handling, long-term detail of associations, and sex specific infant activity budgets are needed to discriminate between these alternatives.

Some studies have found support for allomothering providing the mother the opportunity to forage (Hrdy, 1976). However, when examining the activity budgets for when the infant was not in ventral contact, the hypothesis is not supported in the first couple of months. Similar to what Chism (1995) found when patas infants were allomothered, in the infant's first two month the mother was primarily engaged in social activities when the infant wasn't in ventral contact. Mothers did not spend significantly more time foraging while the infant was off ventral contact until the infant's third month. Other studies in New World primates suggests that allomothering relieves carrying costs. Given mothers are moving significantly less in the first couple of months when their infant is off ventral contact, this suggests that allocare may not be alleviating carrying costs (if one assumes the mother is moving along with the group). Therefore the results suggests the immediate benefits to the mother of allomothering may be increased grooming received (see Figure 3.9A).

4.4.6. IN SUMMARY

- In comparison to other vervet populations, interbirth intervals at Samara are longer. Low quality environments, large troop sizes and higher infant survival may explain some of the variation in the length of interbirth interval.

- Using ventral contact as a measure of maternal investment, a significant interaction was found between maternal rank and infant sex, with daughters of

low-ranking females spending more time in ventral contact than daughters of high-ranking females. This could be a result of females being targeting for allomothering more often. In order to discriminate between the Trivers and Willard hypothesis and the local resource competition hypothesis, more years of data are needed, particularly differences in birth-sex rations between the ranks.

- Weaning in offspring is a dynamic process, with infant contact contingent on maternal behaviour. As the infants gained independence, they were less likely to be in contact while their mother was foraging and moving and more likely to be in contact when the mother was resting, supporting the timing hypothesis. Low rates of ventral contact were observed while the mother was socializing in the first couple of months, presumably as a result of allomothering. The relationship between infant ventral contact and maternal activity needs to be examined further, with particular emphasis on the possible role the infant may play in establishing contact.

- Allomothering occurs in the first three months of infant life, with attempts occurring most frequently in the first month. Juveniles and adult females (including new mothers) participate in allomothering activities. While mothers were most likely to be social when their infant was out of contact for the first couple of months, the role of allomothers/ peer groups during later months may provide the opportunity for a mother to forage unencumbered.

CHAPTER FIVE. GENERAL DISCUSSION

Primates are characterized by a slow reproductive turnover, defined by a relatively long lactation period and high investment in each offspring (Martin, 1995). This thesis focused on the lactation stage, which is the most energetically costly stage of reproduction for female mammals (Glittleman & Thompson, 1988). A lengthy lactation period permits flexibility in reproductive strategies and maternal care. The goal of this thesis was to test current theories of reproductive and investment strategies to cope with the costs of lactation in vervet monkeys.

Next to baboons, vervet monkeys are "one of the most widely distributed and abundant of all African monkeys" (Struhsaker, 1967b). Thus, they are an excellent example a highly successful species able to reproduce in a variety of environments. Vervets share several characteristics with the closely related, well-studied *Papio* genus (baboons), such as: female philopatry, omnivory, savannah dwelling, and both are semi-terrestrial. Vervets differ from baboons in several respects; most notably, vervets are seasonally breeding, have higher birth rates, and have relative to maternal weight larger infant birth weights. Most studies examining maternal investment and reproductive strategies in wild populations of vervet monkeys have originated from the Amboseli population, located in Kenya, close to the equator (Cheney et al., 1988; Hauser & Fairbanks, 1988; Lee, 1984**).** This study took place in the Eastern Cape in South Africa, where the vervets are challenged with lower temperatures and marked seasonality influencing food availability and daylight hours, in comparison to the equatorial populations. An objective of this

thesis was to juxtapose reproductive and investment strategies between my study

population, other vervet populations and other primates.

My study used focal animal sampling (Altmann, 1974) of lactating and non-lactating

females to calculate activity budgets across infant age, as well as to record changes in

mother-infant interactions. Using these methods, I was able to examine how mothers

cope with the costs of lactation, as well as maternal investment strategies. As with most

short-term primate studies, one limitation is my small sample size. Nonetheless, my

sample size is on par with other studies of mother infant pairs (ex. this thesis, sample size

is typically between 7 and 24 mothers depending on the infant month, 15-16 pairs in Lee

1984, 2-11 in Altmann 1980, 10 in Dunbar and Dunbar 1988, 15-23 Barrett et al. 2006a).

5.1. LACTATION COSTS

Atlmann's (1980) proposed maternal feeding time budget model did not fit my study

data, meaning mothers were not increasing time spent foraging in relation to the growing

nutritional demands of their infant. This is comparable to other studies, which have

found only a poor fit (ie. feeding time increased across infant age but fell above or below

predictions, eg. Altmann, 1980; Dunbar & Dunbar, 1988; Lycett et al., 1998) or no fit

with the model (ie. no consistent increase in feeding time across infant age, eg. Barrett et

al., 2006a; Lappan, 2009). Deviations from the model are due to violations of the model

assumptions, most likely the assumptions that mothers maintain their weight and that *A*,

the factor that converts energy requirements into feeding time, remains the same (ie no

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changes in nutrient quality and/or changes in metabolic demand unrelated to infant growth).

