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Maternal Care in Free-Ranging Arboreal Grey-Cheeked Mangabeys (*Lophocebus albigena johnstoni*) in Kibale National Park, Uganda

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Keywords
Maternal behaviour · Maternal experience · Parity · Infant sex · Infant age

Abstract

Maternal styles have been intensively studied in a variety of terrestrial species of primates, but far less in arboreal species. However, to have a balanced view of the evolution of maternal care, it is necessary to investigate this behaviour in the context of habitat. Here, we investigate whether the mother's parity, age and dominance rank, as well as the infant's age and sex, influence maternal care and mother-infant proximity in arboreal grey-cheeked mangabeys (*Lophocebus albigena*). We observed 13 mother-infant dyads in four free-ranging groups for 6 months. Our main finding is that maternal care is a dynamic process affected by a mix of mothers' and infants' characteristics. We found that first-time mothers spent more time watching their infants than multiparous mothers, who carried, groomed and protected their infants more often. We also found that low-ranking mothers prevented their infants from leaving them more often than did high-ranking mothers. Moreover, mothers adjusted their care as infants became older. They groomed and protected female infants more than male infants, behaviours common in female-bonded species. Our study shows the ever-changing dynamics of maternal care related to infant age and highlights the role of the mother's parity and rank in this process.

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Introduction

Primates have a relatively long infant developmental stage compared to other mammals of similar size [Strier, 2007] and therefore need more parental care than other mammals for individuals to become independent [Harvey and Clutton-Brock, 1985]. In most species of non-human primates, only the females take care of infants, with some exceptions, e.g., marmosets (*Callithrix* spp.) and tamarins (*Saguinus* spp.) where males help by carrying infants [Maestripieri, 2011].

Maternal style is the consistent application of particular forms of maternal care by individual females toward multiple infants over time [Berman, 1990]. Maternal styles are often categorized into three types: (1) rejecting mothers that frequently interrupt contact with their infants and stay away from them for a long time; (2) protective mothers that tend to maintain visual contact and spatial proximity with their infants, and (3) laissez-faire mothers that allow their infants to stay close by while also not keeping them from moving away [Hinde, 1974; Rosenblum and Youngstein, 1974; Altmann, 1980; Fairbanks, 1996; Bardi and Huffman, 2002].

The quality of maternal care is influenced by several factors, including the mother's experience in raising offspring, her age and her dominance rank. Experience appears to be a very important factor [Abello and Colell, 2006]. A comparative analysis found that in 15 of 21 studies of primates, infants of younger or primiparous (first-time) mothers had lower survival rates than those of older mothers [Pusey, 2012]. Primiparous mothers are more likely to mistreat or abandon their first infant, resulting in infant death [Schino and Troisi, 2005; Arlet et al., 2014]. For example, in a study of Japanese macaques (*Macaca fuscata*), 40% of infants born to primiparous mothers aged 4, 5 and 6 years or older were abandoned at birth [Schino and Troisi, 2005]. With subsequent births, maternal neglect declines and the quality of maternal care increases [Maestripieri and Carroll, 1998]. Lack of experience may also elevate stress for primiparous mothers, increasing the likelihood that offspring will not thrive emotionally and/or physically [Martin, 2013].

In an earlier study of grey-cheeked mangabeys (*Lophocebus albigena*), we found that infants of older mothers had higher survival rates than those born to younger, first-time mothers [Arlet et al., 2014]. We suggested that this could be related to the mother's age but also to experience. In other species, such as green monkeys (*Chlorocebus sabaeus*), infants of primiparous mothers with allomothering experience (taking care of others' infants), survived better than those of primiparous mothers without such experience [Fairbanks, 1990]. However, there may be some age-related influences on maternal care that are independent of experience. For example, young mothers are still growing [Bercovitch et al., 1998; Setchell et al., 2002] and may face a greater trade-off between foraging for food and taking care of the infant [Setchell et al., 2002]. Moreover, their smaller body size will make carrying their growing offspring more energetically costly [Altmann and Samuels, 1992]. Finally, the quality or quantity of milk they produce may be poorer than that of older (and typically multiparous) mothers, which could affect suckling frequencies [Hinde et al., 2009; Martin, 2013].

Social position may influence maternal behaviour as well by, for example, the extent of aggression directed toward the mother and her infant. In Japanese macaques, low-ranking mothers receive twice as much aggression as high-ranking mothers and are therefore more prone to abandoning their infants, which may be linked to female

stress [Schino and Troisi, 2005]. Infants of lower-ranking mothers are also likely to experience aggression more often than infants of higher-ranking mothers, which may translate into more protective mothering [Smuts and Smuts, 1993].

