



High levels of infant handling by adult males in Rwenzori Angolan colobus (*Colobus angolensis ruwenzorii*) compared to two closely related species, *C. guereza* and *C. vellerosus*

Samantha M. Stead^{1,2} · Iulia Bădescu³ · Dominique L. Raboin^{4,5} · Pascale Sicotte⁶ · Jessica M. Rothman^{7,8,9} · Andrea L. Baden^{7,8,9} · Julie A. Teichroeb¹

Received: 18 December 2020 / Accepted: 30 March 2021
© Japan Monkey Centre 2021

Abstract

Infant handling (holding or carrying) by adult males is rare in mammals; however, high levels have been reported in some primates. Though infant handling is a costly behaviour, there are many benefits that male handlers can accrue. Infant handling by males is most conspicuous in platyrrhines and tends to be uncommon in catarrhines. In the latter species, research on male–infant interactions has focused on low-cost behaviours, such as proximity and grooming. However, to better understand the evolution of infant handling by males, more data on its occurrence across the Primate order are essential, even in species where it is relatively uncommon. We compare the occurrence of infant handling by males in three closely related species of catarrhine: *Colobus vellerosus*, *C. guereza*, and *C. angolensis ruwenzorii*. We collected focal animal samples on infants to quantify infant handling rates and durations, and found that adult male *C. a. ruwenzorii* handled infants much more frequently and for much longer than males in the other two species. We discuss how *C. a. ruwenzorii*'s unique social organization may explain high levels of infant handling by adult males in this species. More long-term and detailed comparisons of infant handling across species and populations will shed light on how sociality has shaped the evolution of this behaviour in the Primate order.

Keywords Black-and-white colobus monkeys · Bonding mechanism · Comparative · Infanticide · Male–infant interactions · Social organization

Introduction

Most eutherian mothers cache their infants (i.e., in nests, burrows, caves, snow dens, vegetation or on ice patches) while they forage and return intermittently to nurse (e.g., Broekhuizen et al. 1986; Sharp et al. 2006). However, six of the 19 eutherian orders, notably Primates and Chiroptera,

contain species where infants are held and carried (hereafter referred to as ‘handled’) by their mothers throughout the active period (Ross 2001). In a subset of these species, individuals other than the mother also handle infants (Rosenbaum and Gettler 2018). Non-mother handlers tend to be females, but in some species, they are also male (Fernandez-Duque et al. 2009; Huck and Fernandez-Duque 2013).

✉ Samantha M. Stead
sam.stead@mail.utoronto.ca

¹ Department of Anthropology, University of Toronto
Scarborough, Toronto, ON, Canada

² School of the Environment, University of Toronto, Toronto,
ON, Canada

³ Département D'Anthropologie, Université de Montréal,
Montréal, Québec, Canada

⁴ Department of Anthropology, Rutgers University,
New Brunswick, NJ, USA

⁵ Center for Human Evolutionary Studies, Rutgers University,
New Brunswick, NJ, USA

⁶ Department of Biology, Concordia University, Montreal, QC,
Canada

⁷ Department of Anthropology, Hunter College of City
University of New York, New York, NY, USA

⁸ Department of Anthropology, The Graduate Center
of the City University of New York, New York, NY, USA