Increasing net food intake to concurrently provision offspring as infant demands increase is one of two female reproductive strategies, termed income breeding by life history theorists (Stearns, 1989). At the other end of the continuum are capital breeders, which use stored energy to provision offspring (Stearns, 1989). Altmann (1980) suggested one of the reasons lactating females weren't feeding to levels predicted may have been because they were losing weight. Bercovitch (1987) confirmed in olive baboons that lactating females weighed 7% less than cycling females, meaning female baboons are acting like capital breeders, using stored energy/own reserves to fuel some of infant growth. Using data from a number of studies, Brockman and van Shaik (2005) placed baboons on the capital breeding side of the spectrum for primates, given that baboons seem to need to obtain a threshold condition in order to ovulate and/or conceive. Vervets, on the other hand, were placed within the income breeding side of the continuum (Brockman & van Schaik, 2005). In my study, lactating females did not increase the amount of time spent foraging to the levels predicted by Altmann's model; however, due to birth seasonality, they may have been able to concurrently offset the costs of lactation through changes in dietary quality.

Timing food availability to different reproductive events is suggested to be the most important ultimate cause of birth seasonality (Butynski, 1988; Di Bitetti & Janson, 2000). Butynski (1988) suggested that guenon birth seasonality was timed so that peak lactation,

and therefore peak nutritional stress, corresponds to peak food abundance. This was supported in the Amboseli vervets, as Lee (1987) found that peak nutritional quality corresponded with peak lactation. My study did corroborate nutritional quality increasing with lactation demands, although nutritional quality in lactating females diets increased beyond peak lactation. The increase in quality beyond peak lactation could be because mothers were regaining condition following lactation, which is indicated by lactating females targeting higher protein items than non-lactating females during late lactation. In addition, the vervets at my study site are located further south from the equator than the Amboseli vervets, and are therefore exposed to greater seasonal variation in temperatures and daylight. Since vervet births are clumped in the late spring, infants are between six and eight months old when daylight hours are the shortest and winter begins. A later peak in food abundance could assist the monkeys in obtaining sufficient energy to cope with decreasing day length and shorter temperatures, which has been noted to increase cortisol levels in baboon populations (Weingrill et al., 2004).

A limitation of my study is a lack of physiological measurements. While vervets may be offsetting some of the costs of lactation by targeting higher quality food, it may not be sufficient to maintain condition. Obtaining field measurements of body weight throughout lactation is an important next step. In addition, more recently, non-invasive collection of C-peptide has been proposed as a method for assessing changes in energy balance (Emery Thompson & Knott, 2008). Pairing physiological changes with time budgets can give a more accurate assessment of the impact of a variety of factors such as nursing an infant and seasonality on energy balance.

5.2. MATERNAL INVESTMENT

Some life history characteristics, such as gestation length, litter size, and life expectancy, are species specific, restricted by evolutionary history. However, even within a species there is flexibility in behaviour patterns, with the variation due to the response of ecological and social settings (Lee & Bowman, 1995). Length of maternal investment is one example of plastic behaviours. For example, in a review of the effects of food supplements on reproductive parameters in various groups of primates (humans, baboons and rhesus monkeys), Lee and Bowman (1995) found food supplements typically decreased interbith interval, increased growth rate and decreased age at first reproduction. Consistent with Lee's (1987) and Hauser and Fairbanks (1988) findings within the Amboseli population, my study data also reflects troops in lower nutrient quality having longer inter-birth intervals (see Table 4.2). Table 4.2 also indicates that troops at Samara also had longer inter-birth intervals than troops at Amboseli, as well as higher probability of survival.

The causes of infant mortality may influence female reproductive strategies. For example, Pennington and Harpending (1988) outline a model, where mortality can be due to care-dependent factors (intrinsic) that can be alleviated by increased parental investment or care-independent factors (extrinsic) like infections diseases that are not effected by parental effort. In situations where extrinsic causes of mortality are high and intrinsic are low, the highest reproductive fitness would be obtained by producing as many offspring as possible. Alternatively, if intrinsic sources of mortality are high and

extrinsic low, highest reproductive fitness would be obtained by investing more in each individual offspring.

An excellent example of how the two causes influence investment is presented on two baboons populations by Barrett et al. (2006b). Baboon infants at DeHoop are born across the year, whereas those in the Drakensberg face harder conditions and have seasonal infant births. Due the seasonal birth peaks, when infants are potentially capable of independently foraging, they are faced with the winter environment when weaning foods aren't available. Therefore, Drakensberg infants are weaned 5-6 months older than infants at DeHoop, and consequently, the Drakensberg females have a long interbirth interval (Barrett et al., 2006b). Yet because Drakensberg infant survival rate is higher, the two populations may have similar lifetime reproductive success. Similarly, if predation rates at Samara are lower than at Amboseli and increased maternal investment increases the chance of survival for infants, lifetime reproductive success may be highest by investing more in each offspring.

At Amboseli, Cheney et al. (1988) suggested the high infant mortality at four months may be due to predation since it coincides with a reduction in carrying by the mother, and the high mortality at eight to nine months with illness, as it coincides with weaning during the dry season. Quantitative comparisons of predation rates, nutrient availability and deaths due to illness/other factors between Amboseli and Samara are needed to test life history strategies between the two sites.