The mother's dominance rank may also interact with characteristics of the infant to affect the quality of maternal care. For example, in vervet monkeys (*Chlorocebus pygerythrus*), high-ranking mothers rejected daughters more often than sons, whereas low-ranking mothers did not [Lee, 1984]. A study of yellow baboons (*Papio cynocephalus*) showed that high-ranking mothers carried daughters more often than sons whereas low-ranking mothers showed no such sex bias [Altmann and Samuels, 1992]. In the same study, high-ranking mothers also tended to carry infants of both sexes for less time than low-ranking mothers [Altmann and Samuels, 1992]. In rhesus macaques (*Macaca mulatta*), mothers prevented female infants from leaving more so than male infants [Mitchell, 1968]. Besides infant sex, numerous studies show that infant age has an important influence on the maternal care. For example, younger infants receive more care than older infants [Altmann, 1980; Goldizen, 1987; Altmann and Samuels, 1992; Onishi and Nakamichi, 2011].

Most studies of maternal style in cercopithecine primates have been conducted on terrestrial or semi-terrestrial species, e.g., green monkeys [Fairbanks and McGuire, 1988], yellow baboons [Altmann 1980] and rhesus macaques [Berman, 1990], which may have more flexibility than committed arboreal cercopithecines (e.g., blue monkeys *Cercopithecus mitis*, red-tailed monkeys *Cercopithecinus ascanius*) where the risk of falling is higher for their infants [Nakamura and Ramadhani, 2014]. With the risk of injury and death from falls greater and the visibility more limited [Nishida et al., 2003], it seems likely that the arboreal environment poses somewhat different challenges than the terrestrial environment for mothers and infants [Förster and Cords, 2002]. Thus, we might expect mothers in arboreal species to be more restrictive toward their infants with regard to leaving the mother or travelling alone. However, there has been comparatively little research on maternal care in arboreal species [Förster and Cords, 2002] to determine whether arboreal cercopithecines, like terrestrial cercopithecines, have multiple maternal styles or must be generally more restrictive because of the limitations of the arboreal habitat. In a study of long-tailed macaques, (*M. fascicularis*), mothers and their infants of 10–20 weeks of age were generally in contact with each other a greater proportion of the time at higher levels in the canopy than at lower levels, suggesting that the risk of falling might contribute to maternal care [Karssemeijer et al., 1990]. In contrast, in arboreal blue monkeys, infants gained spatial independence earlier in life than more terrestrial cercopithecine species, such as patas monkeys *(Erythrocebus patas)*, rhesus and long-tailed macaques and yellow baboons [Nicolson, 1987; Förster and Cords, 2003, 2005]. Perhaps greater precociality is important in the arboreal environment, or alternatively, at least in guenons, it may be related to lower rates of agonism normally expressed within groups [Förster and Cords, 2005].

Here, we present the first detailed study on maternal behaviour in free-ranging grey-cheeked mangabeys. We investigated the effects of the mother's parity, age and dominance rank, as well as the infant's sex and age, on maternal care and on mother-infant proximity. Grey-cheeked mangabeys are closely related to baboons [Harris and Disotell, 1998; Burrell et al., 2009] and, like baboons, they live in multi-male, multi-female groups in which females are the philopatric sex and have stable, linear dominance hierarchies [Chancellor and Isbell, 2009]. However, group sizes are typically

Table 1. Composition of grey-cheeked mangabey study groups in Kibale National Park, Uganda

	BT1	LC1	LC2	MK
Group size	17–23	19–26	13–16	10–15
Adult females	7	7	4–5	4
Adult males	2–6	3–8	1–2	3–4
Subadult females	0–1	0–2	0–1	0–2
Subadult males	1	0	1	0
Juvenile females	1–2	0	1	0–2
Juvenile males	2	5	3	1
Infant females	1	2	0	2
Infant males	3	2	3	0

The values are presented as minimum and maximum of the number of individuals per age-sex class over the study period.

smaller [Waser, 1977; Henzi and Barrett, 2003], and most of their time is spent arboreally. As locomotor and feeding substrate influences a large range of behaviours [Clutton-Brock and Harvey, 1977], we have no reason to expect that the same is not true for maternal care. It seems likely that the highly diverse, visually dense and 3-dimensional environment of arboreal species is a challenge for maternal care and protection.

Because parity influences maternal care in many species, we expected to find that multiparous (experienced) mothers provide better maternal care than primiparous mothers. We also expected the age of the mother, as it tends to be connected with experience, to have an impact on the quality of maternal care. Since the social organization of grey-cheeked mangabeys is similar to that of other papionin species, we expected to find rank effects on maternal care, with high-ranking females spending more time with infants. We also expected differential care of male and female infants, with mothers protecting their daughters more frequently than sons. We also expected mothers to devote more attention and care to younger infants. Finally, since mangabeys are an arboreal species, we expected greater time in direct contact between mothers and infants, i.e., more time spent carrying infants, in comparison to more terrestrial species. As most maternal care studies have been carried out in terrestrial cercopithecine species, our study helps to fill a gap and brings attention to maternal care in less well-known arboreal species.

