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MATERNAL CARE IN GREY-CHEEKED MANGABEYS

Master's Thesis

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1. Introduction

Primates have relatively long infant development compared to other mammals of similar size (Strier, 2007) and therefore need more parental care to reach maturity (Harvey and Clutton-Brock, 1985). In most species of non-human primates, only females take care of infants, with some exceptions in socially monogamous species, like the common marmoset (*Callithrix jacchus*), and tamarins (*Sanguinus spp.*), where fathers help with carrying their infants (Maestripieri, 2011). Consequently, knowledge of the important factors influencing maternal care and infant survival is important, especially in terms of conservation, as 48% of primate species are listed as threatened (IUCN, 2013). Studying the more common or closely related species can give us essential information on how to protect endangered species in the wild and carry out successful breeding programs in captivity. This is especially so as primate mothers can feed their infants with milk for more than one year depending on the species and can even continue care for the rest of their lives (Maestripieri, 2011) and the effects of maternal care have been shown persist beyond the period of dependence (Altmann and Alberts, 2005). As mammals, maternal care consists mainly of breastfeeding, but also of carrying, grooming and protecting the infant either directly from predators and other group members or indirectly from danger by handling (e.g. holding on to the infant to keep it from falling). In addition to these, vocalization can be considered part of maternal care as communication with other group members can avoid danger to the infant. For example, when a grey-cheeked mangabey alarms that an eagle is around, the dominant male climbs up a tree to chase the bird away, so other members can escape (Arlet and Isbell, 2009).

The extent and success of primate maternal care depends on several parameters of the mother and her infant as well, for example, her previous experience (Beck and Power, 1988; Meder, 1990; Lindburg and Fitch-Snyder, 1994; Abello and Colell, 2006; Maestripieri, 2011; Arlet *et al*, 2014), social rank (Bowman and Lee, 1995; Ross and MacLarnon, 1995; Lee, 1999; Altmann and Alberts, 2005), and the age (Seyfarth and Cheney, 1986; Onishi and Nakamichi, 2011) or sex of the infant (Mitchell, 1968; Itoigawa, 1973; Trivers and Willard, 1973; Arlet *et al*, 2014).

The number of infants produced is not the only important feature of a female mammal influencing its fitness. In fact, the survival of infants is the key to reproductive success (Silk *et al,* 2003a,b). Infants of primates need months to years of maternal care to survive depending on the

species, and the more experienced a mother is, the more likely she is to succeed in raising her young (Beck and Power, 1988; Meder, 1990; Lindburg and Fitch-Snyder, 1994; Abello and Colell, 2006; Maestripieri, 2011). How much experience a mother has, may depend on her social rank – higher-ranking females can have better access to other females' infants, and hence the chance to practice taking care of infants with other females' offspring (Henzi and Barret, 2002; Gumert, 2007). However, this might not always be the case as low-ranking baboons have been shown to successfully prevent other females from getting their infants in three-quarters of attempts (Bentley-Condit *et al,* 2001). Secondly, it can depend on whether she has had offspring before – so her parity. Several studies have found it a crucial factor influencing the quality of maternal care, with the most extreme examples of incorrect maternal behaviour coming from hand-reared primates (Beck and Power, 1988; Meder, 1990; Lindburg and Fitch-Snyder, 1994; Abello and Colell, 2006). Primiparous mothers are more likely to mistreat or even abandon their first infant (e.g. 40% of abandonment in primiparous Japanese macaques (*Macaca fuscata*, Schino and Troisi, 2005)), but this probability decreases with each subsequent birth (Maestripieri, 2011). However, primiparous mothers have been recorded to be more protective (Nguyen *et al,* 2012, and references within). Thirdly, experience can be determined by the mother's age (Charpentier and Drea, 2013), because the older the female is, the more she inevitably has seen the behaviour of other females in her group and, in addition, had more time to handle infants whether her own or not. It is possible that older mothers are more competent or efficient at maternal care and are therefore observed to be less restrictive of infants breaking contact at a younger age (Cameron *et al*, 2000; Nguyen *et al*, 2012). Also, the age of the mother has been positively correlated with how well she protects her infant from other group members (Charpentier and Drea, 2013). Furthermore, more experienced mothers may take care of their infants more effectively when it is most crucial without investing more of their resources than mothers with less experience (Cameron *et al,* 2000). Older mothers have been observed to stay in contact longer than young, inexperienced mothers (Hoffman *et al*, 2010), for example, mothers can feed while they are holding their infants.

Age can also influence maternal behaviour in other ways. Older females have longer inter-birth intervals as the female reproductive system ages (olive baboons (*Papio anubis*), Strum and Western, 1982; rhesus macaques (*Macaca mulatta*), Hoffman *et al,* 2010; mountain gorillas (*Gorilla beringei beringei*), Robbins *et al*, 2006), thus having more time to look after their infants. For example, infants of older mothers in grey-cheeked mangabeys (Arlet *et al,* 2014) and macaques (*Macaca spp.,* Paul *et al,* 1993; Silk *et al,* 1993) have been found to have higher

survival rates. On the other hand, few infants of old and very old females of rhesus macaques survive to reproductive age as they are often unable to provide enough milk in the last five to ten years of their maximum lifespan (Hoffman *et al*, 2010).

It has been found in several species, for example, in macaques, that rank influences maternal behaviour mostly through better access to food by dominant females (Maestripieri, 2007). Among grey-cheeked mangabeys (*Lophocebus albigena*), dominant females are able to feed at sites with more valuable food for longer periods of time (Chancellor and Isbell, 2009). Plentiful or better quality food affects the female's condition and thereby the condition of her infant (Altmann and Alberts, 2005; Borries *et al*, 2013): high-ranking mothers have been shown to have shorter inter-birth intervals (Brown, 2001; Johnson, 2003) as growth and maturation processes of the infant are accelerated (Borries *et al*, 2013). Therefore, dominant females can have greater reproductive success if the life spans of females of both ranks are alike. However, a long-term study of rhesus macaques found no statistically significant difference between high- and low-ranking mothers in the number of grand-offspring (Bercovitch and Berard, 1993). Nevertheless, Bales and her colleagues (2002) found that the mother's condition is positively correlated with how much they invest in their offspring. In addition, Silk *et al* (2003a) associated high rank with greater infant survival.

In addition to the mother's own traits, the characteristics of an infant can also affect maternal conduct. Firstly, it has been shown to change immensely with infant age: mothers carry, hold and protect infants more the younger they are, but encourage them to move around more as they grow (Maestripieri, 2011; Onishi and Nakamichi, 2011). Secondly, it is hypothesized that if a mother's investment influences her infant's physical condition as an adult and if the reproductive success of different sexes is differently affected by the individual's condition, then a mother in good condition should bias her investment towards the sex that gives her more grand-offspring (Trivers and Willard, 1973), so in polygynous primates this should be sons for dominant females. This has not been fully proven nor rejected for monkeys (Brown, 2001). But since the infant's own behaviour depends on its sex in some aspects (Brown and Dixson, 2000), the mother's behaviour can vary as well (Mitchell, 1968), although the influence of it on maternal care is not well known (Nguyen *et al,* 2012).

Compared to other females, mothers of young infants feed more, because of the added energy expenditure of lactation (Altmann, 1980; Dunbar and Dunbar, 1988). On the contrary, mothers

of weaned infants who only carry them, spend less time on feeding than other group members, although carrying also spends extra energy (Goldizen, 1987; Price, 1991). However, these mothers have been shown to move less as well (reviewed in Nievergelt and Martin, 1999). Another behavioural aspect that can vary between mothers and other females is how much they are groomed. This is a possible way of earning the handling rights of the mother's infant, and although, the groomer does not always gain access to the infant, the mother seldom grooms the other female in return (Henzi and Barrett, 2002; Aspden, 2005; Frank and Silk, 2009).

Much of the data on maternal behaviour in primates has come from more visible and mostly terrestrial species such as ring-tailed lemurs, vervets, macaques, baboons, and chimpanzees. Some of the results of earlier studies have been inconsistent between and even within species (Brown, 2001; Borries *et al*, 2013). Therefore, to draw general conclusions, it is necessary to study species from other habitats as well, so the species observed are broadened to include information from arboreal primates. These are, for example, the Milne-Edward's sifakas (*Propithecus diadema edwardsi*, Pochron *et al*, 2004), Hanuman langurs (*Semnopithecus,* Sommer *et al*, 1992), capuchins (*Cebus capucinus*, Fedigan *et al*, 2008) and blue monkeys (*Cercopithecus mitis stuhlmanni*, Cords and Chowdhury, 2010). This thesis sets out to supplement the knowledge about maternal behaviour in arboreal primates with the grey-cheeked mangabey, which is closely related to the well-studied but terrestrial baboons, but also several vulnerable (*Cercocebus atys*, *C. torquatus*), endangered (*C. galeritus, C. sanjei*) and critically endangered species (*Rungwecebus kipunji;* IUCN, 2013). We investigated whether and how the aforementioned maternal behaviours are influenced by several variables of the mother and her infant. Moreover, we also compared mothers to other females of similar age. There is no information available about whether and how rank influences maternal behaviour, concerning grey-cheeked mangabeys in the wild. Arlet *et al* (2014) observed that the cycle frequency decreases with age only among low-ranking females, although, no difference in inter-birth intervals was found, yet the infants of older females had higher survival. However, there is no information on how the infant's parameters influence the behaviour of mangabey mothers.

Grey-cheeked mangabeys have only recently been under thorough investigation (Figure 1.1), possibly because arboreal rainforest species are difficult to investigate (Deputte, 1991). Consequently, mother-infant relationships have not been well studied in this species. For example, Thomson Reuters Web of Science does not give any results when searched for "grey-cheeked mangabey mother infant", "mother grey-cheeked mangabey", "*Lophocebus* mother"

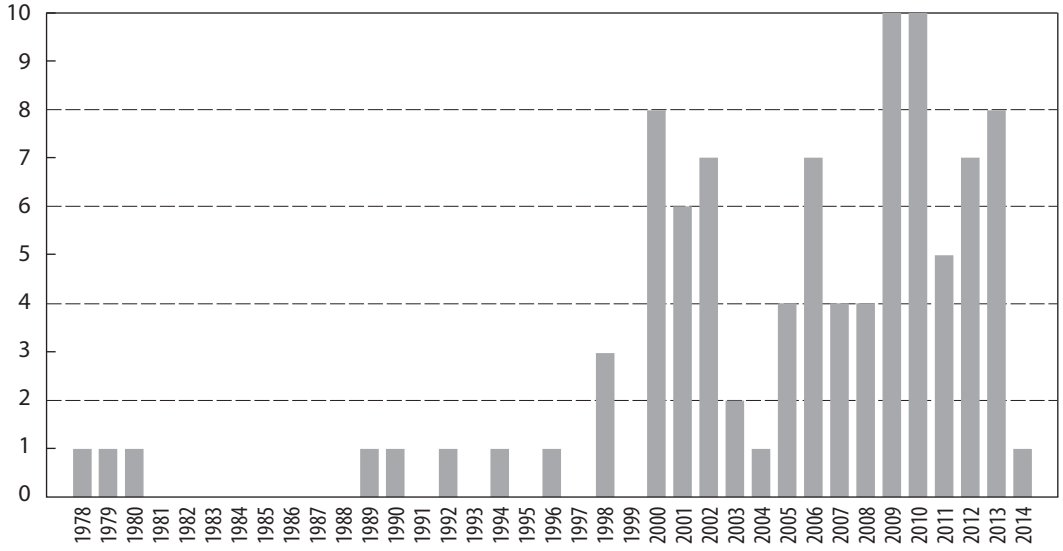

Figure 1.1. Report of published articles in each year in Thomson Reuters Web of Science for "*Lophocebus albigena*".

or "*Lophocebus* maternal". For that reason, this study is an important step to understanding mother-infant relationships in the grey-cheeked mangabey.

The general aim of this study was to describe the factors responsible for variation of maternal behaviour in grey-cheeked mangabeys, and also to find out whether and how the respective behaviours in this species differ from that in other monkeys, especially of their relatives and other arboreal species. Based on the data available on other species, the hypotheses of this study were:

- Older mothers groom, handle and protect their infants more,
  but are less restrictive than younger mothers.
- Primiparous mothers spend less time on caring for their infants,
  but are more protective of them than multiparous mothers;
- Dominant grey-cheeked mangabey mothers provide more maternal care,
  e.g. groom and carry more, but vocalize less;
- The extent of maternal care decreases with infant age: they are groomed,
  carried, held and protected less, but restricted from contact and suckling more;
- Mothers are more restricting of their daughters than sons, but there is no difference
  in carrying and handling the infant based on its sex;
- Compared to other females, mothers feed, sit and are groomed more,
  but move and groom less.