The ability of mothers to increase investment based on increased risk of intrinsic mortality factors is a function of the infant being able to communicate its need for more investment (Bateson, 1994). Trivers (1974) stated that 'weaning conflict', as assessed by infant tantrums, is a result of the infant trying to obtain more investment than the mother is willing to give. Bateson (1994), on the other hand, suggested that infant tantrums are infants signaling an honest need for more investment, and given that mothers have imperfect knowledge of their offspring's condition, mothers should respond by increasing investment. Furthermore, Bateson (1994) highlighted the active role the infant plays in monitoring its mother's condition as well. An example of the dynamic nature of mother-offspring contact is infant ventral contact being contingent on maternal activity.

Atlmann (1980) and Dunbar (1988) suggest that weaning tantrum may be related to the timing of the infant's access to milk, particularly for ground dwelling species like primates, where ventrally clinging infants interfere with a mother's activity. In their own studies of baboons (Altmann, 1980) and gelada (Barrett et al., 1995), they found support for infant contact decreasing faster across infant age while the mother was foraging compared to resting and socializing. My results support the timing hypothesis, as infant ventral contact decreased earlier while the mother was foraging and moving in comparison to when she was resting. However, while Barrett et al. (1995) found maternal rejection was highest while the mother was feeding, my results indicate higher rejections while the mother was resting. I found no difference in maternal activity following infant rejection, which suggests mother may reject their infants while resting to engage in an activity in which the infant would be an inconvenience (eg. foraging,

moving).   More details are needed on mother-infant dynamics to elucidate the causality

of maternal activity and infant ventral contact. For example, perhaps as the infants get

larger mothers stop foraging when the infant starts nursing. In addition, or alternatively,

infants may initiate contact while the mother is already engage in a resting or social

activity.

Mother-infant contact is also contingent on other troop members, particularly in species

which allow allomothering. For example, mothers were more likely to be engaged in

grooming while the infant was off-ventral contact than while on ventral contact in the

infant's first two months, when allomothering rates were highest. Furthermore, females

were allomothered at a higher rate in their first month than males, which may result in the

differential investment noticed between sex and rank.

Differential investment in offspring based on infant sex and maternal ranks has been

postulated by two evolutionary hypotheses. The Trivers-Willard hypothesis predicts that

females in good condition will invest more in the sex that has the greater variability in

reproductive success (which is often sons), whereas females in poor condition will invest

more in offspring that have stable reproductive success (usually daughters) (Trivers &

Willard, 1973). The local resource competition model suggests that because females

compete for resources in societies with female philopatry, females will try to limit the

production of daughters by other females (Silk, 1983). Therefore, low-ranking females

who are unable to protect their daughters from aggression from other females are

expected to have a male-biased sex ratio (Silk, 1983).   Due to a lack of sufficient birth-

sex ratio data and inconclusive results for investment favouring either direction, I'm unable to support either hypothesis. The significant interaction of infant sex and maternal rank, with daughters of low-ranking females spending more time in ventral contact than daughters of high-ranking females, could be a result of a number of factors. For example, since females were targeted for allomothering more frequently, and low-ranking females typically are unable to control access to their infants in the way that high-ranking females can, low-ranking females may provide more ventral contact to daughter to protect against other group members (eg. Gomendio, 1990). Long term data is needed to determine whether the difference in ventral contact is sufficient to significantly influence interbirth interval, and thus investment in future offspring, in low-ranking females after having daughters.

5.3. CONCLUSION

In summary, in my study troops of vervet monkeys, lactating females offset the costs of lactation primarily by targeting high quality diet items, and spending more time feeding than non-lactating females. The dynamic nature of mother-infant interactions was highlighted, with maternal activity and other troop members influencing infant ventral contact. The findings from this thesis highlight the complex interaction of ecological and social conditions on maternal investment.

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APPENDIX A – CHAPTER THREE APPENDIX

Due to differences in troops, the data were separated for certain analyses. The pooled results are presented in this appendix.

A.1. BASELINE FEMALES

Figure A.1. shows the seasonal changes for all baseline females across the study period.
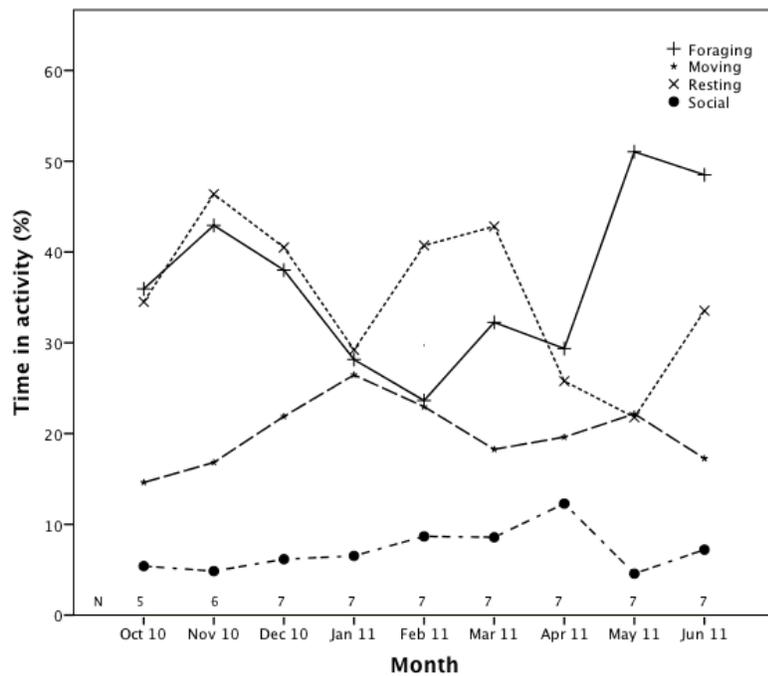