Methods

Study Area and Subjects

The study site, Kibale National Park, Uganda, is a 795-km^2 moist, evergreen, medium-altitude forest with areas of swampland, grassland, thicket and colonizing forest [Chapman and Lambert, 2000]. We collected data from the end of July 2011 to March 2012 on four groups of grey-cheeked mangabeys: Lower Camp 1 (LC1), Lower Camp 2 (LC2), Butanzi 1 (BT1), and Mikana (MK), which ranged in size from 10 to 26 individuals (1–8 adult males, 4–7 adult females, and 0–3 infants; Table 1) [Janmaat et al., 2009].

Table 2. Mothers' and infants' characteristics

Group/ female	Age, years	Rank	Parity	Infant age, months	Infant sex
BT1					
Kagezi	8	2	PP	0.5	m
Kadogo	10	3	MP	0.5	f
Mwirima	7	4	MP	4.0	m
Muhimbo	7	7	PP	5.0	m
LC1					
Nyakato	14	1	MP	9.0	m
Ngonzi	9	5	MP	4.0	f
Namara	11	6	MP	4.0	f
Kaisiki	9	7	MP	4.0	m
LC2					
Kiiki2	13	1	MP	9.0	m
Kissa2	8	2	PP	10.0	m
Tindereya	12	4	MP	5.0	m
MK					
Kakende	12	1	MP	0.5	f
Broom	8	2	PP	0.5	f

Age of females is given in years and age of infants in months (at the end of the study). Age of the females older than 10 years was estimated. Parity: PP, primiparous females (first-time mothers); MP, multiparous females (experienced mothers). Infant sex: m, male; f, female.

We have monitored these groups monthly since 1999, with continuous observation since 2004 (LC1, BT1, MK) or 2010 (LC2) up to 2014. All animals were habituated and individually recognized [Arlet et al., 2014]. We identified females using natural markings such as relative body size, nipple colour and size, and tail characteristics (scars, shape and thickness of hair [Strum and Western, 1982]. In our study, we recorded the behaviour of all females with infants (n = 13), and we knew the birth dates of their infants. In our study, we included 8 male and 5 female infants (Table 2). Most infants are weaned between 6 and 7 months [Veromann, 2011]. Grey-cheeked mangabey females mature between 5 and 6.2 years, and they have their first births between 6.8 and 7.8 years [Deputte, 1992; Arlet et al., 2014, 2015]. Our 13 adult female subjects, all with infants, were characterised as either primiparous or multiparous based on their known histories (Table 2).

Female dominance ranks were based on Arlet et al. [2014] using 91 agonistic interactions from the 2011–2012 study period. We recorded all dyadic agonistic interactions per group, including non-physical threats (e.g., facial displays), approach-avoids (i.e., moving away from another who is approaching), supplants (i.e., taking the place of another), physical contacts (e.g., biting, tail-pulling and pushing), and chases (i.e., aggressively pursuing another). We constructed dominance matrices for each study group, with rank order determined by minimizing the number of reversals against the hierarchy (i.e., interactions below the diagonal). The ranks of our subjects were stable during the 6-month study as no changes were found when comparing the first half of the study with the second half.

Behavioural Observations

Two authors (M.E.A. and L.-L.V.-J.) and field assistant Richard Kaseregenyu (R.K.) collected data from July 2011 until March 2012 (M.E.A. and L.-L.V.-J. July-September 2011, R.K. September-December 2011 and M.E.A. January-March 2012). Observers were trained by the same person and collected behavioural data simultaneously on the same females' behaviour to

Table 3. Description of maternal behaviours in grey-cheeked mangabeys (modified from Patterson, 2001)

Behaviour	Description
Watch infant	Female observes infant
Hold infant	Female cradles infant while sitting
Carry infant	Female transports infant
Groom infant	Female uses her mouth and hands to pick through infant's fur
Protect infant	Female prevents group member from touching or taking her infant
Restrict infant from leaving	Female keeps her infant from leaving
Restrict infant from contact	Female keeps her infant from contact with group members
Restrict infant from suckling	Female keeps her infant from taking her nipple into its mouth

test for interobserver reliability (Spearman test: $r_s = 0.87$, $p < 0.001$, $n = 620$). We carried out the observations as a rotation between groups – we followed one group for 6 days every 5 weeks [Arlet et al., 2009]. We opportunistically determined the focal sampling order in each group by first sighting of an adult female that had not yet been sampled during that particular round, while taking care to balance morning and afternoon sampling. We collected 247 h of focal observations, with a mean ± SD of 17.6 ± 13.9 h per female.