2. Materials and Methods

2.1. Study area and subjects

The study material was collected on females and infants of grey-cheeked mangabeys in Kibale National Park (0°13'–0°41'N and 30°19'–30°32'E), Uganda. Kibale National Park (795 km^2) is a moist, evergreen, medium altitude forest with areas of swampland, grassland, thicket, and colonizing forest (Chapman and Lambert, 2000). The data was collected from July 2011 to March 2012 on five groups of grey-cheeked mangabeys: Lower Camp 1 (LC1), Lower Camp 2 (LC2), Butanzi 1 (But1), Mikana (MIK) and a control group named CC. Grey-cheeked mangabeys have been studied in Kibale since the 1970s and the studied groups were habituated with humans (Arlet *et al*, 2014). The groups consisted of 11 to 25 monkeys (Table 2.1).

Grey-cheeked mangabeys are predominantly frugivorous (Waser, 1977; Chancellor and Isbell, 2009) medium-sized dimorphic arboreal monkeys who live in forests of Central Africa (Harris and Disotell, 1998; Burrell *et al*, 2009). As they are closely related to baboons, they live in multi-male, multi-female groups, but group sizes tend to be smaller than in baboons (Waser, 1977; Henzi and Barrett, 2003). Females typically remain in their natal groups after they reach adulthood and remain there throughout their lives like baboons and macaques (Altmann *et al,* 1996). Furthermore, female mangabeys have stable, linear dominance hierarchies where the daughter's rank is attained in accordance with her mother's (Chancellor and Isbell, 2009). Subadult males disperse from their group of origin when they reach sexual maturity (Arlet *et al,* 2008). Joining another troop, immigrant males compete with resident males for dominance and access to oestrous females (Olupot and Waser, 2001, Arlet *et al,* 2007). Grey-cheeked mangabeys are aseasonal breeders (Wallis, 1983; Arlet *et al*, 2007). Consequently, the infants in this study are not at the same age.

2.2. Identification and the basic traits of the females and infants

In 2004, Rebecca L. Chancellor and her field assistants were the first to identify females individually. The traits used were relative body size, nipple size, nipple colour and different tail characteristics like scars, shape and the thickness of hair (Arlet *et al,* 2014). The same features were used to identify female mangabeys matured after Chancellor's and before our study (Tables 2.2 and 2.3).

Table 2.1. Compositions of groups of grey-cheeked mangabeys in Kibale National Park, Uganda between August 2011 and March 2012.

Group code	But1	LC1	LC2	MIK	CC
Group size	16–19	20–25	13–14	11–12	13–20
Adult females	7	7	4–5	4	4–7
Adult males	1–4	3-6	1	3–4	3–4
Subadult[3] females	1	1–2	0–1	0–2	1–2
Subadult[3] males	1	0	1	0	1–2
Juvenile[2] females	1	0	1	0–2	0–1
Juvenile[2] males	2	3–4	3	2	2–4
Infant[1] females	1	2	0	1	0
Infant[1] males	2	4	3	1	0

[1] Infants are individuals younger than 18 months old. [2] Juveniles are 18 months to 3–4 years.
[3] Subadults are immature mangabeys up to the age of 6–7 years when they become sexually mature (Waser, 1974).

The ages of twelve females were estimated, because they were born before studies had started in 2004. The estimate of age was based on the relative size of the female, the skin condition of her sexual swelling, nipple length, how much the skin was wrinkled on the face and neck, sagged around the face, and the extent of hair thinning (Arlet *et al,* 2014). The ages of the females born after 2004 are known exactly (Table 2.3). The age estimates for LC2 group were not available, as this group has been studied only since 2010.

Female dominance ranking was based on Arlet *et al* (2014) matrices for groups LC1, But1, MIK and CC until 2012. These troops had fairly stable linear dominance hierarchies that were divided into high- and low-ranking (in other words, dominant and subordinate) individuals on the basis of their matrilineal ranks. There was no dominance rank data available for group LC2, so three mothers were left out from analyses regarding the influences of dominance on mother-infant relationships.

Data on 16 infants was collected (Table 2.2); these were defined as animals younger than 18 months old (Waser, 1974). The oldest infant in the study was 14 months old at the end of the observation period. The birth dates for infants born before the study began were estimated based on variation in coat colour. There were six mothers with infants in LC1, four mothers with infants in But1, three mothers with infants in LC2, two mothers with infants in MIK,

and CC group consisted only of controls as no females had infants during our study period (Table 2.3). The parity of the mother was characterized as primi- or multiparous. Four of the mothers were primiparous – caring for their first infant, and 10 were multiparous, having had at least one infant before the one they were caring for during the observation period. The parity for two mothers was unknown. Dominant mothers had five male and three female infants, and subordinate females had three males and two females. The particular interest was in studying mothers with infants, because the mother pays the most attention to its offspring before the juvenile age (Altmann and Alberts, 2005), so the differences in maternal care should come out more pronounced in this period.

Table 2.2. Mothers and infants in the groups of grey-cheeked mangabeys. Females without infants are excluded from this model[1].

Group Female (ID)	Infant (ID)	Infant's date of birth	Sex	First infant	Infant survived until juvenile
LC1					
Kiiki (KI)	Kyamanywa (Yn)	Jan 2011	m	No	Yes
Namara (NM)	Makune (Ak)	Nov 2011	f	No	Yes
Nsungwa (Ns)	Busobozi (Bs)	Dec 2010	m	No	Yes
Nyakato (Nt)	Tusime (Ts)	June 2011	m	No	Yes
Kaisiki (SK)	Asimwe (We)	Nov 2011	m	No	Yes
Ngonzi (ZI)	Birungi (Gn)	Nov 2011	f	Yes	No
But1					
Muhimbo (Hm)	Kiswasa (Ks)[2]	March 2011	m	Yes	No
Muhimbo (Hm)	Kaheeru (Ee)	Feb 2012	m	No	No
Mwirima (WI)	Banura (Na)	Nov 2011	m	No	No
Kadogo (DO)	Zahura (Za)	Feb 2012	f	No	Not known[3]
Kagezi (GZ)	Katusabe (Us)	March 2012	m	Yes	No
LC2					
Kiiki2 (Ki2)	Nturanabo (Nn)	June 2011	m	No	Not known
Kissa2 (Ks2)	Ndyanabo (Nd)	May 2011	m	NI[4]	Not known
Tindereya (Td)	Bagamba (Aa)	Oct 2011	m	NI	Not known
MIK					
Broom (RO)	Gonza (ZO)	March 2012	f	Yes	Not known
Kakende (KD)	Kisembo (KM)	March 2012	f	No	NI[4]

[1] Females who did not have infants during this study are KO and DM from group LC1; KB from But1; Hr and BK from LC2; WO and NB from MIK; KU, KE, IR, BO, MZ, GI, TB and KU from CC.
[2] Kiswasa (Ks) died during the study on 20th August 2011. [3] Not known – the infant was not a juvenile at the end of the study, but had not died. [4] NI – no information.

Table 2.3. Ages, age estimates and dominance rank of female grey-cheeked mangabeys of studied groups in Kibale National Park, 2012.

Group	Female	Age	Rank
LC1	KI	16–20	High
	NM	8–12	Low
	Ns	12–16	High
	Nt	16–20	High
	SK	9	Low
	ZI	9	Low
	KO	12–16	Low
	DM	5	High
But1	Hm	7	Low
	WI	7	High
	DO	10	High
	GZ	7	High
	KB	23	Low
LC2[1]	Ki2	Not known	Not known
	Ks2	Not known	Not known
	Td	Not known	Not known
	Hr	Not known	Not known
	BK	Not known	Not known
MIK	RO	8	High
	KD	12–16	High
	WO	9	Low
	NB	16–20	Low
CC	KU	19–23	High
	KE	19–23	Low
	IR	8	Low
	BO	13–15	High
	MZ	16–20	Low
	GI	8	High
	TB	Not known[2]	Low

[1] No age or rank information was available for LC2.

[2] TB immigrated to the CC group in 2009 taking the lowest rank in the female hierarchy, but her age was not estimated.

2.3. Observation

From the end of July 2011 to September 2011, two observers (Linda-Liisa Veromann and Richard Kaseregenyu) collected behavioural data for 6–10 hours per day between 7 am to 5 pm for five consecutive days per week. From mid-September 2011 until the second week of March 2012, the mangabeys' behaviour was recorded for 8 hours per day by one observer (Richard Kaseregenyu). Inter-observer reliability was established by sampling the same animal simultaneously during the first week of observation and again one month into the study. The observations were carried out as a rotation between groups – one group was followed for one week every five weeks. No data was collected during rain, on Sundays and Mondays and holidays. Focal-animal sampling and all occurrence behaviour data collection were used (Altmann, 1974).

The focal sampling order in each group was opportunistically determined by first sighting of an adult female that had not yet been sampled during a particular round (usually a day), while taking care to balance morning and afternoon sampling for each individual to minimize the effect of behavioural changes during the course of the day. So, the female's rank, age or parity did not determine when or where she was observed and the order of study subjects was incidental. Each focal sampling lasted approximately 1–1.5 hours. The total amount of data was altogether 343 hours and the median time recorded per female was 4.6 hours (range: 1 hour for GZ who gave birth to her infant on the last day of the last round of her group, to about 37 hours for Ki2 and Ks2 who had the oldest infants in the study, thus the whole observation period).

We predominantly followed females with infants (N = 15). For comparison, we also collected data from females without infants (N = 22), who were the same age as the mothers, and of both ranks. Eight females had infants during the study and were thus observed at first as controls, as their behaviour did not differ from non-pregnant non-mothers statistically significantly, and then as mothers. The behaviours of focal females were recorded all day, divided into 90-minute sampling blocks for females with infants, and 60-minute for adult females with no infants. During focal sampling of females with infants, we recorded distance to the infants every time it changed, nearest animal and all occurrences of interactions with infants and other group members within 10 m of the focal female (NN 10 m, Figure 2.1). We recorded behaviours connected with the infant in addition to main activities of the daily budget of females. The exact definitions of behaviours were established before collecting the data (Table 2.4) and it was marked on the data sheets as the duration of that behaviour

FOCAL DATA SHEET **Date: 1.09.11** **Group: LC2** **Female: Ki2** **Infant: Nn** **Infant sex: male**

Time start	Time end	Place	F/M/B/S	Nn 10m	Sit	Suckling	Watching infant	Groom	Feed	Introd. food	Restrict leave	Restrict contact	Restrict suckling	Protect from	Handling whom	Aggressive to infant	Vocals	Stand	Move	Carring (V or D)	Distance from inf	Comment
11:17:30	11:18:26	W Kar	M	?	Y				Y												0	
11:18:26	11:19:40	W Kar	M	?	Y				Y												0,1	Inf moving very close to Ki2
11:19:40	11:22:37	W Kar	M	?	Y				Y												0	
11:22:37	11:22:41	W Kar	M	?															Y	V	0	
11:22:41	11:23:01	W Kar	M	?	Y																0	
11:23:01	11:23:08	W Kar	M	?													Gts		Y	V	0	
11:23:08	11:23:44	W Kar	M	?	Y				Y												0	
11:23:44	11:30:04	W Kar	M	?	Y				Y												0–1	Inf moving around
11:30:04	11:30:50	W Kar	M	?	Y				Y												0–2	Inf moving around
11:30:50	11:31:50	W Kar	M	?													SB		Y	V	0	Submitted to IB
11:31:50	11:33:07	W Kar	M	?	Y				Y												0	
11:33:07	11:40:33	W Kar	M	?	Y				Y												0–1	Inf moving around
11:40:33	11:44:52	W Kar	M	?	Y				Y												0	
11:44:52	11:47:22	W Kar	M	?	Y				Y												0–1	Inf moving around

Figure 2.1. An example of a spreadsheet used for collecting data on grey-cheeked mangabeys in Kibale National Park.

in seconds, except the distance from infant, which was marked in meters. Figure 2.1 shows detailed behaviours collected during this study.

Mothers were very rarely aggressive to infants and were not observed watching their infant or introducing it food often enough for us to make meaningful comparisons in their occurrences, so these behaviours were left out of the analyses.

Table 2.4. The activity descriptions for focal observations of grey-cheeked mangabeys (modified from Patterson, 2001).