Figure A.1. Activity budget of the baseline females for the duration of the study

A.2. ALTMANN'S MODEL

Combined data from the two troops are illustrated in Figure A2. There was a very good qualitative fit between observed and predicted values, i.e., the overall shape of both graphs conformed to prediction, despite observed values generally falling below those predicted (correlation of mean monthly values and predicted $\Delta i=0.003$kg/day: $r=0.943$, $p<0.001$; $\Delta i=0.005$kg/day: $r=0.932$, $p=0.001$; $N=8$).
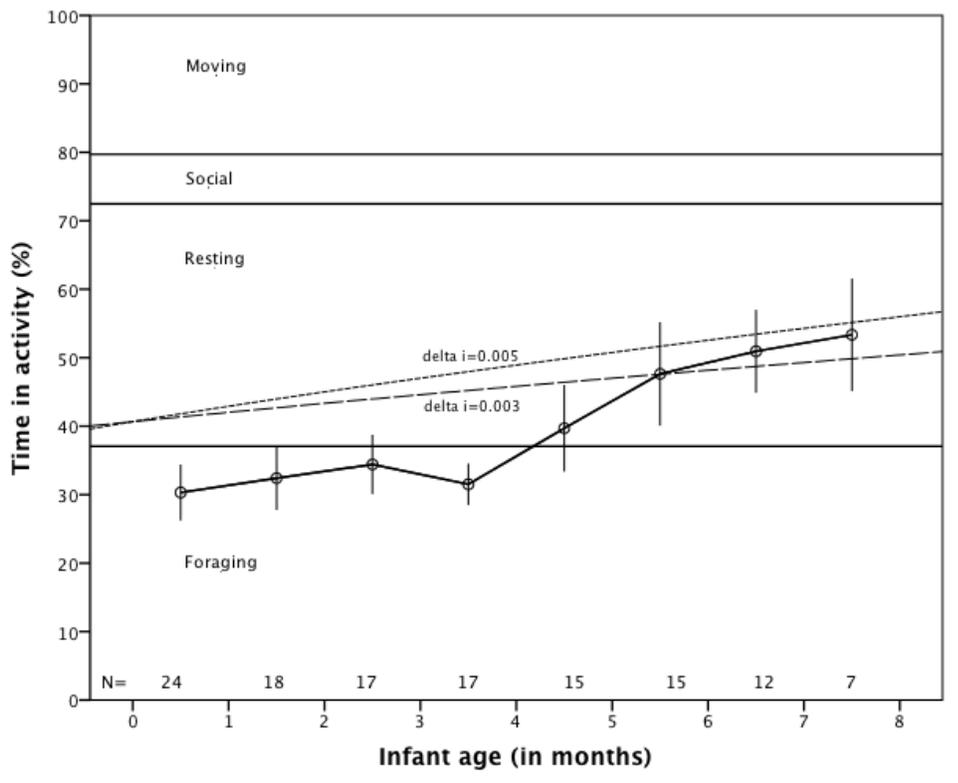

Figure A.2. Altmann's predicted model with $\Delta i=0.003$ kg/day (thin dotted line) or $\Delta i=0.005$kg/day (thick dotted line) compared to observed values (solid line) for both troops combined. The horizontal lines represent the mean time budgets of the mothers throughout the study months. Error bars represent 95% confidence intervals.

Standard least squares regression with REML was used to assess the relationship between maternal feeding time and infant age, with Mother I.D. entered as a random effect. There was a statistically significant relationship between infant age and percent of time spent foraging (t=8.25, p<0.001 df=1, adj. R^2=0. 4217) when allowing for variability across individual time spent foraging. given by the equation:

$f_t = 26.43 + 3.35i_{age}$

A.3. MOTHERS COMPARED TO BASELINE FEMALES

A.3.1. FORAGING

Maternal foraging time was significantly below baseline values at birth (t=-3.462, df=22, p=0.002) and then increased above baseline following month two (Month 2: t=2.554, df=16, p=0.021; Month 3: t=2.611, df=16, p=0.019; Month 4: t=2.700, df=14, p=0.017), illustrated in Figure A.3.
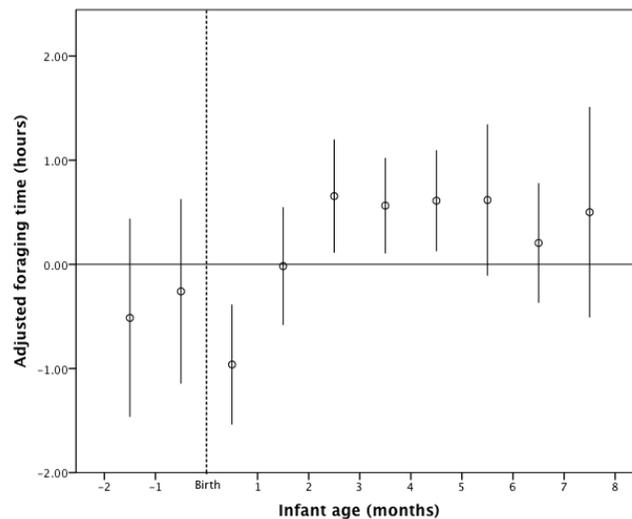