⁹ The New York Consortium in Evolutionary Primatology,
New York, NY, USA

Infant handling is costly due to increased energy expenditure during movement, reduced feeding efficiency, and decreased agility when fleeing from predators (Achenbach and Snowdon 2006; Altmann and Samuels 1992; Schradin and Anzenberger 2001). Despite these costs, infant handling can have many fitness benefits for adult males. First, males can improve their reproductive success by handling their own offspring if this improves the offspring's survival and/or future reproductive success ('paternal care' hypothesis, Charpentier et al. 2008; Huchard et al. 2012). Indeed, several studies show that males selectively interact with their own offspring (e.g., *Macaca mulatta*, Langos et al. 2013; *Papio cynocephalus*, Buchan et al. 2003; *P. anubis*, Städele et al. 2019; *Pan troglodytes*, Murray et al. 2016; *Semnopithecus entellus*, Borries et al. 1999), though more data are needed to determine how this impacts offspring fitness. Second, males may handle non-descendant young to impress females and improve their chance of being selected as a subsequent mate ('mating effort' hypothesis, Smuts 1985; *Saguinus oedipus*, Price 1990; *M. sylvanus*, Ménard et al. 2001; *M. nigra*, Kerhoas et al. 2016; *Gorilla beringei*, Rosenbaum et al. 2018). Moreover, if infant handling reduces the mother's energetic burden and allows her to return to estrus faster, males will have the opportunity to sire her subsequent offspring sooner ('maternal relief' hypothesis; Hatchwell 1999; Heinsohn 2004). Third, in several species, males use infant handling as a way to bond with one another and/or manage social conflict ('agonistic buffering' Deag and Crook 1971; 'bridging' Ogawa 1995; 'triadic male–infant interactions' Taub 1980; 'male–infant–male interactions' Zhao 1996). Reports of this behaviour have come from Barbary macaques (*Macaca sylvana*, Deag and Crook 1971; Deag 1980; Taub 1980), Tibetan macaques (*M. thibetana*, Ogawa 1995; Bauer et al. 2013), Assamese macaques (*M. assamensis*, Kalbitz et al. 2017), chacma baboons (*Papio ursinus*, Busse & Hamilton 1981; Ransom & Ransom 1971), and geladas (*Theropithecus gelada*, Dunbar 1984). These interactions vary in form and function. For instance, Barbary macaque males often transfer infants between one another in affiliative contexts, whereas for chacma baboons and geladas, males often use infants in agonistic contexts apparently as a way to reduce their likelihood of being aggressed (Paul et al. 2000). Lastly, males may handle infants as a way to bond with the infants and form future allies (Dunayer and Berman 2017). Social bonds are known to facilitate coalition formation, access to resources, protection against harassment, and stress mitigation (Berghänel et al. 2011; Ostner and Schülke 2014; Young et al. 2014; Haunhorst et al. 2017; Schülke et al. 2010). Thus, there are several ways that males can improve their fitness by handling infants, despite the associated costs. It is likely that these hypotheses are not mutually exclusive and that different combinations can explain infant handling by males across the Primate order.

High levels of infant handling by males have been observed in platyrrhines, such as tamarins, marmosets, owl monkeys, and titi monkeys (review: Fernandez-Duque et al. 2009; Huck and Fernandez-Duque 2013; Whitten 1987; Wright 1984; Mendoza and Mason 1986; Fragaszy 1982). In these species, males are the primary handlers for at least a portion of the infant's early life. In catarrhines, high levels of infant handling by males are uncommon. Siamangs are an exception, with one study showing infants to be carried by male(s) 12–27% of the time at 16–18 months of age (Lappan 2008). Most research on male–infant interactions in catarrhines has focused on low-cost behaviours, such as maintaining or tolerating infant proximity, grooming and playing, and affiliative behaviours, such as touching and lipsmacking (Kerhoas et al. 2016; Langos et al. 2013, 2015; Minge et al. 2016; Murray et al. 2016; Rosenbaum et al. 2018; Fox 2015; but see Borries et al. 1999; Buchan et al. 2003; Xiang et al. 2009). However, due to the high costs of infant handling, even low rates could have fitness costs for the male, and possible fitness benefits for the infant, and its mother. Therefore, documenting its prevalence is important, even if rates are not as high as those observed in platyrrhine species. A more comprehensive data set on infant handling by adult males will also provide a stronger comparative framework that we can use to explore the evolution of this behaviour across the Primate order (Gettler et al. 2020). Comparisons of infant handling across closely related species will reveal how socio-ecology and phylogeny have influenced the evolution of these behaviours.

Here, we explore infant handling by males in three closely related catarrhine species: ursine or white-thighed colobus (*Colobus vellerosus*), mantled guereza (*C. guereza*), and Rwenzori Angolan colobus (*C. a. ruwenzorii*). Fashing (2011) was the first to note that infant handling by males may be more frequent in *C. a. ruwenzorii* than in other species of black-and-white colobus. We use quantitative data to show that infant handling by adult males is significantly greater in *C. a. ruwenzorii* than in these other two closely related species. We discuss how the unique social organization of *C. a. ruwenzorii* may have led to high levels of infant handling by adult males in this subspecies.

Methods

Study sites and study species

Colobus vellerosus

From June to November 2010, infant handling by adult males was recorded by IB in a population of *C. vellerosus* at the Boabeng-Fiema Monkey Sanctuary (BFMS), a forest fragment situated within a network of smaller fragments

in the Brong-Ahafo region of central Ghana (350 m elevation, 7° 43' N and 1° 42' W). The 1.92 km² BFMS fragment consists of dry semi-deciduous forest and is located in the forest-savanna transition zone of Ghana. The population of *C. vellerosus* at BFMS has been studied under the supervision of PS since 2000. A total of 152.90 hours of focal observation were recorded for nine study infants (male = 3, female = 5, unknown = 1) (Bădescu et al. 2015). Infants were distributed across four groups, which ranged in size from 19 to 27 and were one-male/multi-female ($N=6$ infants) and multi-male/multi-female ($N=3$ infants).