Activity	Description
Sitting (s)[1]	The mangabey is sitting on a branch or on the ground
Standing (s)	Standing up, but not moving anywhere
Moving (s)	Walking, running and jumping
Suckling (s)	The infant is holding the mother's nipple in its mouth
Watching infant (s)	The mother is turning her head and/or body toward the infant while the infant is sitting or moving
Grooming (s)	The focal female is using her mouth and hands to pick through someone's fur (including self-grooming) or is groomed by someone else
Feeding (s)	Consuming any food or water and foraging (picking up, searching food objects)
Introducing food (c)[2]	The mother is offering her infant edible objects
Restricting from leaving (c)	The mother is restricting her infant from leaving, i.e.breaking contact with her
Restricting from contact (c)	The mother does not allow the infant to climb onto her or hold on to her ventral side while she is moving
Restricting from suckling (c)	The mother does not allow the infant to take her nipple into its mouth
Protecting from somebody (c)	The mother restricts another member of the group from handling the infant
Handling somebody (s)	A focal female is holding or carrying someone's infant or a focal mother is holding someone else's infant
Aggressive to infant (s)	Biting, slapping or chasing the infant
Vocalizing (s)	Emitting a sound: grunting, staccato barking, alarming or screaming
Carrying (s)	Carrying an infant on one's ventral or dorsal side

[1] s – behaviour was recorded as an amount of time: observations written down in seconds, analysis done with minutes. [2] c – behaviour was recorded as counts of actions and analysis done with the number divided with the time followed.

Two compendious behaviours were also included in the analyses: overall time spent in contact with the infant and total time spent on vocalizing. Contact between the mother and her infant is fundamental for normal offspring growth, as it provides transportation (carrying), protection (carrying, holding the infant during sitting and standing), nourishment (suckling) and also thermoregulation (all of the aforementioned; Altmann, 1980).

2.4. Statistical analysis

The ages of the mothers and infants were considered as continuous factors – infant age in months and age of the mother in years. The mean values were calculated from the estimated ages of the mothers, for example Ns from Lower Camp 1 had an age estimate of 16–20, so she was included in the analysis as an 18-year-old mother.

To avoid pseudo-replication, the data for an individual female (or infant) was averaged or summed up, depending on the type of data, and included in the models as one single data-point. Behaviours that occurred during another action, like carrying an infant while moving or standing, are a percentage of the total time we observed the female doing the longer activity.

STATISTICA 10 (StatSoft Inc. USA) was used for all the analyses. Analyses were done by Linda-Liisa Veromann in consultation with Ants Kaasik. Due to small sample size, it was not usually possible to analyse more than four factors in the same model. Residuals of models analysed with General Linear Models and ANCOVA did not differ statistically significantly from a normal distribution.

Simple regression was used for one-way analysis of continuous factors (the age of the mother and the age of the infant) and General linear models Univariate Tests of Significance Sigma-restricted parameterization (ANOVA) for categorical factors (the social rank and parity of the mother and the sex of the infant) on grooming, carrying, standing, sitting, overall time in contact, average distance between mother and infant, protecting and restricting from suckling, leaving and contact. The results were tested with Bonferroni correction.

Advanced linear models Analysis of Covariance (ANCOVA) Univariate Tests of Significance Sigma-restricted parameterization was used to analyse the effect of the social rank and parity of the mother on grooming her infant, carrying, standing and sitting with her infant, overall

time in contact with it, the average distance between the mother and her infant, restricting from leaving, restricting from suckling, restricting from contact and protecting from other group members (dependent factors) with the age of the infant and/or the age of the mother being the continuous factors, or covariates. Since the age of the infant can be an important factor of how much the mother needs to hold and carry the infant and the rank of the mother is not correlated with the age of the mother in grey-cheeked mangabeys (Arlet *et al*, 2014), the age of the infant and the mother were included in the model. General linear models (GLM) Univariate Tests of Significance Sigma-restricted parameterization was used to analyse the effect of the age of the mother and the age of the infant on the same behaviours. Due to a small sample size, larger models were not possible in this program.

The influence of infant age in combination with the sex of the infant was analysed with an ANCOVA Univariate Tests of Significance Sigma-restricted parameterization, where the continuous predictor was infant age, the dependent factor either grooming, carrying, standing, sitting or overall time in contact with the infant and the categorical factor was the sex of the infant.

The statistical significance of the influence of the infant's age and sex, the mother's age and parity on her vocalizations were calculated with generalized linear/nonlinear models Poisson model and *log* link function with type III empirical standard error (GLZ), because vocalization data had a strongly unbalanced nature and was in a Poisson distribution. However, it was possible to test the effect of parity and rank (categorical predictor) separately in a larger model with the dependent factor being either grunting, staccato barking, alarming or overall time spent on vocalization, the covariates the age of the mother and the age of the infant with ANCOVA, because the residuals did not differ significantly from a normal distribution. One female, Muhimbo, was left out from the analyses with her second infant, Kaheeru, because her vocalizations deviated from the average six times.

Comparison data about other females with normal distributions was analysed using one-way ANOVA: comparisons of feeding, grooming, moving, sitting, standing, vocalizing, holding, carrying and standing with an infant between mothers and females without infants. Group influences were tested for each behaviour, but they were not statistically significant.

3. Results

3.1. The correlations between behaviours and between the parameters of mothers and infants

I tested whether the behaviours observed correlated with each other. Time spent on grooming correlated negatively with the time spent on carrying the infant (regression analysis: $F_{1,14}=15.01$; $p=0.002$) and alarming positively with the time spent on standing with the infant ($F_{1,14}=34.67$; $p<0.0001$), but as most of them have multiple trade-offs in the mother's daily budget, I did not find the time spent on any of the other behaviours statistically significantly dependent on any other activity.

The overall time spent in contact with the infant correlated positively with sitting with the infant for mothers (regression analysis: $F_{1,14}=81.2$; $p<0.0001$) as it was the most common behaviour of those where the mother was in physical contact with it. Maternal care was still analysed with both to illustrate the influence of holding the infant and the effect of other behaviours on overall time in contact with it. The total time spent on vocalizing correlated positively with grunting ($F_{1,14}=3651$; $p<0.0001$). Although, the correlation is very strong, the results were presented with both behaviours to make the effect of grunting and all the vocalizations together comparable and to illustrate the large proportion of grunting of all the vocalizations.

In addition, I tested whether the parameters of the mother (age, rank, parity) and the infant (age, sex) were dependent on one another. I found that none of the parameters depended on any other and therefore needed to be tested and presented separately.

3.2. The effect of the age of the mother on infant care

Older females groomed their infants significantly more than younger females (regression analysis: $F_{1,11}=5.09$, $p=0.045$, Figure 3.1), but spent less time carrying them ($F_{1,11}=7.13$, $p=0.022$). When the age of the infant was regarded in the analysis as a covariate, the effect of the age of the mother on the time spent on grooming remained statistically significant (GLM: $F_{1,10}=5.15$, $p=0.047$), but not on how much they carried their infants ($F_{1,10}=0.051$, $p=0.84$).

However, the time spent on carrying and grooming did not depend significantly on the age of the mother when the mother's rank or parity was also added to the model. No connection was

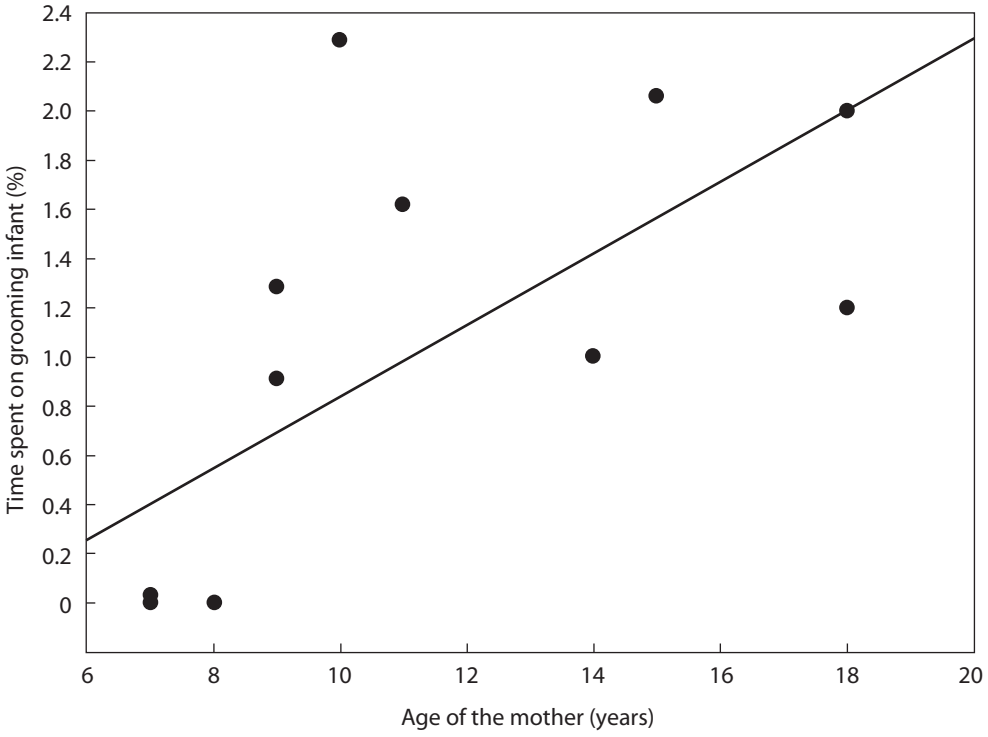

Figure 3.1. The effect of the age of the mother on how much she grooms her infant.

found between the time mothers spent standing (regression analysis: $F_{1,11}=0.037$, $p=0.85$) or sitting with the infants ($F_{1,11}=0.13$, $p=0.72$). There was also no difference between older and younger mothers in the overall time spent in contact (carrying, holding the infant while she is standing or sitting, and grooming it) with their infant (regression analysis: $F_{1,11}=0.23$, $p=0.64$), regardless of the age of the infant (GLM: $F_{1,10}=1.32$, $p=0.28$). Furthermore, the age of the mother did not affect the average distance between her and her infant when the age of the infant was included in the model ($F_{1,10}=0.061$, $p=0.8$).

Moreover, when considering the age of the infant and the mother in the model, no differences were found among females in how restrictive they were: how often they restricted the infant from suckling (GLM: $F_{1,10}=2.23$, $p=0.17$), restricted the infant from leaving ($F_{1,10}=0.34$, $p=0.57$) or restricted physical contact with them ($F_{1,10}=0.027$, $p=0.87$). Because no age information was available for three mothers of 15, there was not enough data to analyse these parameters in larger models. However, overall, older mothers protected their infants more often than their younger counterparts when the age of the infant was included in the model (GLM: $p=0.028$; Table 3.1).

Table 3.1. The effect of the age of the mother on the frequency of protecting her infant (general linear models, analysis of covariance: age of the infant).

Effect	df	SS	F	p
Age of the infant	1	3.92	9.39	0.028
Age of the mother	1	0.004	8.82	0.031
Error	10	1.66		

3.3. The effect of the parity of the mother on infant care

Maternal care seemed not to be contingent on whether the mother was caring for her first infant or had had infants before. There was no statistically significant difference between primiparous and multiparous females on the time spent on grooming (ANCOVA: $F_{1,11}=2.04$, $p=0.18$), carrying ($F_{1,11}=0.072$, $p=0.79$), holding the infant while standing ($F_{1,11}=2.41$, $p=0.15$), sitting with it ($F_{1,11}=0.24$, $p=0.64$) or the overall time spent in contact with it ($F_{1,11}=0.49$, $p=0.5$) considering the age of the infant. Also, the average distance between the mother and her infant did not depend on the mother's parity when the age of the infant was included in the model ($F_{1,11}=0.0001$, $p=0.99$). Furthermore, when the age of the infant was considered, primi- and multiparous mothers protected ($F_{1,11}=2.32$, $p=0.16$) and restricted their infants similarly (from suckling: $F_{1,11}=2.16$, $p=0.17$; from leaving: $F_{1,11}=0.95$, $p=0.35$; from contact: $F_{1,11}=1.46$, $p=0.25$).

3.4. The effect of the social rank of the mother on maternal care

Dominance rank of 12 females with infants was known: eight were high-ranking and only four were low-ranking. However, there were 12 high- and 12 low-ranking females with known ranks in total in four groups during our research. The rank of 3 mothers from the LC2 group was unknown. Also, no evidence was found that rank is a statistically significant factor in determining the sex of the infant ($p=1$). Dominant mothers had five male and three female and subordinates had three male and two female infants.

High-ranking mothers spent significantly more time sitting and in contact with their infants than low-ranking mothers. These results were also statistically significant when the age of the infant and the age of the mother were used in the analysis as covariates (Table 3.2). However, there

Table 3.2. The effect of the social rank of the mother on maternal care (ANCOVA).