Figure A.3. Mother foraging hours compared to baseline

A.3.2. MOVING

Maternal moving time was significantly below baseline values in the last month of pregnancy (t=-3.380, df=19, p=0.003) and at birth (t=-3.408, df=22, p=0.003) and then increased above baseline in month six (t=2.324, df=11, p=0.040), illustrated in Figure A.4.
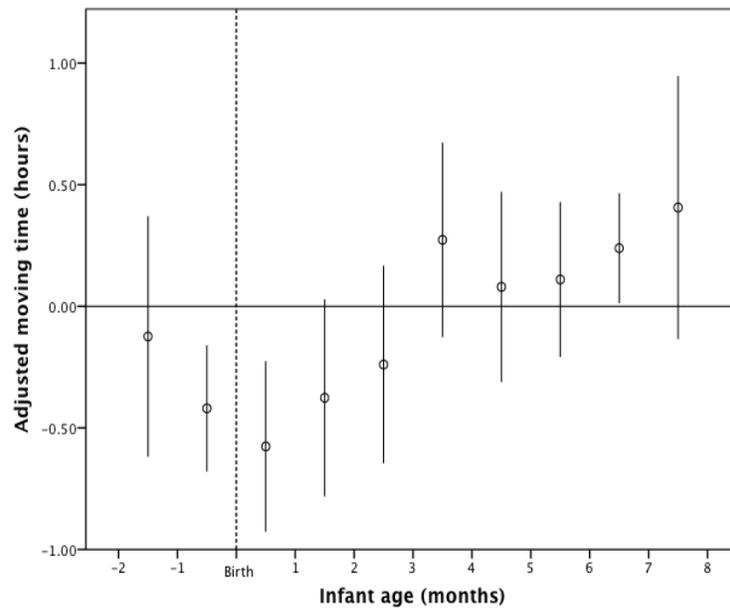

Figure A.4. Moving time of mothers compared to baseline

A.3.3. RESTING

Maternal resting time was significantly above baseline values at birth (t=-4.337, df=22, p<0.001) and then decreased below baseline following month three (Month 3: t=-2.753

df=16, *p*=0.014; Month 4: *t*=-4.032, *df*=14, *p*=0.001; Month 5: *t*=-3.091, *df*=14, *p*=0.008;

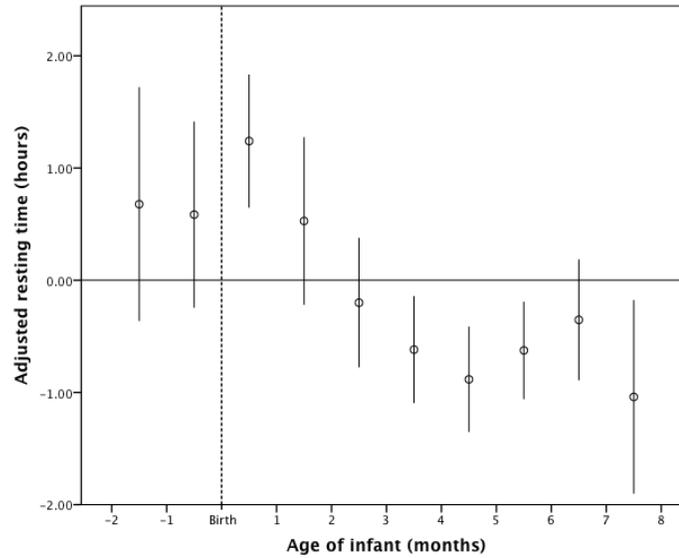Month 7: *t*=-2.948, *df*=6, *p*=0.026), illustrated in Figure A.5.

Figure A.5. Resting time of mothers compared to baseline females

A.3.4. SOCIAL

Maternal social time was below baseline following month two (Month 2: *t*=-2.224 *df*=16,

p=0.041; Month 3: *t*=-2.210, *df*=16, *p*=0.042; Month 5: *t*=-2.193, *df*=14, *p*=0.046), which
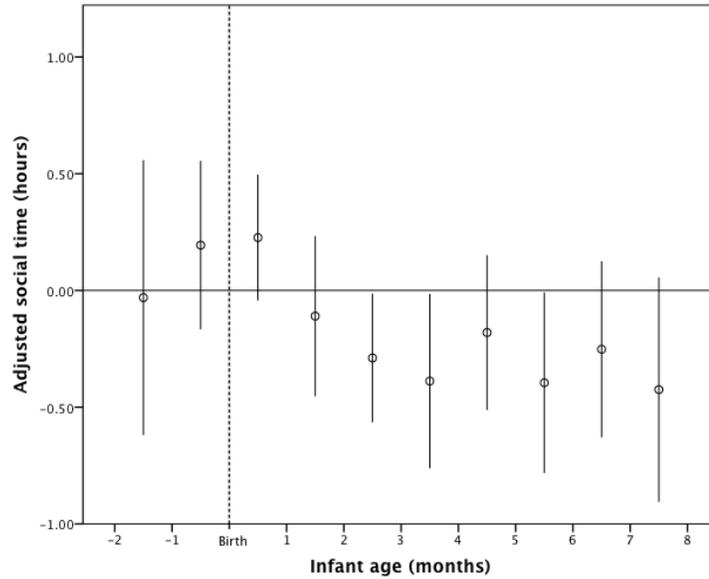
is illustrated in Figure A.6.