We focal-sampled each female with an infant for 90 min per day (excluding time out of sight) for a total of 6 days over 6 months. During that time, we recorded behaviours designated as "watch," "hold," "carry" and "groom." For analyses, we used occurrences of these behaviours and quantified them as rates per unit time. We also recorded all occurrences of behaviours designated as "protect," "restrict leaving mother's proximity," "restrict contact with others" and "restrict suckling" and quantified them for analyses as rates per unit time. We provide operational definitions in Table 3. We estimated proximity between mothers and infants (in metres) every time the behaviour changed, and every time the distance between the mother and infant changed. All observers were trained to estimate focal female distances to the infant and we found a high degree of reliability between observers' estimates (Spearman test: $r_s = 0.9$, $p < 0.01$, $n = 370$).

Statistical Analysis

We used generalized linear mixed models with identity link function to examine predictors of the expression of maternal behaviours. We considered models with the following predictors as main effects: mothers' parity (primiparous vs. multiparous), age (in years), dominance rank (1, 2, 3, etc.; estimated for all females in each group), infant age (in months) and infant sex. We included group and infant identity as random factors. In our model, the dependent variable was the number of each behaviour recorded per month of observation (i.e., per month of infant age) divided by monthly observation time in minutes (to counterbalance the differences in sampling effort and to acknowledge developmental changes over time). The ranks and ages of the mothers and the ages of their infants were both fixed factors and were considered continuous factors, whereas parity and infant sex were categorical factors.

We used generalized linear mixed models with identity link function to test the influence of mothers' parity, age, dominance rank, and infant age and sex on mother-driven proximity to infants. We considered group and infant identity as random factors. Here, the dependent variable was average proximity of the infant from the mother per month, calculated from every instance the distance between the mother and infant changed. As above, the dependent variable was the number of each behaviour recorded per month of observation, mother's rank and age and infant's age were continuous factors, and parity and infant sex were categorical factors.

The study design, with repeated observations of each female in a group over the observation period, calls for statistical models that incorporate several factors (of maternal care). Our data meet the assumptions of normality of generalized linear mixed models. We used STATISTICA 10 (StatSoft Inc., USA) for all the analyses with a significance threshold set at 0.05.