	Mother's rank + age of the infant		Mother's rank + age of the infant + age of the mother	
	$F_{1,10}$	p	$F_{1,9}$	p
Sit holding infant	8.52	0.015	5.87	0.038
Time in contact	8.08	0.017	5.57	0.043

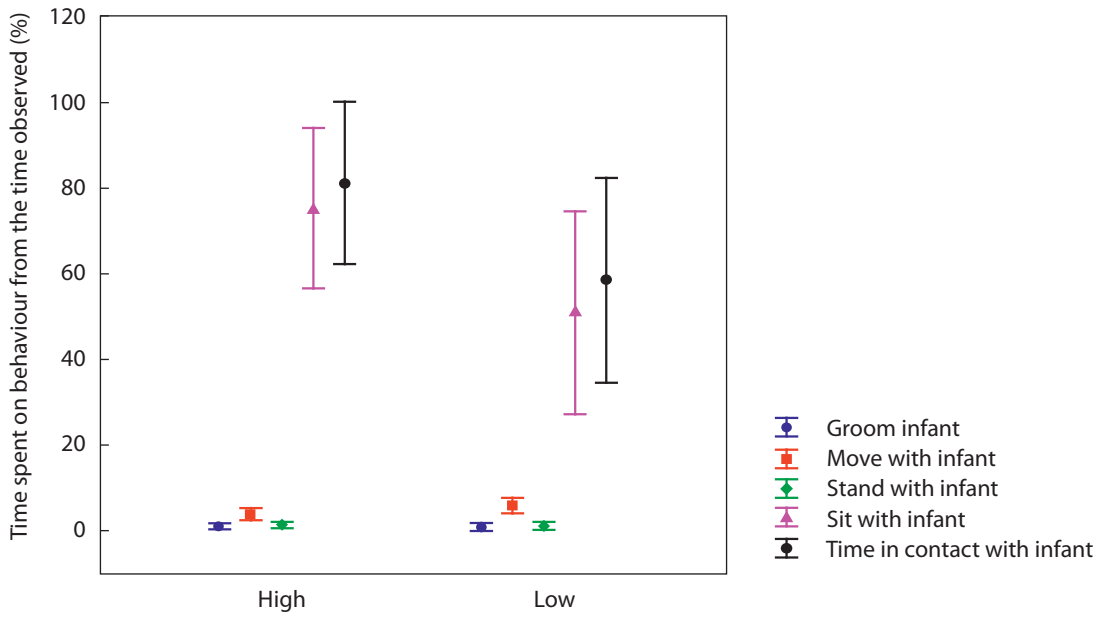

Figure 3.2. The mean percentage of time spent on different actions of maternal care depending on the mother's rank (high or low). Vertical bars denote 0.95 confidence intervals.

was no statistically significant difference in the time high- and low-ranking mothers groomed (ANCOVA: $F_{1,10}=0.009$, $p=0.92$), carried ($F_{1,10}=0.025$, $p=0.88$) or stood holding their infants ($F_{1,10}=0.26$, $p=0.62$, Figure 3.2). Furthermore, the average distance between a mother and her infant did not vary significantly among high- and low-ranking mothers, when the age of the infant was applied as a covariate ($F_{1,10}=1.29$, $p=0.28$).

The number of times a mother restricted her infant from suckling (ANCOVA: $F_{1,10}=0.67$, $p=0.43$) and from contact with her ($F_{1,10}=0.9$, $p=0.36$) depended rather on the infant's age than on the mother's rank. Also, no statistically significant difference was found between ranks in how often they protected their infants from other group members ($F_{1,10}=1.14$, $p=0.31$) or restricted from

leaving ($F_{1,10}=0.25$, $p=0.63$). When the influence of rank was combined with the sex of the infant, it did not affect how much she restricted her infant from leaving, contact or suckling ($F_{1,8}=0.13$, $p=0.72$, $F_{1,8}=0.96$, $p=0.36$ and $F_{1,8}=0.29$, $p=0.61$, respectively), but for suckling, the age of the infant did.

3.5. The effect of the mother's parameters on vocal communication

Younger females grunted more often (GLZ: $\chi^2=15$, $df=1$, $p=0.0001$) and also vocalized more overall ($\chi^2=12.6$, $df=1$, $p=0.0003$). However, the significance of these differences disappeared when the age of the infant was included in the models (grunting: $\chi^2=1.16$, $df=1$, $p=0.28$; total vocalizations: $\chi^2=1.04$, $df=1$, $p=0.31$) and vocalizations depended rather on the age of the infant. In addition, the frequencies of staccato barking and alarming were similar in mothers of different ages (accordingly: $\chi^2=0.02$, $df=1$, $p=0.88$; $\chi^2=0.48$, $df=1$, $p=0.49$). Also, there was no statistically significant difference between older and younger females in vocalizing when the age of the infant and the dominance rank or parity of the mother were included in the model.

Generally, the mother's parity had no influence on her vocalizations. Regarding infant age in the analyses, both primiparous and multiparous mothers grunted ($\chi^2=0.18$, $df=1$, $p=0.67$), staccato barked ($\chi^2=0.13$, $df=1$, $p=0.72$), alarmed ($\chi^2=0.001$, $df=1$, $p=0.97$) and vocalized similarly overall ($\chi^2=0.06$, $df=1$, $p=0.8$).

In total, mothers with lower dominance status grunted (GLZ: $\chi^2=6.3$, $df=1$, $p=0.012$) and vocalized more overall ($\chi^2=4.35$, $df=1$, $p=0.037$) regardless of their infant's age, but not statistically significantly when the mother's own age was included in the model. There was no significant difference between ranks in the time spent on staccato barking and alarming ($\chi^2=0.13$, $df=1$, $p=0.71$ and $\chi^2=0.046$, $df=1$, $p=0.83$ respectively), also when the age of the infant was included in the model ($\chi^2=0.12$, $df=1$, $p=0.72$ and $\chi^2=0.025$, $df=1$, $p=0.87$, respectively).

3.6. The influence of the age of the infant on maternal care

Many parameters of maternal care tested were affected by the age of her infant. It had a significant impact on grooming time: the older the infants were, the more they were groomed by their mothers (Figure 3.3), regardless of the sex of the infant, but the less they were carried. Furthermore, younger infants were held more while sitting and the overall time handling

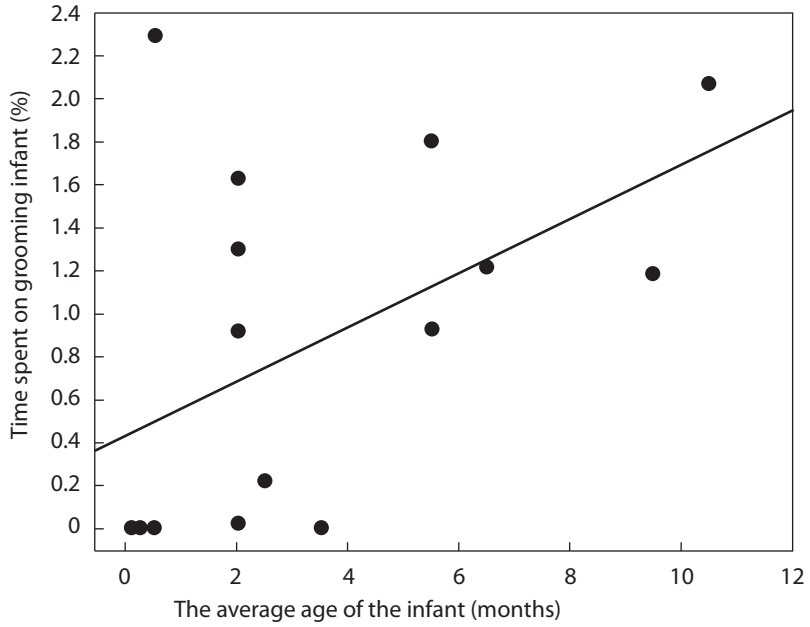

Figure 3.3. The effect of the age of the infant on the average percent of time spent on grooming it.

the infant was longer when only the effect of the age of the infant was calculated in the model, but not after Bonferroni correction. Also, the latter two became non-significant when infant sex or both infant sex and the social rank of the mother were included in the model (Table 3.3). How much the mother held her infant while she was standing did not depend on the age of the infant in any of the models tested ($p > 0.38$). Nonetheless, the average distance between mothers and infants grew with infant age (Table 3.3), with the longest observed

Table 3.3. The effect of the age of the infant on its mother's behaviour (regression analysis was used for only the effect of the age of the infant, ANCOVA was used for other models).

	Age of the infant		Age of the infant + sex of the infant		Age of the infant + rank of the mother		Age of the infant + sex of the infant + rank of the mother	
	$F_{1,14}$	p	$F_{1,13}$	p	$F_{1,10}$	p	$F_{1,8}$	p
Groom infant	4.63	0.049[1]	8.63	0.012	3.14	0.11	3.61	0.094
Carry	31.5	<0.0001	54.2	<0.0001	30.3	0.0003	34	0.0004
Sit holding infant	4.97	0.042[1]	2	0.18	8.54	0.015	3.44	0.1
Time in contact	4.58	0.05[1]	2.23	0.16	9.6	0.011	4.2	0.075
Distance	60.6	<0.0001	40.5	<0.0001	87.6	<0.0001	45.3	0.0001

[1] These p values were not statisically significant after Bonferroni correction.

average distance being 2.59 meters between Nsungwa whose infant Busobozi was the oldest (14 months) at the end of the study. This correlation remained when both the rank of the mother and the sex of the infant were added to the model (ANCOVA: $F_{1,8}=45.26$, $p=0.0001$).

The age of the infant also affected some aspects of the restrictive and protective behaviour of the mother. The act of a mother protecting her infant from other members of the group was observed a total of 61 times over the observation period. It was mainly observed with younger infants: 71% or 44 times of these were when the infant was four months old or younger with the remaining 29% or 17 times were with infants from five to ten months old. Mothers were not observed restricting other individuals from holding their infants when the latter were older than ten months. Nevertheless, the frequency of protecting the infant did not deviate with the age of the infant statistically significantly when tested separately from other parameters (regression analysis: $F_{1,14}=1.35$; $p=0.26$), but older infants were protected less when the age of the mother was included (GLM: $F_{1,10}=9.39$; $p=0.028$), but not when Kagezi (GZ), who protected her infant several times more than the average was left out ($F_{1,9}=0.93$; $p=0.36$). There was a trend of protecting decreasing with the age of the infant when the rank of the mother and the sex of the infant were added to the model (ANCOVA: $F_{1,8}=5.19$; $p=0.052$).

Mothers restricted their infants from suckling 24 times during the observation time, 14 times when the infants were between six to eight months old (Figure 3.4). The time spent on restrict-

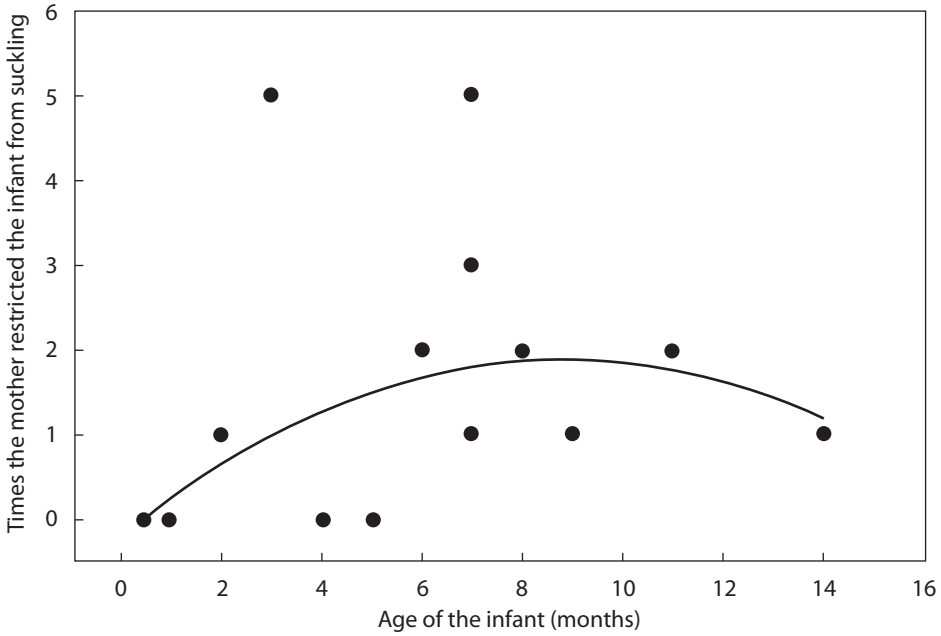

Figure 3.4. Mothers restricted their 6 to 8 month-old infants from suckling most.

ing the infant from suckling increased with the age of the infant (regression analysis: $F_{1,14}=54{,}2$; $p<0.0001$), regardless of the social rank of the mother (ANCOVA: $F_{1,10}=55.9$, $p<0.0001$), her parity ($F_{1,11}=51.9$, $p<0.0001$), her age (GLM: $F_{1,10}=33.7$, $p=0.0002$), all of them combined (ANCOVA: $F_{1,7}=24.5$, $p=0.002$) or the sex of the infant ($F_{1,13}=31.9$, $p=0.0001$).