Figure A.6 Social time of mothers compared to baseline females

A.3.4.2. GROOMING

Due to slight skew in opposite directions for differences in amount of grooming in some of the months, the non-parametric equivalent of the paired *t*-test was used, the Wilcoxon signed rank test. Mothers were groomed significantly more in the first month of infant life ($N=23$, $z=3.832$, $p<0.001$) but not thereafter. They groomed others significantly less between months two to seven (month 2: $N=17$, $z=-2.059$, $p=0.039$; month 3: $N=17$, $z=-3.101$, $p=0.002$; month four: $N=15$, $z=-2.613$, $p=0.009$; month five: $N=15$, $z=-3.408$, $p=0.001$; month six: $N=12$, $z=-3.059$, $p=0.002$; month seven: $N=7$, $z=-2.366$, $p=0.018$). The difference in mean grooming rates is presented in Figure A.7.
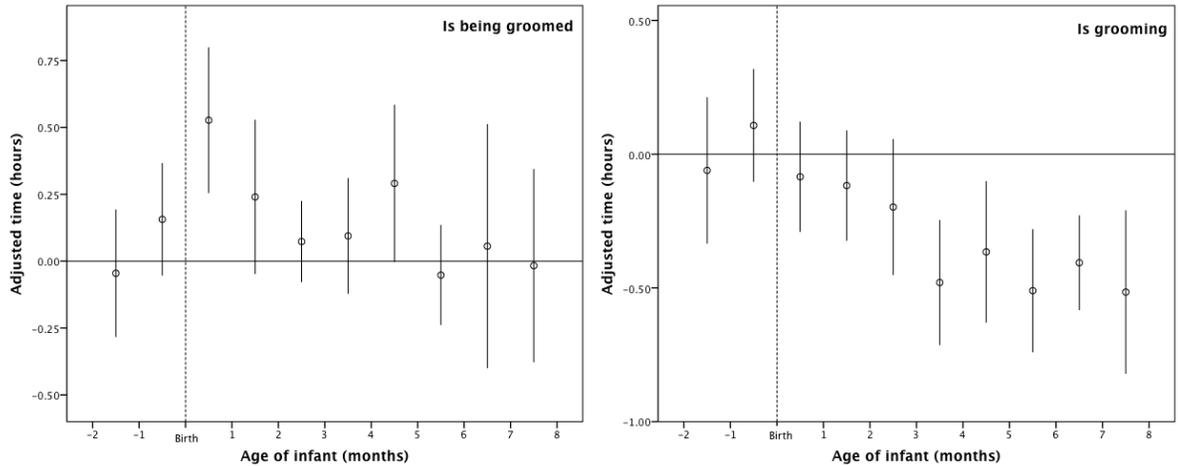
Figure A.7. Mean maternal time being groomed (on the left) and is groomed (on the right) relative to baseline females (in hours) by infant months. Error bars represent 95% confidence intervals.

A.4 ECOLOGICAL FACTORS

A.4.1 NUTRIENT INTAKE

The mean energy intake (MJ/ kg dried mass) and mean raw protein (g/ kg dried mass) in the diet was examined for each mother over the last two months of pregnancy and the first eight months of infant life. Figure A.8 shows that mean energy intake (per dried mass) steadily increases, while mean raw protein (per dried mass) in the diet shows much greater fluctuation. There was a significant effect of infant month (F=6.1221 df=9, p=<0.0001), but no significant effect of troop I.D. (F=0.053, df=1, p=0.82) on average energy in the diet. Tukey's HSD was used to detect significant differences between two months before birth and infant months three, five, six and seven. A significant differences was also detected between month zero and month five and month seven with month zero, one, two and four. There was a significant main effect of infant month

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(F=34.16, df=9, p<0.0001) on average protein in diet, and a significant effect of troop

(F=4.74, df=1, p=0.043). Tukey's HSD was used to detect significant differences

between month zero and month six, and the last month with months zero to five.
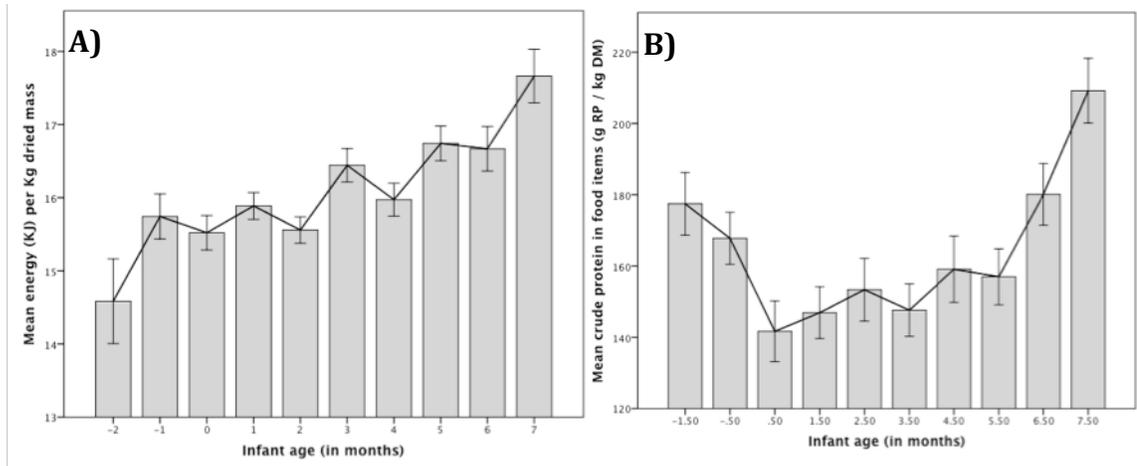

Figure A.8 A) Mean total energy (MJ) per dried mass (kg) and B) mean crude protein (in g) per dried mass (kg) (on the right) over months of infant age. Error bars represent ± 1 standard error.