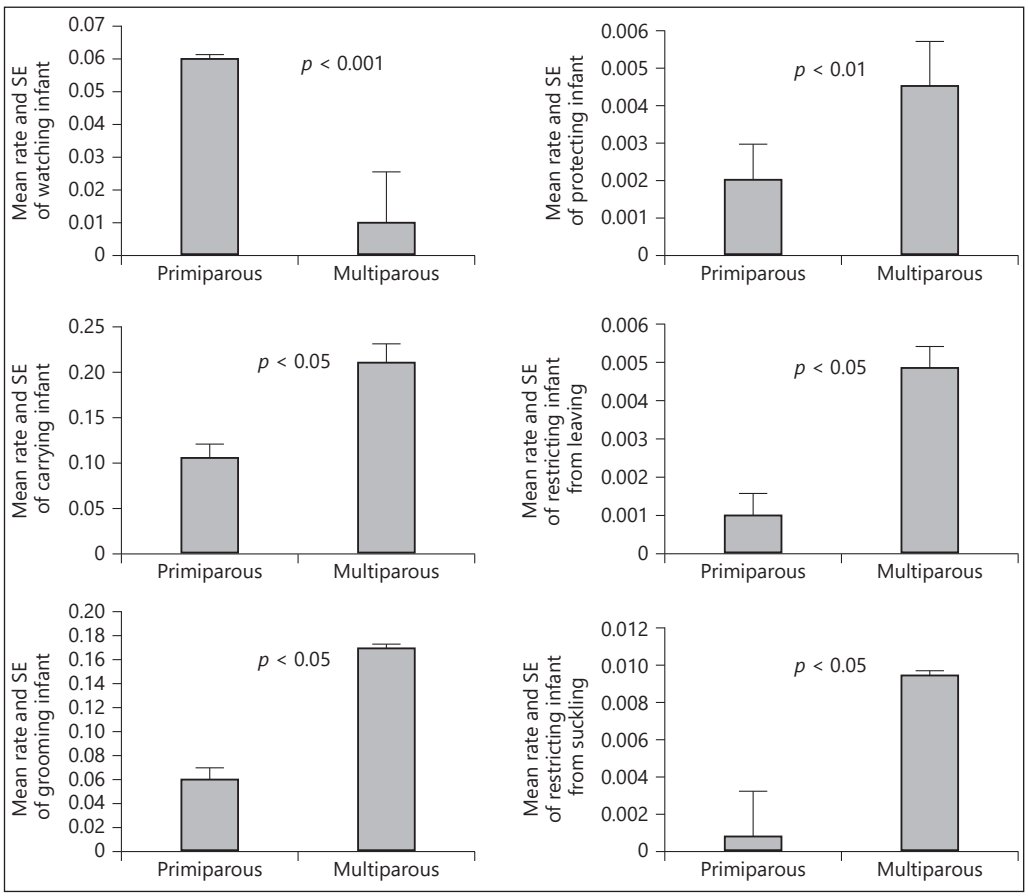

Fig. 1. Relation between mother's rearing experience and the rate of maternal behaviours. The number of observations represents the mean number of observations per female per minute. Error bars are standard errors.

Results

Influence of Mother's Parity, Rank and Age on Maternal Behaviours

We found that mother's parity, but not age or rank, influenced most forms of maternal care. Primiparous mothers watched their infants longer than did multiparous mothers (primiparous: mean ± SD = 0.06 ± 0.004 min; multiparous: mean ± SD = 0.01 ± 0.0005 min) but multiparous mothers carried (primiparous: mean ± SD = 0.09 ± 0.02/min; multiparous: mean ± SD = 0.17 ± 0.005/min) and groomed (primiparous: mean ± SD = 0.06 ± 0.002/min; multiparous: mean ± SD = 0.17 ± 0.0005/min) their infants more often, and were more protective than primiparous mothers (primiparous: mean ± SD = 0.002 ± 0.0006/min; multiparous: mean ± SD = 0.004 ± 0.0006/min; $p < 0.05$ in all cases; Table 4, Fig. 1). Multiparous mothers restricted their infants from leaving (primiparous: mean ± SD = 0.001 ± 0.003/min; multiparous: mean ± SD = 0.004 ± 0.009/min) and from suckling (primiparous: mean

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Table 4. Influence of mother's and infant's characteristics on maternal behaviours

	df	Watch			Hold			Carry			Groom			Protect			Restrict leave			Restrict contact			Restrict suckling		
		F	β	*p*	*F*	β	*p*	*F*	β	*p*	*F*	β	*p*	*F*	β	*p*	*F*	β	*p*	*F*	β	*p*	*F*	β	*p*
Female age	1	0.03	–0.11	0.87	1.05	0.25	0.31	1.32	–0.23	0.26	0.15	0.09	0.69	3.32	0.39	0.08	2.95	–0.4	0.09	0.4	–0.14	0.53	1.08	–0.23	0.3
Female parity	1	16.5	–0.75	**<0.001**	3.03	0.34	0.09	4.52	0.39	**0.04**	2.86	0.4	**0.03**	13.1	–0.5	**0.004**	5.16	0.47	**0.03**	3.88	0.38	0.052	1.16	0.42	**0.02**
Female rank	6	0.94	–0.27	0.34	0.19	–0.09	0.67	0.41	0.12	0.53	1.12	–0.21	0.29	3.41	–0.33	0.07	7.99	0.56	**<0.001**	2.02	0.32	0.08	0.13	–0.09	0.72
Infant age	1	7.49	–0.64	**0.009**	12.9	–0.53	**0.001**	22.01	–0.66	**<0.001**	0.85	–0.14	0.36	8.4	–0.47	**0.006**	7.13	–0.49	**0.01**	0.77	–0.16	0.38	6.75	–0.48	**0.013**
Infant sex	1	0.35	0.18	0.56	4.85	0.17	0.34	0.31	–0.07	0.58	9.13	0.51	**0.004**	9.59	0.58	**0.001**	18.11	–0.64	**<0.001**	0.28	–0.07	0.6	3.26	0.32	0.08

F/*p*: statistical values of generalized linear mixed model test with significant differences in bold.