The restriction from leaving (N=40) did not depend on infant age (regression analysis: $F_{1,14}=0.11$, $p=0.75$), but the older the infants were, the less they were restricted from contact with the mother (N=35; $F_{1,14}=5.12$; $p=0.036$). This association remains when the sex of the infant is included in the model (ANCOVA: $F_{1,13}=5.15$, $p=0.036$), but disappears when the social rank of the mother is added ($F_{1,10}=2.78$, $p=0.12$). Nonetheless, one female, Mwirima from Butanzi 1 group, restricted her infant 11 times when he was less than a month old, while the overall average was 2.06 times. If she was excluded from the analysis, the results were not statistically significant ($p>0.1$).

3.7. The effect of infant sex on maternal care

How much the mother held her infant while she was sitting depended more on the age of her infant than on its sex, possibly because female infants were younger during the study (ANCOVA: $F_{1,13}=1.25$, $p=0.28$; Table 3.3). The time spent on grooming the infant did not depend on infant sex either ($F_{1,13}=3.42$, $p=0.09$) nor did the average distance between the mother and her infant ($F_{1,13}=0{,}21$, $p=0.65$). However, females were carried significantly more when the age of the infant was considered in the model (Table 3.4), but not when the rank of the mother was included ($F_{1,8}=4.38$, $p=0.07$).

There was no difference between male and female infants in how many times they were protected from other group members tested separately (GLM: $F_{1,14}=0.05$, $p=0.82$) or regarding

Table 3.4. Infant sex influenced how much it was carried (ANCOVA).

Effect	df	SS	F	p
Age of the infant	1	8363	54.2	<0.0001
Sex of the infant	1	1223	7.93	0.015
Error	13	2005		

infant age (ANCOVA: $F_{1,13}=1.23$, $p=0.28$). There was no statistically significant difference between sexes in the frequency of the mothers' physical contact restrictions, when the ages of the infants were used as a covariate ($F_{1,13}=1.02$, $p=0.33$). Only males were restricted from suckling during our study (N=24).

3.8. The influence of infant's parameters on the mother's vocalizations

The older the infant the less its mother grunted (GLZ: $\chi^2=11.1$, df=1, $p=0.0008$) and vocalized overall ($\chi^2=8.29$, df=1, $p=0.004$), regardless of the age of the mother (grunting: $\chi^2=6.49$, df=1, $p=0.011$; overall vocalizations: $\chi^2=4.48$, df=1, $p=0.034$). Grunting was the most common vocalization (mean: 3.46%; mean time spent on staccato barking was 0.22% and alarming 0.18%). On the other hand, the time spent on staccato barking ($\chi^2=0.01$, df=1, $p=0.9$) or alarming ($\chi^2=0.92$, df=1, $p=0.34$) by the mother did not depend on infant age. When the social rank of the mother was included in the model in addition to her infant's age, the results were not statistically significant (ANCOVA, grunts: $F_{1,9}=0.84$, $p=0.38$, and overall vocalizations: $F_{1,9}=0.76$, $p=0.41$). However, when parity was included in the model, the older the infants were, the more their mothers alarmed ($F_{1,11}=6.39$, $p=0.028$).

Infant's sex had no noteworthy influence on its mother's vocalizations if all females were included in the analysis. When the female who grunted most often (Muhimbo with her second infant Kaheeru) was excluded, mothers with female infants tended to grunt (GLZ: $\chi^2=12.5$, df=1, $p=0.0004$) and vocalize more overall ($\chi^2=12$, df=1, $p=0.0005$) than mothers of males. This correlation remained regardless of the age of the infant for both ($\chi^2=7.03$, df=1, $p=0.008$ and $\chi^2=8.03$, df=1, $p=0.005$ respectively).

3.9. Comparison between mothers and females without infants

Females were divided into mothers and females without infants although eight mothers were pregnant some of the study period, because they did not differ from non-pregnant non-mothers statistically significantly (Table 3.5).

There were small differences in the percentage of time spent on sitting and feeding between females with infants and females without infants (Figure 3.5). Of the overall time followed, mothers were sitting on average 87.5% and females without infants 91% (ANOVA: $F_{1,36}=2.4$,

p=0.13). They spent 45.8% and 49% on feeding respectively, so there were no differences between the two groups in these behaviours ($F_{1,36}$=0.19, p=0.67). The percentage of time spent on standing was similar as well: 2.7% for mothers and 2.1% for females without infants ($F_{1,36}$=1.4, p=0.24). Time spent on carrying someone's infant while moving or holding one

Table 3.5. The effect of being pregnant or not on the main daily activities of females.

	Effect: pregnant or not pregnant	
Behaviour	$F_{1,20}$	p
Sit	2.05	0.17
Feed	0.003	0.96
Move	2.65	0.12
Stand	2.83	0.11
Alarm	1.82	0.19
Grunts	0.44	0.51
Staccato bark	0.047	0.83
Sit with infant	0.23	0.63
Groom by someone	3.21	0.088
Groom	0.096	0.76
Groom herself	0.006	0.94
Groom an infant	0.56	0.46

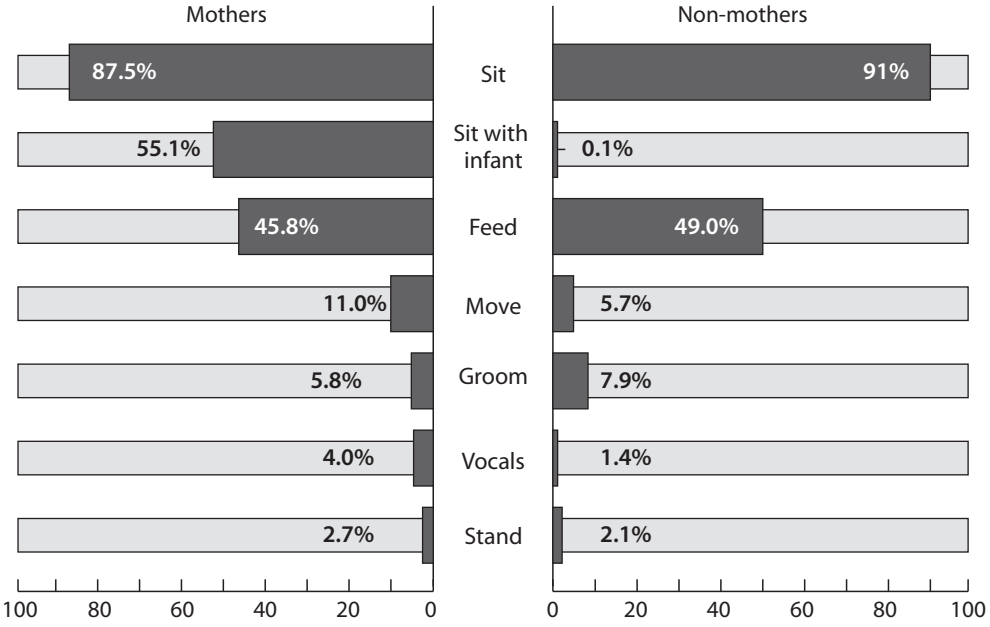

Figure 3.5. The difference between mothers (left) and females without infants (right) in their daily budget.

while the female was standing was 0% of time recorded for females without infants, but 6.5% ($F_{1,36}=24.3$, $p<0.001$) and 2.9% ($F_{1,36}=4.19$, $p=0.065$) for mothers. However, females who did not have infants at the time of the study, held infants while they were sitting, but only 0.08% of the time and most of these females did not hold infants at all (19 from 22). Mothers, on the other hand, sat with infants on average 55.1% of the recorded period ($F_{1,36}=85.7$, $p<0.001$).

Mothers moved almost twice as much as other females (11% for mothers, 5.7% for females without infants; $F_{1,36}=5$, $p=0.032$), but vocalized similarly to females without infants: 0.2% of time was spent alarming ($F_{1,36}=3.28$, $p=0.079$), 3.5% on grunting ($F_{1,36}=2.3$, $p=0.14$) and 0.3% staccato barking ($F_{1,36}=1.88$, $p=0.18$), while females without infants' figures were 0.04%, 1.2% and 0.2%, respectively.

Other group members groomed mothers (7.5% of time followed) as other females (5.6% of time followed; $F_{1,36}=0.15$, $p=0.7$). Mothers spent a comparable amount of time with other females on grooming overall (4.6% and 6.3% of the daily budget, respectively; $F_{1,36}=0.34$, $p=0.593$) and also themselves (0.4% of daily budget for mothers, 1.4% for other females; $F_{1,36}=2.64$, $p=0.11$). Mothers spent more time grooming infants than other females did (0.8% and 0.2% of daily budgets; $F_{1,36}=5.34$, $p=0.027$) as could be expected.

4. Discussion

4.1. Correlations between parameters

The time spent on grooming correlated negatively with the time spent on carrying the infant and alarming positively with the time spent on standing with the infant. The first is likely because grooming and carrying are mutually exclusive behaviours, although there are other activities that cannot be performed at the same time, for example, sitting and moving, but these did not render significant. Alarming can be positively correlated with standing, because when the animals are disturbed enough to alarm, they are likely to stand up in distress to be ready to escape. However, since standing does not always mean the mangabey is alarming, both behaviours were included separately in the analyses. We did not find the time spent on any of the other behaviours statistically significantly dependent on any other activity likely because most of them have multiple trade-offs in the mother's daily budget.

4.2. Does the age of the mother influence maternal care?

Older females have more experience in behaviour necessary for their own survival (Nguyen *et al*, 2012; Charpentier and Drea, 2013). For example, it has been found that raising an infant can reduce the mother's capability to feed and avoid predators (Altmann and Samuels, 1992), so more experienced mothers might feed more efficiently. Thus, older mothers may have more time to engage in less vital forms of maternal care, like grooming, that aid with hygiene and social bonding with the infant, rather than strict survival. We found in the study that older females groomed their infants more than younger ones, regardless of infant age. Even so, when parity was added to the model, grooming did not emerge as statistically relevant, which can be a result of our small sample, because adding factors to a model with a small amount of data can hide the effect of the tested factor, but does not mean that the effect does not exist. Additionally, the hypothesis of older mothers possibly having more time for less consequential activities is further supported by our finding that other forms of maternal care necessary for successful raising of an infant did not depend on the age of the mother. This included carrying the infant while changing locations, holding it while standing or sitting, and restricting it from leaving. Furthermore, the average distance between the mother and her infant did not depend on her age. This differs from our original hypothesis stated in the introduction, but it is likely because most of the previous information comes from more terrestrial species,

for example, baboons (Nguyen *et al*, 2012). Staying in contact with the infant is especially important for arboreal monkeys when the infant is very young and does not have the necessary strength and balance to hold on to branches when they move or leap from tree to tree (see the case of Muhimbo's infant, Kiswasa below), which is a common way of travel for mangabeys (Stern and Goldstone, 2005). Also, Altmann and Samuels (1992) calculated for yellow baboons (*Papio cynocephalus*) that during nutritional dependence of the infant, it is more energetically efficient for the mother to carry rather than let the infant move on its own. In contrast, Hoffman *et al* (2010) found that in rhesus macaques the time spent in contact with infants increased with female age, but it may not be strictly comparable since macaques are much more terrestrial than mangabeys. However, it has been observed for baboon mothers that the proportion of time spent on carrying their infants during rapid travel does not change with infant age as quickly as the overall time spent carrying (Altmann and Samuels, 1992), which can be compared to carrying infants from tree to tree, because in both scenarios the infant would be otherwise left behind due to its inability to keep up. In addition, grey-cheeked mangabeys in Kibale have the most injuries compared to other sympatric arboreal monkeys (red colobus, *Piliocolobus tephrosceles*, black-and-white colobus, *Colobus guereza*, and red-tailed monkey, *Cercopithecus ascanius*), inflicted most often by intra-species aggression, falling and possibly predation (Arlet *et al*, 2009). Mothers can protect their infants from all of these best by carrying and staying in contact with them.