Standard least squares regression with REML was used to determine whether there was a

significant difference in mean energy and mean protein in the diet (as separate dependent

variables) across infant age (as continuous). Only values from parturition to month seven

were used. Mother I.D. was entered as a random effect to control for repeated measures

of individuals. Infant age had a significant effect on energy intake (β=0.23 t=5.99,

p<0.0001). Infant age had a significant effect on protein intake (β=6.33, t=4.52,

p<0.0001). As the infant gets older, protein and energy intake in the diet significantly

increases.

Average energy and protein in the maternal diet were compared to baseline female diet for RST and RBM combined (see Figure A.9). Wilcoxon signed ranked test was used to compared energy in the diet of mothers to the diet of baseline females since the data could not be normalized, and paired *t*-tests were used to compared protein intake. Mean energy in the diet was below baseline in month two ($z=2.343$, $p=0.019$), and above baseline values for month 5 ($z=2.215$, $p=0.27$), month 7 ($z=2.197$, $p=0.028$). Mean protein in diet was above baseline levels for the last two months of pregnancy and first two months of infant life (although this was only significant two months before birth: $t=3.307$, $df=8$, $p=0.011$), as well as in the later infant months (month 6: $t=2.185$, $df=14$, $p=0.046$; month 7: $t=3.775$, $df=11$, $p=0.003$; month 8: $t=6.209$, $df=6$, $p=0.001$).
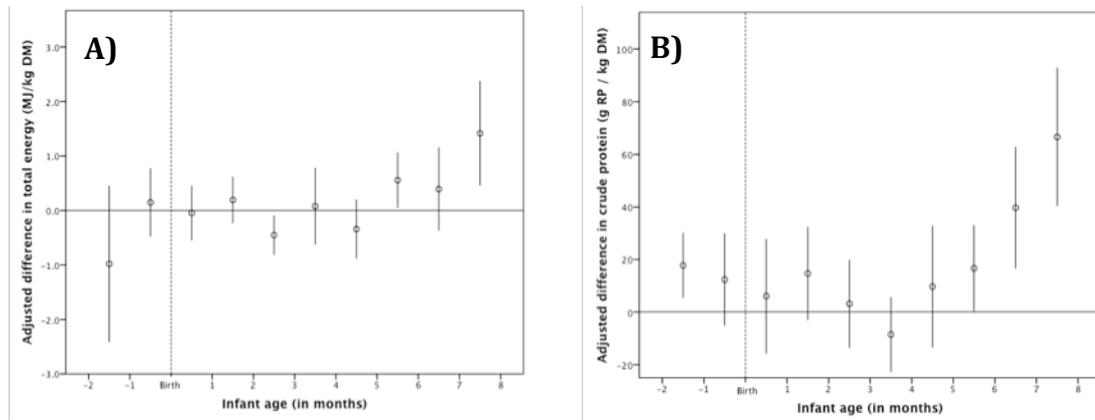

Figure A.9 A) Mean total energy (MJ) per dried mass and B) mean crude protein (g) per dried mass (kg) of maternal diet relative to baseline females over age of infant months.

A.4.2 SEASONAL VARIATION

In order to determine if a random slope should be included in the percent of foraging time model while incorporating seasonal effects, the individuals were

plotted over infant age (Figure A.10). The same procedure was applied for foraging

time in hours. (Figure A.11). Due to the differences in change over time between
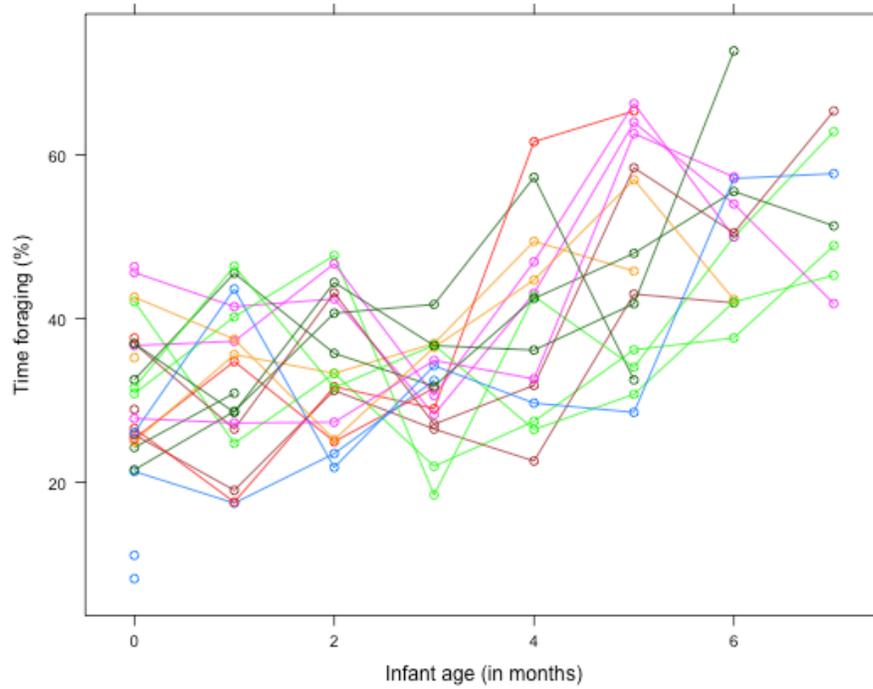
individuals, a random slope was included.