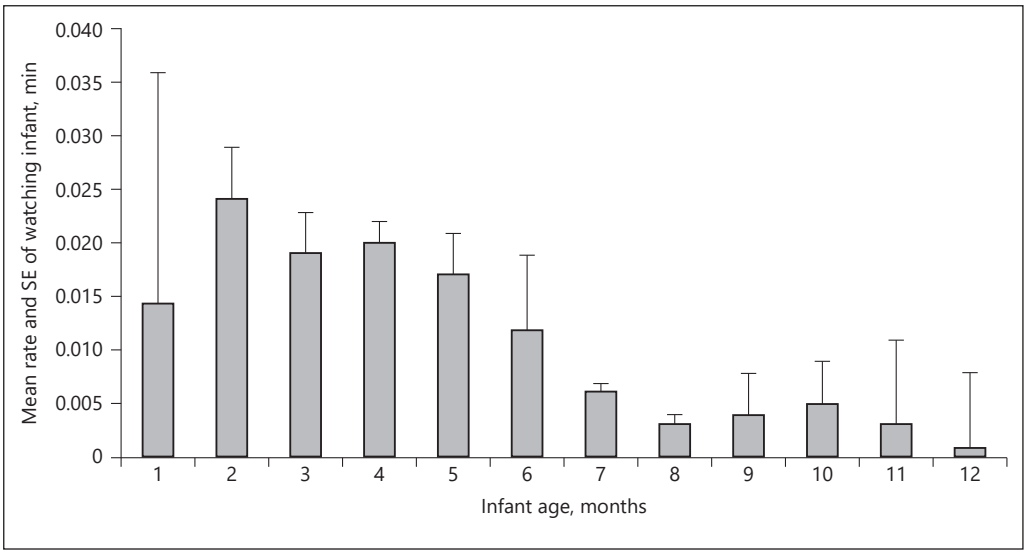

Fig. 2. Relation between age of infants and the time mothers spent watching them. The number of observations represents the monthly number of observations per minute. Error bars are standard errors.

± SD = 0.0007 ± 0.002/min; multiparous: mean ± SD = 0.009 ± 0.002/min) more often than primiparous mothers. All mothers displayed comparable holding (primiparous: mean ± SD = 0.06 ± 0.07/min; multiparous: mean ± SD = 0.1 ± 0.13/min) and restricting from contact regardless of their maternal experience (primiparous: mean ± SD = 0.003 ± 0.005/min; multiparous: mean ± SD = 0.01 ± 0.01/min; $p > 0.05$). Restricting infants from leaving was correlated with dominance rank, as low-ranking mothers (rank: 5–7) restricted their infants more than higher-ranking mothers (rank 1–4: mean ± SD = 0.001 ± 0.003/min; rank 5–7: mean ± SD = 0.012 ± 0.018/min; Spearman correlation: $r = 0.53$, $p < 0.05$). Mother's age had no effect on any measure.

Influence of Infant's Age and Sex on Maternal Behaviours

In our study, most measures of maternal care were affected by the age of the infant (Table 4). Mothers with 3-month-old infants spent, on average, 36% of their time carrying those infants whereas mothers with 6-month-old infants spent, on average, 15% of their time carrying them. The younger the infant was, the longer its mother spent watching it (1–3 months: mean ± SD = 0.02 ± 0.002/min; 4–6 months: mean ± SD = 0.01 ± 0.001/min; >6 months: mean ± SD = 0.005 ± 0.004/min; Fig. 2), holding it (1–3 months: mean ± SD = 0.17 ± 0.09/min; 4–6 months: mean ± SD = 0.04 ± 0.07/min; >6 months: mean ± SD = 0.0 ± 0.0/min) and carrying it (1–3 months: mean ± SD = 0.34 ± 0.2/min; 4–6 months: mean ± SD = 0.15 ± 0.1/min; >6 months: mean ± SD = 0.02 ± 0.05/min).

Younger infants were also more protected than older ones (1–3 months: mean ± SD = 0.006 ± 0.002/min; 4–6 months: mean ± SD = 0.003 ± 0.005/min; >6 months: mean ± SD = 0.0 ± 0.0/min; Fig. 3); most cases of protection (71%) were observed with infants younger than 4 months. We did not observe protection of infants older

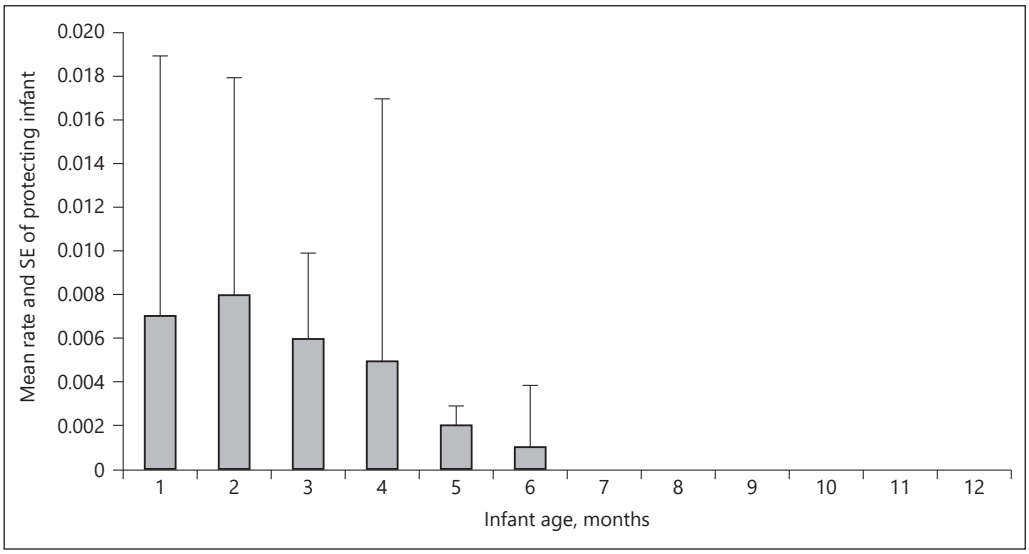

Fig. 3. Relation between age of infants and the time mothers spent protecting them. The number of observations represents the monthly number of observations per minute. Error bars are standard errors.