Although, the time spent on other forms of maternal care that concern how much the mother is in contact with her infant were mostly not determined by her age, the frequency of a mother protecting her infant was. To specify, older mothers protected their infants from other group members more often irrespective of infant age. Our finding may partly explain the result of Arlet and colleagues (2014) that infants of older grey-cheeked mangabey females had higher survival than infants of younger mothers. Also, a long-term study of lemurs found, in concurrence with our results, that the strongest effect of maternal age in protective behaviours is from other group members. Charpentier and Drea (2013) established that older mothers protected their infants more efficiently, especially from bite wounds from conspecifics.

4.3. Do primiparous grey-cheeked mangabeys care less for their infants than multiparous?

In concordance with studies by Bales *et al* (2002) and Charpentier and Drea (2013), but contrary to most other studies, we did not observe significant differences between primi- and multiparous mothers in their maternal behaviour. This might be because of small sample size or because these monkeys live in social groups where they can obtain maternal experience from how their mothers raised them. It has been shown that in great apes, good maternal skills are learnt best from one's own mother and by observing correct maternal behaviour in a social group (Abello and Colell, 2006). In addition, females can learn by observing their mothers care of their siblings, other mothers care of their infants as well as from allomothering before giving birth themselves (Bales *et al,* 2002). More and long-term research is needed to answer this question in grey-cheeked mangabeys.

It has been observed that primiparous mothers are more likely to mishandle and even neglect their infants (Maestripieri, 2011 and references within). The only case of neglect in our study was a first-time mother, who often did not carry her infant when she was moving from one tree to another. She changed her behaviour with her second infant. Therefore, it may have been the lack of experience that caused the accident. Furthermore, primiparous mothers abandon their infants more often or may handle them incompetently, but the chances of this reduce with each new infant (Maestripieri and Carroll, 1998a,b; Schino and Troisi, 2005). However, no abandonment or mishandling of the infants was observed during our study period.

Predation, disease, accidental falls and infanticide are the main reasons of infant mortality among nonhuman primates, with mortality rates of wild populations higher than those in captivity (McFarland, 1988; Morland, 1990). The death of one infant was witnessed because of falling, but no infants went missing, were killed by predators or by infanticidal group members during the study. The incident happened at 14:33:00 on August 20th 2011 in Butanzi 1 during a fight between males. Several females of the group were in oestrous and males that guard these females chase and attack other males (Arlet *et al*, 2009), so there had been bouts of fighting and chasing every day during that week of our observation. Muhimbo, a primiparous mother, left her seven-month-old infant Kiswasa behind on a tree when she moved away. The males started fighting on that tree, shaking the branches and the infant, being too young to be able to hold on, fell and died.

4.4. Are dominant females better mothers?

High-ranking females had twice as many infants as low-ranking females in this study, which is probably because dominant females have better access to resources (Henzi and Barret, 2002; Aspden, 2005; Maestripieri, 2007) and are therefore in a better condition to conceive and give birth. For example, it has been shown that the mother's weight is an important determinant of infant growth and intra-specific variation of infant weight (Bowman and Lee, 1995; Ross and MacLarnon, 1995; Lee, 1999; Altmann and Alberts, 2005). It has been observed that high-ranking females of grey-cheeked mangabeys have better access to certain food objects (Chancellor and Isbell, 2009). Furthermore, the constraints of consuming low quality food have been shown to cause energetic constraints on Goeldi's monkey (*Callimico goeldii*) females' reproduction (Porter and Garber, 2004 in Ross *et al,* 2010). In addition, offspring of high-ranking savannah baboon mothers have been observed to have higher growth rates and younger age at first reproduction (Altmann and Alberts, 2005). Therefore, similarly to other primates, dominant mangabey females are able have more infants than subordinate females.

There was no difference between high- and low-ranking females in the time they spent grooming their infants. Although, dominant females usually groom other individuals less and are groomed more (Cheney, 1990; Gumert, 2007), there may not be a difference in how long they groom their own infants compared to low-ranking females in grey-cheeked mangabeys. However, we received evidence that dominant mothers sit holding their infants and spend more time in contact with them than subordinate females. This may again be because they have better access to resources and can sit feeding with the infant for longer bouts and additionally, resulting from this, have more time to rest and stay in contact with their infants. Yet, there was no difference between social ranks in the average distance between mothers and their young or carrying infants. This can be due to the small sample size, but can still show the importance of carrying, especially in an arboreal species. For example, Ross *et al* (2010) observed that mothers of Goeldi's monkey transport infants for longer than closely related common marmosets and their infants grow faster, concluding that Goeldi's monkey infants can devote their energy to growth instead of early independence. So, in addition to carrying keeping the infant from falling, it also helps the infant to gain weight faster.

Low-ranking baboon and macaque mothers have been found to be more protective and restrictive of their offspring, possibly due to greater risk of social aggression (White and Hinde, 1975;

Altmann, 1980; Nguyen *et al,* 2012). However, the mother's social rank did not affect the frequency of restricting the infant from suckling, contact, leaving or from other group members handling it in our study. This can be explained with these behaviours being more dependent on the infant's age in this sample as they are connected with weaning and the infant maturing (discussed below). So, although dominant mangabey females have more infants, we do not have definitive evidence for if they actually are better mothers yet.

4.5. How do vocalizations vary between different mothers?

Our study confirmed that grunting (social, contact call) is the most common vocalization among grey-cheeked mangabeys (Chalmers, 1968). The older the infant, the less its mother grunted, but alarming did not differ. Yet, alarming increased with infant age, but the difference in grunting was not significant when her parity was considered, which can be due to the small sample. However, there was no significant difference in staccato barking either way. There are several reasons a grey-cheeked mangabey might grunt, one of which is in response to a sudden movement, for example when another monkey approaches, or to a disturbance, like a sudden noise. Also, it correlates with the reduction of aggressive behaviour towards the grunter and may even play an integral part in keeping peace within a group (Chalmers, 1968). Therefore, it is likely that the mother grunts more when the infant is younger, because it is more vulnerable and may be more easily hurt when the mother is attacked. Also, since female monkeys are the more attracted to the infant the younger it is (Silk *et al,* 2003b), it might be necessary for the mother to grunt frequently to ensure the infant's safety as it is approached more often. Nevertheless, when maternal rank was considered, there was no significant difference in the time spent on grunting as the infant got older. However, mothers with a lower dominance status grunted more, regardless of the age of the infant. These females may receive more antagonistic behaviour from other group members, which suggests further that grunting is necessary to sustain non-violent conduct towards the mother and therefore to keep the infant safe. In addition, mothers with daughters grunted more, possibly because daughters remain in the natal group and therefore behaviour connected with hierarchy is directed towards them, so more grunting may also serve as a precautionary measure.

All females spent a comparable amount of time on staccato barking and most on alarming as well. The only exception was that the older the infant, the more the mother spent on alarming, when the age and parity of the mother were included in the model, but this can again be due

to the small sample, because adding factors to be model can render the tested factor statistically significant by chance. However, the staccato barking did not depend on either factor of the mother. The similarity of time spent on alarming and staccato barking among different mothers with infants of different ages and of both sexes and mothers and other females may be because of the functions of these vocalizations. Mangabeys, like other monkeys, alarm when there is danger around to warn the group, for example from an eagle (Arlet and Isbell, 2009) or chimpanzees (personal observation). Staccato barking is used both for alarming and making one's position known to others (Brown, 1989). Therefore, these sounds are communicated for the wellbeing of all the members of the group including infants of all ages, so mothers should vocalize for alarming purposes equally. Also, a female needs to staccato bark as well to let the group know of her position to avoid being left behind whether or not she has an infant and regardless of its age, so the group can stay intact.

4.6. Does maternal care change with infant age?

The age of the infant was one of the most important factors influencing maternal care. Younger infants were held more by their mothers while they moved and sat. This is correlated with the infant's ability to hold on to the surface they are on. Infants need someone to carry them when they are younger and consequently unable to jump the gaps between branches. However, in our study, there was only a non-significant trend in the amount of time spent standing holding the infant decreasing with its age. This may be due to a small sample size as it has been observed in several species that mothers spend less time holding them as they get older: macaques (Schino *et al,* 1993; Maestripieri, 2011), baboons (Nash, 1978; Altmann and Samuels, 1992) and lemurs (Volampeno *et al*, 2011).

Since younger infants were handled for longer periods of time, the average distance increased with infant age regardless of the social rank of the mother or the sex of the infant. In several species of primates, the time spent away from the mother and the distance to her have been shown to increase as the infant ages (Altmann and Samuels, 1992; Onishi and Nakamichi, 2011 and references within). Older infants begin to explore the surrounding area using the mother as a safe base when tired, hungry or in distress (Hinde and Atkinson, 1970), therefore breaking contact with the mother and venturing longer periods of time to further distances, while the mother is increasingly encouraging this behaviour (Maestripieri, 2011). This is probably because the infant is less vulnerable to predation and intra-group aggression as its locomotive

abilities and capability to recognise threats improve (Seyfarth and Cheney, 1986; Onishi and Nakamichi, 2011).

Grey-cheeked mangabey mothers restricted their infants from suckling most when they were 6–8 months old, the frequency of restraint increased until then and even showed some decreasing trend after. This inverted U-shaped curve in restricting from suckling can be because infants are gradually less dependent on the mother's milk as they grow and therefore try to suckle less frequently and, in addition, the mother starts the process of weaning. Before the infant is six months old, restricting it from suckling too often may result in the infant's death due to malnutrition. Infants older than 8 months are almost weaned and do not try to suckle as frequently, so the mother needs to restrict them less. However, the overall statistics showed restricting from suckling increasing with infant age regardless of the parameters of the mother. We did not observe a significant correlation between infant age and restricting it from leaving, although a significant correlation has been found in other studies on Old World primates (Schino *et al,* 1993 and references within). This may be because we witnessed restriction from leaving only 40 times over the study period and we had infant ages spanning from birth to 14 months. We also found evidence that mothers restricted their infants from contact less when they were older, which can be because of similar reasons to restricting from suckling, but we are cautious in drawing conclusions as one female deviated drastically from the average in our small sample.

Mothers of younger infants (less than 5 months), restricted another individual from handling her infant more than 70% of the times, but it was not statistically significant. Nevertheless, it has been observed in other species and may be because younger infants are more fragile, easier to hurt due to mistreatment or suffer from malnutrition and dehydration, and more prone to predation (Schradin and Anzenberger, 2003; Förster and Cords, 2005). However, during the first months of infant life, other group members are very interested in handling infants (Hrdy, 1999; Silk *et al*, 2003b). Later, the mother may favour others handling her infant as it becomes less dependent on her. This will leave more time for her to feed and reduce the energetic cost of moving (Schradin and Anzenberger, 2003; Förster and Cords, 2005).

We found evidence that, contrary to most other forms of maternal care, the older the infant, the more its mother groomed it, which can be explained in two ways. Firstly, grooming is an important behaviour for reinforcing social relationships (Dunbar and Dunbar, 1988; Aureli *et al*, 1999; Henzi and Barrett, 2002; Aspden, 2005), which might be the reason older infants

are groomed more. As they start to mature, they are more part of the group as individuals. This would be further supported if female infants were groomed more as they remain in their natal group whereas the males disperse. Accordingly, the mothers should invest more time in grooming female infants to reinforce their relationship. However, we did not find a significant difference between the time mothers spent grooming female and male infants. Secondly, infants are infected with more parasites as they mature and start to interact with other members of the group, so they need more cleaning (Arlet, personal comment). By contrast, in snub-nosed monkeys (*Rhinopithecus roxellana*) grooming, like carrying, has been shown to decrease with infant age (Luo *et al*, 2011).

4.7. Does maternal care depend on the infant's sex?

The sex of the infants did not affect maternal care in the aspects of grooming or holding, nor did it influence the overall time spent in contact with the infant among grey-cheeked mangabeys. Infant sex was not found to affect the time spent in contact in rhesus macaques (Hoffman *et al*, 2010) or maternal care in general in golden tamarins either (*Leontopithecus rosalia,* Bales *et al,* 2002). However, we did find evidence that female infants were carried more than males, but not when the rank of the mother was included in the model. A similar difference in carrying has been shown among baboons, yet, only among high-ranking mothers, but not when rank was left out of the model (Altmann and Samuels, 1992).