Figure A.10.   Time foraging (%) for individual mothers for infant age (in months)
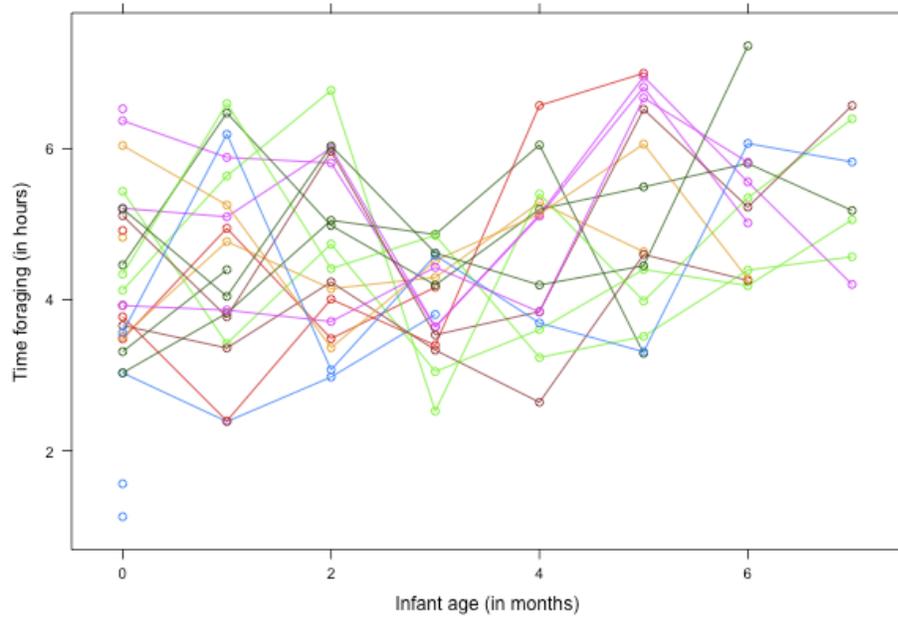
Figure A.11. Time foraging (in hours) for individual mothers for infant age (in months)

APPENDIX B – CHAPTER FOUR APPENDIX

In order to examine the differences in degree of association with activity and infant

month, Kendall-Tau B was used to examine the percent of time in ventral contact and

infant month for each individual for each maternal maintenance activity (foraging,

moving, resting, and social). Only individuals who had a full set of data for the first six

months were included in the analysis (N=15), with the coefficients reported in Appendix

B. In contrast to Green (1995), who found that for vervets up to twelve weeks of age

most of the correlations were not significant and therefore infant age was not a significant

factor in explaining time in ventral contact, I found infant age was a significant factor for

all maternal activities other than time spent in ventral contact while socializing. The

difference is likely due to the longer duration of my study.

Table A1: Kendall Tau-B coefficents for each individual activity for association between time in ventral contact over infant age while the mother was engaged in the four maternal maintenance activities (*N*=6, six months for each individual). Non-significant cells are shaded.

Mother ID	Feeding		Moving		Resting		Social	
	τ	*P*	τ	*p*	τ	*p*	τ	*p*
El	-0.966	0.007*	-0.828	0.022*	-0.867	0.015*	-0.400	0.327
Fa	-0.733	0.039*	-0.966	0.007*	-0.867	0.015*	-0.600	0.091
Gi	-1.00	<0.001*	-1.00	<0.001*	-1.00	<0.001*	-0.545	0.150
He	-0.745	0.044*	-1.00	<0.001*	-0.733	0.039*	-0.200	0.624
Ho	-0.894	0.016*	-0.966	0.007*	-0.867	0.015*	-0.414	0.251
Iz	-0.894	0.016*	-0.867	0.015*	-0.828	0.022*	-0.667	0.174
Lo	-0.966	0.007*	-0.966	0.007*	-0.733	0.039*	-0.801	0.105
Pr	-0.966	0.007*	-0.966	0.007*	-0.733	0.039*	-0.600	0.142
Sa	-0.828	0.022*	-0.966	0.007*	-1.00	<0.001*	-0.828	0.022*
Te	-0.894	0.016*	-0.966	0.007*	-0.690	0.056	-0.316	0.448
Ts	-0.966	0.007*	-1.00	<0.001*	-0.867	0.015*	-0.733	0.039*
Um	-0.966	0.007*	-0.966	0.007*	-1.00	<0.001*	-0.400	0.327
Wi	-0.894	0.016*	-0.867	0.015*	-0.733	0.039*	-0.149	0.687
Xa	-0.966	0.007*	-0.966	0.007*	-0.867	0.015*	0.298	0.421
Ye	-0.966	0.007*	-0.867	0.015*	-0.733	0.039*	-0.258	0.564

*p<0.005