Table 5. Influence of mother's and infant's characteristics on mother-infant distance

	df	*F*	*p*
Female age	1	1.44	0.24
Female parity	1	2.03	0.16
Female rank	1	2.61	0.11
Infant age	1	87.8	<0.001
Infant sex	1	1.79	0.19

F/*p*: statistical values of generalized linear mixed model test.

than 7 months. Mothers restricted younger infants from leaving more often than older infants (1–3 months: mean ± SD = 0.008 ± 0.01/min; 4–6 months: mean ± SD = 0.002 ± 0.004/min; >6 months: mean ± SD = 0.0008 ± 0.002/min). Older infants were restricted more often than younger infants from suckling (1–3 months: mean ± SD = 0.00 ± 0.00/min; 4–6 months: mean ± SD = 0.001 ± 0.003/min; >6 months: mean ± SD = 0.17 ± 0.27/min).

Mothers groomed female infants more often than they groomed male infants (daughters: mean ± SD = 0.09 ± 0.012/min; sons: mean ± SD = 0.016 ± 0.02/min) and protected infant females more often than infant males (daughters: mean ± SD = 0.008 ± 0.01/min; sons: mean ± SD = 0.001 ± 0.005/min). Infant females were restricted from leaving more often than infant males (daughters: mean ± SD = 0.007 ± 0.01/min; sons: mean ± SD = 0.003 ± 0.008/min).

Influence of Mothers' and Infants' Characteristics on Mother-Infant Proximity

We found that mother-infant proximity was influenced only by infant age (Table 5). As might be expected, distances between mothers and infants increased with age as infants were moving away from mothers and increasingly interacting with other group members (Spearman correlation: $r = 0.88$, $p < 0.05$). At 1–3 months, the mean distance ± SD between mothers and infants was 1.9 ± 0.85 m, at 4–6 months, it was 4.9 ± 0.77 m, and at >6 months, it was 8.7 ± 1.67 m.

Discussion

The study of maternal behaviour in cercopithecine primates is largely restricted to species that spend much of their time on the ground. Because of the greater risk of injury from falling from trees, cercopithecine species that are arboreal may express maternal behaviour somewhat differently, especially to keep infants from moving independently.

Our study is the first to investigate maternal behaviour in grey-cheeked mangabeys, an arboreal cercopithecine primate species. We found that, as with many other species, the mother's parity strongly influenced maternal care in that multiparous mothers carried, groomed, protected their infants, and prevented their infants from leaving, more often than primiparous mothers. Therefore, the difference in the quality of maternal care between primiparous and multiparous mothers may be directly related to their acquired experience with infants, possibly even of losing them in the past. Our study showed that multiparous mothers carried their infants twice as much as primiparous mothers did.

Differences between primiparous and multiparous mothers in maternal behaviour may help to explain the lower survival rates of infants of primiparous mothers in this population [Arlet et al., 2014]. Nearly 25% of infant deaths during a 9-year study occurred because infants fell from trees during bouts of fighting between males [Arlet et al., 2014]. Our study showed that grey-cheeked mangabey mothers with 3-month-old infants carried them for more time (36%) than has been reported for the terrestrial yellow baboons (25%) [Altmann and Samuels, 1992], which could be a response to the infant's high risk of falling at this young age. However, mangabeys and yellow baboons were similar in how much time they carried older, 6-month-old infants (mangabeys: 15%, baboons: 16%) [Altmann and Samuels, 1992]. In the arboreal environment in which grey-cheeked mangabeys live, it might be particularly beneficial for mothers to be attentive to their very young infants, but it may take primiparous mothers time to learn that. Here we found that multiparous mothers carried their infants twice as much as primiparous mothers did. In our study we found that parity had an effect on maternal care, as is found in terrestrial species. Therefore, we can expect that other, more universal types of experience or age-related factors also affect offspring survival in grey-cheeked mangabeys, e.g., the tendency to neglect infants by primiparous mothers [Maestripieri and Carroll, 1998; Schino and Troisi, 2005). However, we found that primiparous females watched their infants more than experienced mothers, which may be related to attraction towards "novelty," in this case an infant, as watching behaviour itself was not connected with protective behaviour, carrying or holding by first-time mothers. We detected the effect of mother's rank only on restricting infants from leaving, with low-ranking females restricting their infants from leav-