Our data also indicated that infant sex does not influence how much a mother restricts or protects her infant. This is contrary to most other Old World monkeys where all mothers usually restrain their daughters, while restricting their sons more from establishing contact with them (Mitchell, 1968; Itoigawa, 1973). In addition, newborn baboon males were recently found to also initiate breaking contact with the mother more frequently than females and mothers are more tolerant of them doing so (Nguyen *et al*, 2012). It has been observed that in species where the females take part in physical aggression in addition to males, they play as much or even exceed males in time spent playing (Starin, 1990) and therefore, mothers must restrain both sexes equally for it to be possible. However, males are usually the ones that fight as adults in grey-cheeked mangabeys (Olupot and Waser 2001, Arlet *et al,* 2007), so it is possible that these results may be due to a small sample. Because of this, long-term research and a larger sample are needed to make definite conclusions and to further investigate the influence of infant sex on maternal care.

4.8. How does the daily budget differ between mothers and females without infants?

Mothers spend extra energy due to lactation. In some species of primates, it has been observed that lactating mothers spend a larger percentage of their day feeding than other females (baboons, *Papio* – Altmann, 1980; Dunbar and Dunbar, 1988; common marmosets – reviewed in Nievergelt and Martin, 1999), but mothers, who only carry infants, feed less (reviewed in Nievergelt and Martin, 1999). Furthermore, carriers feed and forage less compared to other group members (non-mothers and males who do not carry infants) as well (Goldizen, 1987; Price, 1991), but the time spent of feeding has also been found to increase with infant age (Altmann, 1980; Dunbar and Dunbar, 1988). However, in our study, there was no significant difference in the time mothers spent feeding compared to non-mothers, which may be the result of food availability in the area (all females feed similarly to meet basic nutritional needs in lack of food or eat until full when food is abundant) or a small sample size. Similarly, van Noordwijk *et al* (2013) observed that orangutans, who likewise reproduce aseasonally, also do not have a peak in feeding as they are lactating. Moreover, in this research, we did not measure the amount of food eaten, only the time spent on feeding. Mothers need more energy than other adult females, so there might still be a difference in the energy consumed despite the similarities in time spent on feeding. This question should be studied long-term in grey-cheeked mangabeys in the future.

Mothers spent a significantly larger portion of their daily budget on moving than other females. This could be linked to similar amounts of time spent feeding – mothers could be searching for better quality food. Some mothers in our study were still lactating, others had older infants, although it has been observed that mothers who have weaned their infants, but still carry them, move less (reviewed in Nievergelt and Martin, 1999). This may be due to mothers who do not carry their offspring at all times anymore, following the latter in the canopy to ensure their safety.

Although allomothering or handling someone else's infant is common among primates and recorded for several species (Silk, 1999; Maestripieri, 2001; Silk *et al,* 2003b; Förster and Cords, 2005; Maestripieri, 2007), we did not observe any females carrying or holding other female's infants while standing. Females without infants, except three, did not handle other's infants as they were sitting either, so the time spent on allomothering was less than 0.1% of the overall time recorded. Mothers on the other hand, spent more than half of the observation period sitting with their infants and were observed on occasion handling another's infant in addition to their own.

Of the three females allomothering, one was pregnant herself, which shows that, as in most primates (Silk *et al*, 2003b), mangabey females, who do not have their own offspring to care for, are still attracted to infants. Furthermore, it suggests that mangabeys allomother due to the female's attraction to infants according to the responsiveness hypothesis – the more responsive a female is, the higher chance that she reacts to her own infant's needs and she is the most responsive when it is absolutely necessary (Silk, 1999; Maestripieri, 2001; Silk *et al,* 2003b). On the other hand, one of the three non-mother handlers was five years old, about two years before sexual maturation, so she might be an example of how natural selection might have favoured attraction to infants to practice mothering skills. It has been shown that females who handle and are generally more interested in infants before adulthood rear their first-born more successfully (Fairbanks, 1990). Further long-term research is needed to fully understand allomothering, its extent and importance among mangabeys.

Grooming has important functions in addition to hygiene – establishing, maintaining and improving social relationships, reducing tension and it can be a service in return for another or a way to get access to infants (Dunbar and Dunbar, 1988; Aureli *et al,* 1999; Henzi and Barrett, 2002; Aspden, 2005). In the aspect of building and preserving social relationships and hygiene, there might not be a significant difference between mothers and other females, since all group members need to groom others for social reasons. Rather, there is usually a variation in the time spent on grooming between dominant and subordinate females, the latter grooming more and the first less (Cheney, 1990; Gumert, 2007). On the other hand, there should be an asymmetry in the time mothers are groomed compared to other females, since grooming is used to get hold of the infant and, in this case, the mother rarely reciprocates by grooming (Henzi and Barrett, 2002; Aspden, 2005). Nevertheless, we did not find a statistically significant difference in the time mothers and non-mothers were groomed nor in the time they spent grooming others or themselves. This could be because of the lack of allomothering observed during the study period; since we did not see many occasions of infant handling, we did not witness the grooming preceding it.

Summary

Like all mammals, infants of primates need maternal care to survive, but differences between individuals can affect the extent and success of this care. As many species of primates are threatened or endangered, it is necessary to know the factors influencing the mother–infant relationship. However, most information available is from visible, mostly terrestrial species. We observed maternal behaviour and studied factors influencing maternal care in grey-cheeked mangabeys in Kibale National Park in Uganda, an arboreal species closely related to both well-studied baboons and many threatened and even endangered mangabey species.

The main findings:

1) The results that older mothers protected infants more than younger mothers, and spent more time on grooming, support the hypothesis based on previous studies. However, carrying, holding and restricting the infant did not depend on the age of the mother, which was associated with the arboreal habitat of mangabeys.
2) Even though most studies have found differences in maternal care due to the parity of the mother, no significant differences were found between mothers with their first infant and mothers who had had offspring before, contrary to the initial hypothesis. Primiparous and multiparous females took similar care of their infants, although one incident of neglect resulting in the death of an infant was recorded for a first-time mother.
3) Similarly to previous studies, dominant females had twice as many infants as subordinate and stayed in contact with their infants for a longer time than low-ranking females.
4) As expected, subordinate females and also mothers with younger infants grunted more.
5) Infant age influenced maternal care the most: younger infants received more care.
6) No evidence was found that maternal care depends on infant sex, except for carrying and grunting.
7) Females with infants moved almost twice as much as females without infants, but did not differ in other main behaviours of the daily budget.

Further and long-term research is needed to determine more thoroughly which factors influence the maternal behaviour in grey-cheeked mangabeys.

Kokkuvõte

Sarnaselt teiste imetajatega vajavad primaatide järglased ellujäämiseks emahoolt, kuid isenditevahelised erinevused võivad selle ulatust ja edukust mõjutada. Kuna paljud primaadid on ohustatud või hävimisohus, on oluline teada, millised faktorid mõjutavad neil liikidel ema ja järglase vahelist suhet. Enamik uuringuid on läbi viidud nende liikide kohta, kes on kergesti vaadeldavad ja peamiselt maapealse eluviisiga. Meie vaatlesime emade käitumist ja uurisime tegureid, mis mõjutavad emahoolt mantelmangabeidel, kes on lähedalt suguluses nii põhjalikult uuritud, kuid maapealse eluviisiga paavianitega kui ka mitme ohustatud ja hävimisohus mangabeiliigiga. Välitööd viidi läbi Kibale Rahvuspargis, Ugandas.

Vaatluse põhitulemused:

1) Leidsime toetust varasema kirjanduse põhjal tehtud hüpoteesile, et vanemad emad kaitsevad oma järglasi teiste grupiliikmete eest rohkem ja veedavad enam aega järglasi sugedes kui nooremad emad. Kandmine, järglaste hoidmine ja nende keelamine ei sõltunud siiski ema vanusest, mida saab põhjendada mantelmangabeide elupaigaga puude võrades.
2) Kuigi enamikes uuringutes on leitud, et ema paarsus mõjutab emahoolt, ei leidnud me, vastupidiselt hüpoteesile, statistiliselt olulisi erinevusi esimest poega kasvatavate emade ja teist või enamat poega kasvatavate emade vahel. Kuigi esmasünnitajad hoolitsesid üldiselt oma järglaste eest varem poeginud emadega sarnaselt, toimus vaatluse ajal üks hooletusest põhjustatud ja poja surmaga lõppenud õnnetus just esmasünnitajaga.
3) Varem kirjanduses avaldatuga sarnaselt poegisid ka meie uuringus dominantsed emased umbes kaks korda enam ja olid nendega pikema osa päevast kontaktis kui madala staatusega emased.
4) Vastavalt oodatule häälitsesid röhkides rohkem madala sotsiaalse staatusega ja ka nooremate järglastega emad.
5) Järglase vanus mõjutas emahoolt kõige rohkem: mida noorem oli imik, seda rohkem emahoolt ta sai.
6) Me ei leidnud tõendeid, et järglase sugu mõjutaks emahoolt peale kandmise ja röhkimise.
7) Järglastega emased liikusid peaaegu kaks korda rohkem kui ilma järglasteta emased, kuid teised uurimise all olnud tegevused, mis võtavad põhiosa nende päeva ajakavast, ei erinenud.

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References

Abello, M. T. and Colell, M. (2006). Analysis of factors that affect maternal behaviour and breeding success in great apes in captivity. *Int. Zoo Yb.* 40: 323–340.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour.* 49: 227–267.

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

Altmann, J. and Samuels, A. (1992). Costs of maternal care: infant-carrying in baboons. *Behav. Ecol. Sociobiol.* 29: 391–398.

Altmann, J., Alberts, S., Hainesi, S., Dubach, J., Muruthi, P., Coote, T., Gefen, E., Cheesman, D. J., Mututua, R. S., Saiyalels, S. N., Wayne, R., Lacy, R. and Bruford, M. W. (1996). Behavior predicts genetic structure in a wild primate group. *Proc. Natl. Acad. Sci.* 93: 5797–5801.

Altmann, J. and Alberts, S. (2005). Growth rates in a wild primate population: ecological influences and maternal effects. *Behav. Ecol. Sociobiol.* 57: 490–501.

Arlet, M. E., Molleman, F. and Chapman, C. A. (2007). Indications for female mate choice in grey-cheeked mangabeys *Lophocebus albigena johnstoni* in Kibale National Park, Uganda. *Acta. Ethol.* 10: 89–95.

Arlet, M. E., Molleman, F. and Chapman, C. A. (2008). Mating tactics in male grey-cheeked mangabeys (*Lophocebus albigena*). *Ethology*. 114: 851–862.

Arlet, M. E. and Isbell, L. A. (2009). Variation in behavioral and hormonal responses of adult male gray-cheeked mangabeys (*Lophocebus albigena*) to crowned eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behav. Ecol. Sociobiol.* 63: 491–499.

Arlet, M. E., Carey, J. R. and Molleman, F. (2009). Species, age and sex differences in type and frequencies of injuries and impairments among four arboreal primate species in Kibale National Park, Uganda. *Primates.* 50: 65–73.

Arlet, M. E., Isbell, L.A., Molleman, F., Kaasik, A., Chancellor, R.L., Chapman, C.A., Mänd, R. and Carey, J. R. (2014). Maternal investment and infant survival in gray-cheeked mangabeys (*Lophocebus albigena*). *Int. J. Prim.* 35: 476–490.

Aspden, R. E. (2005). Investing in infants: applying the biological market to the interest in other's offspring. *D. A. J.* 13.

Aureli, F., Preston, S. D., de Waal, F. B. M. (1999). Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): A pilot study. *J. Comp. Psychol*. 113: 59–65.

Bales, K., French, J. A. and Dietz, J. M. (2002). Explaining variation in maternal care in a cooperatively breeding mammal. *Anim. Behav.* 63: 453–461.

Beck, B. B. and Power, M. L. (1988): Correlates of sexual and maternal competence in captive gorillas. *Zoo Biol.* 7: 339–350.

Bentley-Condit, V. K., Moore, T. and Smith, E.D. (2001). Analysis of infant handling and the effects of female rank among Tana River adult female yellow baboons (*Papio cynocephalus cynocephalus*) using permutation/randomization tests. *Am. J. Primatol.* 55: 117–130.

Bercovitch, F. B. and Berard, J. D. (1993). Life history costs and consequences of rapid reproductive maturation in female rhesus macaques. *Behav. Ecol*. *Sociobiol.* 32: 103–109.

Borries, C., Gordon, A. D. and Koenig, A. (2013). Beware of primate life history data: a plea for data standards and a repository. PLoS ONE 8: e67200. doi:10.1371/journal.pone.0067200.

Bowman, J. and Lee, P.C. (1995). Growth and threshold weaning weights among captive rhesus macaques. *Am. J. Phys. Anthropol.* 96: 159–175.