ing more often than high-ranking females. For species with frequent rank-related agonism, greater restrictiveness from leaving by low-ranking mothers is to be expected. For example, in rhesus macaques, lower-ranking mothers were more restrictive and less willing to allow their infant to be approached by others [Maestripieri, 2005]. This difference may have a stronger phylogenetic than substrate signal. For instance, the rate of agonism between female grey-cheeked mangabeys is similar to that of Japanese macaques and lower than that of chacma baboons [Chancellor and Isbell, 2009], both of which spend more time on the ground than mangabeys but are, along with mangabeys, papionins. In contrast, the rate of agonism between female mangabeys is higher than that of both terrestrial patas monkeys and arboreal blue monkeys, which are cercopithecins [Chancellor and Isbell, 2009]. As the rate of agonism between high- and low-ranking female grey-cheeked mangabeys varied between 12 and 64% (of all agonistic interactions between females) and depended on the group [Arlet, unpubl. observation], restricting infants from leaving may be related to female-female aggression in some groups but may also be influenced by increased aggression (and stress) within the group when migrating males were present [Arlet et al., 2007, 2008, 2013].

The age of the infant was an important factor influencing the dynamic of maternal care. Not surprisingly, as infants became older, all measured maternal behaviours decreased except for grooming. Mother-infant distances also increased. Similarly, in captive rhesus macaques, cradling, retrieving and restraining were inversely correlated with infant age [Seay, 1966]. Younger infants appear to be at greater risk of being accidentally harmed than older infants, and when taken from the mother, they may become malnourished and dehydrated [Maestripieri, 1994]. When the infant is older and less dependent on its mother, it may be safer for the mother to allow others to handle her infant, which then frees her to feed more efficiently and reduce travel costs [Förster and Cords, 2005].

Finally, we found that female infants were groomed longer, protected more often and were prevented from leaving more often than were sons. In our previous study we found that male infants have higher mortality than female infants [Arlet et al., 2014], and our present findings may help to explain why. There are at least two non-exclusive explanations for this sex bias in maternal care. As a proximate explanation, more frequent grooming and greater protection of daughters may be a consequence of infant temperament. For instance, in squirrel monkeys (*Saimiri sciureus*), rhesus macaques and patas monkeys, male infants play more than female infants [Biben, 1986; Rowell and Chism, 1986; Brown and Dixson, 2000]. As an ultimate explanation, sex bias in maternal grooming, protecting and preventing infants from leaving may be the result of selection on mothers and daughters to become more bonded than mothers and sons. Like other cercopithecine primates, female grey-cheeked mangabeys typically stay in their natal groups for life, and they form the social core of the groups whereas males emigrate when they reach sexual maturity [Olupot and Waser, 2001, 2005]. In species with female-philopatric groups, when mortality is higher for infant males than females and maternal investment is biased toward females [e.g., Maestripieri, 2001], it might be expected that mothers will also behave in other ways that promote infant female survival.

In summary, variation in the maternal behaviours we measured could be attributed to factors related to arboreal life to some degree (e.g., because primiparous mothers were less experienced, they may have been less protective than multiparous mothers by carrying their infants less, which could lead to falls and increased infant mortal-

ity), but they also reflect the mother's parity independent of arboreality, her rank and the infant's age and sex. Thus, maternal care in grey-cheeked mangabeys generally resembles that of the more terrestrial papionin primates. As most primates spend at least some of their time in trees, mothers must balance keeping infants safe from falls with allowing them the mobility to gain experience for navigating arboreal pathways. This challenge may be accentuated in highly arboreal species such as grey-cheeked mangabeys. As mothers gain experience, they may learn to better balance restrictiveness and permissiveness, while at the same time, as infants grow older and more competent, it may be less costly for mothers to relinquish some of their control. Whether there is enough variation in maternal care in grey-cheeked mangabeys that individuals can be classified as rejecting mothers, protective mothers or laissez-faire mothers will require long-term observations as primiparous mothers become multiparous.

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Statement of Ethics

All data were collected from habituated, wild animals without interfering with their activities. The research complied with the laws of Uganda, and the protocols were approved by the Uganda Wildlife Authority and Uganda National Council for Science and Technology at the time the field research was conducted.

Disclosure Statement

The authors confirm that there are no conflicts of interest involved in publishing this work.

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Author Contributions

All authors made substantial contributions to this paper. L.-L.V.-J. and M.A. collected data, M.A. analysed data and drafted the article, L.I., R.M. and A.L. revised it critically for important intellectual content. All authors gave final approval of the submitted version and have no competing interests.

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