Brown, C. H. (1989). The active space of blue monkey and grey-cheeked mangabey vocalizations. *Anim. Behav.* 37: 1023–1034.

Brown, G. R. and Dixson, A. F. (2000). The development of behavioural sex differences in infant rhesus macaques (*Macaca mulatta*). *Primates* 41: 63–77.

Brown, G. R. (2001). Sex-biased investment in nonhuman primates: can Trivers and Willard's theory be tested? *Anim. Behav.* 61: 683–694.

Burrell, A. S., Jolly, C. J., Tosi, A. J. and Disotell, T. R. (2009). Mitochondrial evidence for the hybrid origin of the kipunji, *Rungwecebus kipunji* (Primates: Papionini). *Mol. Phylogenet. Evol.* 51: 340–348.

Cameron, E. Z., Linklater, W. L., Stafford, K. J. and Minot, E. O. (2000). Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? *Behav. Ecol. Sociobiol.* 47: 243–249.

Chalmers, N. R. (1968). The visual and vocal communication of free living mangabeys in Uganda. *Folia Primat.* 9: 258–280.

Chancellor, R. L. and Isbell, L. A. (2009). Food site residence time and female competitive relationship in wild gray-cheeked mangabeys (*Lophocebus albigena*). *Behav. Ecol. Sociobiol.* 63: 1447–1458.

Chapman, C. A. and Lambert, J. E. (2000). Habitat alteration and the conservation of African primates: a case study of Kibale National Park, Uganda. *Am. J. Primatol.* 50: 169–186.

Charpentier, M. J. E. and Drea, C. M. (2013). Victims of infanticide and conspecific bite wounding in a female-dominant primate: a long-term study. PLoS ONE 8: e82830. doi:10.1371/journal.pone.0082830.

Cheney, D. L. (1990). How monkeys see the world: inside the mind of another species. University of Chicago Press, Chicago, pp 37–39.

Cords, M. and Chowdhury, S. (2010). Life History of *Cercopithecus mitis stuhlmanni* in the Kakamega Forest, Kenya. *Int. J. Prim.* 31: 433–455.

Deputte, B. L. (1991). Reproductive parameters of captive grey-cheeked mangabeys. *Folia Primatol.* 57: 57–69.

Dunbar, R. I. M. and Dunbar, P. (1988). Maternal time budgets of gelada baboons. *Anim. Behav.* 36: 970–980.

Fairbanks, L.A. (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Anim. Behav*. 40: 553–562.

Fedigan, L. M., Carnegie, S. D. and Jack, K. M. (2008). Predictors of reproductive success in female white-faced capuchins (*Cebus capucinus*). *Am. J. Phys. Anthropol.* 137: 82–90.

Frank, R. E. and Silk, J.B. (2009). Grooming exchange between mothers and non-mothers: the price of natal attraction in wild baboons. *Behaviour.* 146: 889–906.

Förster, S. and Cords, M. (2005). Socialization of infant blue monkeys (*Cercopithecus mitis stuhlmanni*): allomaternal interactions and sex differences. *Behaviour*. 142: 869–896.

Goldizen, A. (1987). Tamarins and marmosets: communal care of offspring. In: Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R., Struhsaker, T. (eds) Primate societies. University of Chicago Press, Chicago, pp 4–43.

Gumert, M. D. (2007). Grooming and infant handling interchange in *Macaca fascicularis*: the relationship between infant supply and grooming payment. *Int. J. Prim.* 28: 1059–1074.

Harris, E. E. and Disotell, T. R. (1998). Nuclear gene trees and the phylogenetic relationships of the mangabeys (Primates: *Papionini*). *Mol. Biol. Evol.* 15: 892–900.

Harvey, P. H. and Clutton-Brock, T. H. (1985). Life history variation in primates. *Evolution* 39: 559–581.

Henzi, S. P. and Barrett, L. (2002). Infants as a commodity in a baboon market. *Anim. Behav.* 63: 915–921.

Henzi, S. P. and Barrett, L. (2003). Evolutionary ecology, sexual conflict, and behavioral differentiation among baboon populations. *Evol. Anthropol.* 12: 217–230.

Hinde, R. A. and Atkinson, S. (1970). Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. *Anim. Behav.* 18: 169–176.

Hoffman, C. L., Higham, J. P., Mas-Rivera, A., Ayala, J. E. and Maestripieri, D. (2010). Terminal investment and senescence in rhesus macaques (*Macaca mulatta*) on Cayo Santiago. *Behav. Ecol*. 21: 972–978.

Hrdy, S. B. (1999). Mother Nature: a history of mothers, infants, and natural selection. Random House.

Itoigawa, N. (1973). Group organization of a natural troop of Japanese monkeys and mother infant interactions. *In*: Behavioral regulators of behavior in primates (ed: Carpenter, C. R.). Lewisburg, PA: Bucknell University Press, p. 229–243.

Johnson, S. E. (2003). Life history and the competitive environment: trajectories of growth, maturation, and reproductive output among chacma baboons. *Am. J. Phys. Anthropol.* 120: 83–98.

Lee, P. (1999). Comparative ecology of postnatal growth and weaning among haplorhine primates. In: Lee P (ed) Comparative primate socioecology. Cambridge University Press, Cambridge, pp 111–139.

Lindburg, D. G. and Fitch-Snyder, H. (1994). Use of behavior to evaluate reproductive problems in captive mammals. *Zoo Biol.* 13: 433–445.

Luo, F., Chen, J., Yu, P. and Bao, W. (2011). Infant-care behaviors exhibited toward 0–6 month-old infants of a provisioned group of Sichuan snub-nosed monkey in Shennongjia National Nature Reserve. *Acta Theriol. Sinica.* 31: 422–427.

Maestripieri, D. and Carroll KA. (1998a). Child abuse and neglect: usefulness of the animal data. *Psychol. Bull.* 123: 211–223.

Maestripieri, D. and Carroll, K.A. (1998b). Risk factors for infant abuse and neglect in group-living rhesus monkeys. *Psych. Sci.* 9: 143–145.

Maestripieri, D. (2001). Is there mother-infant bonding in primates? *Dev. Rev.* 21: 93–120.

Maestripieri, D. (2007). Macachiavellian intelligence. The University of Chicago Press, Chicago and London.

Maestripieri, D. (2011). Emotion, stress and maternal motivation in primates. *Am. J. Primatol*. 73: 516–529.

McFarland, S. M. (1988). Demography patterns and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. *Am. J. Primatol.* 15: 45–67.

Meder, A. (1990): Integration of hand-reared gorillas into breeding groups. *Zoo Biol.* 9: 157–164.

Mitchell, G. D. (1968). Attachment differences in male and female infant monkeys. *Child Dev.* 39: 611–620.

Morland, H. S. (1990). Parental behavior and infant development in ruffed lemurs (*Varecia variegata*) in a Northeast Madagascar rain forest. *Am. J. Primatol.* 20: 253–265.

Nash, L. T. (1978). The development of the mother-infant relationship in wild baboons (*Papio anubis*). *Anim. Behav.* 26: 746–759.

Nguyen, N., Gesquiere, L., Alberts, S. C. and Altmann J. (2012). Sex differences in the mother-neonate relationship in wild baboons: social, experimental and hormonal correlates. *Anim. Behav.* 83: 891–903.

Nievergelt, C. and Martin, R. (1999). Energy intake during reproduction in captive common marmosets (*Callithrix jacchus*). *Phys. Behav.* 65: 849–854.

van Noordwijk, M. A., Willems, E. P., Utami Atmoko, S. S., Kuzawa, C. W. and van Schaik, C. P. (2013). Multi-year lactation and its consequences in Bornean orangutans (*Pongo pygmaeus wurmbii*). *Behav. Ecol. Sociobiol.* 67: 805–814.

Olupot, W. and Waser, P. M. (2001). Correlates of intergroup transfer in male grey-cheeked mangabeys. *Int. J. Primatol.* 19: 169–187.

Onishi, K. and Nakamichi, M. (2011). Maternal infant monitoring in a group of free-ranging Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.* 32: 209–222.

Patterson, J. D. (2001). Primate behavior: an exercise workbook, 2nd ed. Prospect Heights, IL: Waveland Press.

Paul, A., Kuester, J. and Podzuweit, D. (1993). Reproductive senescence and terminal investment in female Barbary macaques (*Macaca sylvanus*) at Salem. *Int. J. Primatol.* 14: 105–124.

Pochron, S. T., Tucker, W. T. and Wright, P. C. (2004). Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986–2000 in Ranomafana National Park, Madagascar. *Am. J. Phys. Anthro.* 125: 61–72.

Porter, L. and Garber, P. (2004). Goeldi's monkeys: a primate paradox? *Evol. Anthropol.* 13: 104–115.

Price, E. (1991). Infant-carrying as a courtship strategy of breeding cotton-top tamarin males. *Anim. Behav.* 40: 784–786.

Robbins, A. M., Robbins, M. M., Gerald-Steklis, N. and Steklis H. D. (2006). Age-related patterns of reproductive success among female mountain gorillas. *Am. J. Phys. Anthropol.* 131: 511–521.

Ross, A. C., Porter, L. M., Power, M. L. and Sodaro, V. (2010). Maternal care and infant development in *Callimico goeldii* and *Callithrix jacchus*. *Primates.* 51: 315–325.

Ross, C. and MacLarnon, A. (1995). Ecological and social correlates of maternal expenditure on infant growth in haplorhine primates. In: Pryce, C. R., Martin, R. D. (eds) Motherhood in human and nonhuman primates. Karger, Basel, pp 37–46.

Schino, G., D'Amato, F. R., De Angelis, N. and Troisi, A. (1993). Development of mother-infant relationships in Japanese macaques (*Macaca fuscata*). *Boll. Zool.* 60: 301–306.

Schino, G. and Troisi, A. (2005). Neonatal abandonment in Japanese macaques. *Am. J. Phys. Anthropol.* 126: 447–452.

Schradin, C. and Anzenberger, G. (2003). Mothers, not fathers, determine the delayed onset of male carrying in Goeldi's monkey (*Callimico goeldii*). *J. Hum. Evol.* 45: 389–399.

Seyfarth, R. M. and Cheney, D. L. (1986). Vocal development in vervet monkeys. *Anim. Behav.* 34: 1640–1658.

Silk, J. B., Short, J., Roberts, J. and Kusnitz, J. (1993). Gestation length in rhesus macaques (*Macaca mulatta*). *Am. J. Primatol.* 14: 95–104.

Silk, J. B. (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Anim. Behav.* 57: 1021–1032.

Silk, J. B., Alberts, S. C. and Altmann, J. (2003a). Social bonds of female baboons enhance infant survival. *Science.* 302: 1231–1234.

Silk, J. B., Rendall, D., Cheney, D. L. and Seyfarth, R. M. (2003b). Natal attraction in adult female baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana. *Ethology.* 109: 627–644.

Sommer, V., Srivastava, A. and Borries, C. (1992). Cycles, sexuality, and conception in free-ranging langurs (*Presbytis entellus*). *Am. J. Primatol.* 28: 1–27.

Starin, E.D. (1990). Object manipulation by wild red colobus monkeys living in the Abuko Nature Reserve, The Gambia. *Primates.* 31: 385–391.

Stern, M. and Goldstone, R. (2005). Red colobus as prey: the leaping habits of five sympatric old world monkeys. *Folia Primatol.* 76: 100–112.

Strier, K. (2007). Primate behavioral ecology (3rd edition). Allyn & Bacon, pp 64, 71, 77.

Strum, S. C. and Western, J. D. (1982). Variation in fecundity with age and environment in olive baboons (*Papio anubis*). *Am. J. Primatol.* 3: 61–76.

Trivers, R. L. and Willard, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science.* 179: 90–92.

Volampeno, M. S. N., Masters, J. C. and Downs, C. T. (2011). Life history traits, maternal behavior and infant development of blue-eyed black lemurs (*Eulemur flavifrons*). *Am. J. Primatol.* 73: 474–484.

Wallis, S. J. (1983). Sexual behaviour and reproduction of *Cercocebus albigena johnstoni* in Kibale Forest, western Uganda. *Int. J. Primatol.* 4: 153–166.

Waser, P. M. (1974). Intergroup interaction in a forest monkey: the mangabey *Cercocebus albigena*. Dissertation, The Rockefeller University, New York, USA.

Waser, P. M. (1977). Feeding, ranging and group size in the mangabey, *Cercocebus albigena*. In Clutton-Brock TH (ed) Primate ecology, Academic Press, London, pp 183–222.

White, L. E. and Hinde, R. A. (1975). Some factors affecting mother-infant relations in rhesus monkeys. *Anim. Behav.* 23: 527–542.

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