Colobus guereza

From June through December 2017, infant handling by adult males was recorded by DLR in a population of *C. guereza* at Kanyawara research site in Kibale National Park (KNP) in western Uganda (1110–1600 m elevation, 0° 7' 48"–0° 24' 36" N and 30° 11' 24"–30° 19' 12" E). KNP is a tropical evergreen forest located east of the Rwenzori Mountains. Eight groups from this population have been studied by JMR since 2008. A total of 127.35 focal follow hours were recorded for four study infants (male = 2, female = 2). Infants were distributed across three groups, which ranged in size from 10 to 11 individuals and were one-male/multi-female ($N=2$ infants) and multi-male/multi-female ($N=2$ infants).

Colobus angolensis ruwenzorii

From June to August 2017, infant handling by adult males was recorded by SMS in a population of *C. a. ruwenzorii* in the Masaka region of central Uganda, near Lake Nabugabo. This population ranges within a fragment of tropical moist forest (1134–1167 m elevation, 0° 20' 29" S–31° 52' 1" E), a portion of which is protected by the Manwa Forest Reserve (~2.8 km²). This population of *C. a. ruwenzorii* has been studied under the supervision of JAT since 2013. A total of 49.32 hours of focal observation were recorded for five study infants (male = 2, female = 3). Infants were distributed across four core units, which ranged in size from 6 to 14 individuals and were one-male/multi-female ($N=3$ infants) and multi-male/multi-female ($N=2$ infants).

Social organization

Colobus vellerosus and *C. guereza* both live in bi-sexual groups that can be one-male/multi-female or multi-male/multi-female (*C. guereza*, Kibale, Uganda, mean = 8, range 4–13, Gogarten et al. 2014; Kakamega Forest, Kenya, mean = 12.8, range = 7–21, $N=5$, Fashing 2001; *C. vellerosus*, Boabeng-Fiema, Ghana, mean = 15, range = 9–38, $N=15$, Wong and Sicotte 2006; Bia National Park, Ghana, mean = 16, range = 16, $N=2$, Oates 1994; Saj et al. 2005).

Both species exhibit male-biased dispersal with facultative female dispersal (*C. guereza*, Harris et al. 2009; *C. vellerosus*, Teichroeb et al. 2009, 2011; Wikberg et al. 2012). Groups in these species are cohesive and relatively intolerant of one another; intergroup encounters often lead to aggression (Harris 2006; Sicotte and Macintosh 2004).

In contrast, *C. a. ruwenzorii* live in multi-level societies, whereby smaller social groups (core units) associate and dissociate non-randomly with one another throughout the day (Nyungwe Forest, Rwanda, Miller et al. 2020; Nabugabo, Uganda, Stead and Teichroeb 2019). When they associate with each other, they can form groups of several hundred. Core units can be one-male/multi-female or multi-male/multi-female (Nabugabo, Uganda, core unit mean size = 11, range = 4–23, $N=12$, Stead and Teichroeb 2019). At Nabugabo, data indicate that at least three tiers occur in the *C. a. ruwenzorii* society, with core units clustering preferentially into clans, and clans sharing a home range in a band tier (Stead and Teichroeb 2019). Preliminary data at Nabugabo suggest that males disperse mostly between core units within the band, while females tend to disperse to and from core units outside of the band (Arseneau-Robar et al. 2018; Stead and Teichroeb 2019). In sum, the social organization of *C. a. ruwenzorii* differs dramatically from those of *C. vellerosus* and *C. guereza* (Fig. 1).

Data collection

Colobus infants are born with a pure white natal coat that slowly transitions to grey and eventually to the adult black-and-white coat. We included data from infants with a white or grey coat color (under 5 months of age) only due to limited comparable data from black-and-white infants. We conducted focal animal samples on infants to record all instances of infant handling by adult males (Altmann 1974). Focal animal samples on *C. guereza* were collected for 5 min, whereas focal samples on *C. vellerosus* and *C. a. ruwenzorii* were collected for 10 min. For *C. vellerosus* and *C. a. ruwenzorii*, if focal animals were lost before the end of the 10-min focal period, the sample was still included in the analysis if it was over 5 min in length. During the focal periods, all bouts of infant handling by adult males were recorded. Infant handling was defined as a male actively using its arms or legs to hold or carry the infant (Bădescu et al. 2015). There was no time requirement, and so some of the handling bouts were very short in duration. An infant handling bout was considered distinct from other bouts if the identity of the handler changed or if contact was broken between the infant and the handler for more than 30 s (Bădescu et al. 2015). Only handling bouts by adult males were considered in this analysis. Adult males were defined as a male that had achieved full body size (larger than adult females) and regularly participated in loud call bouts and

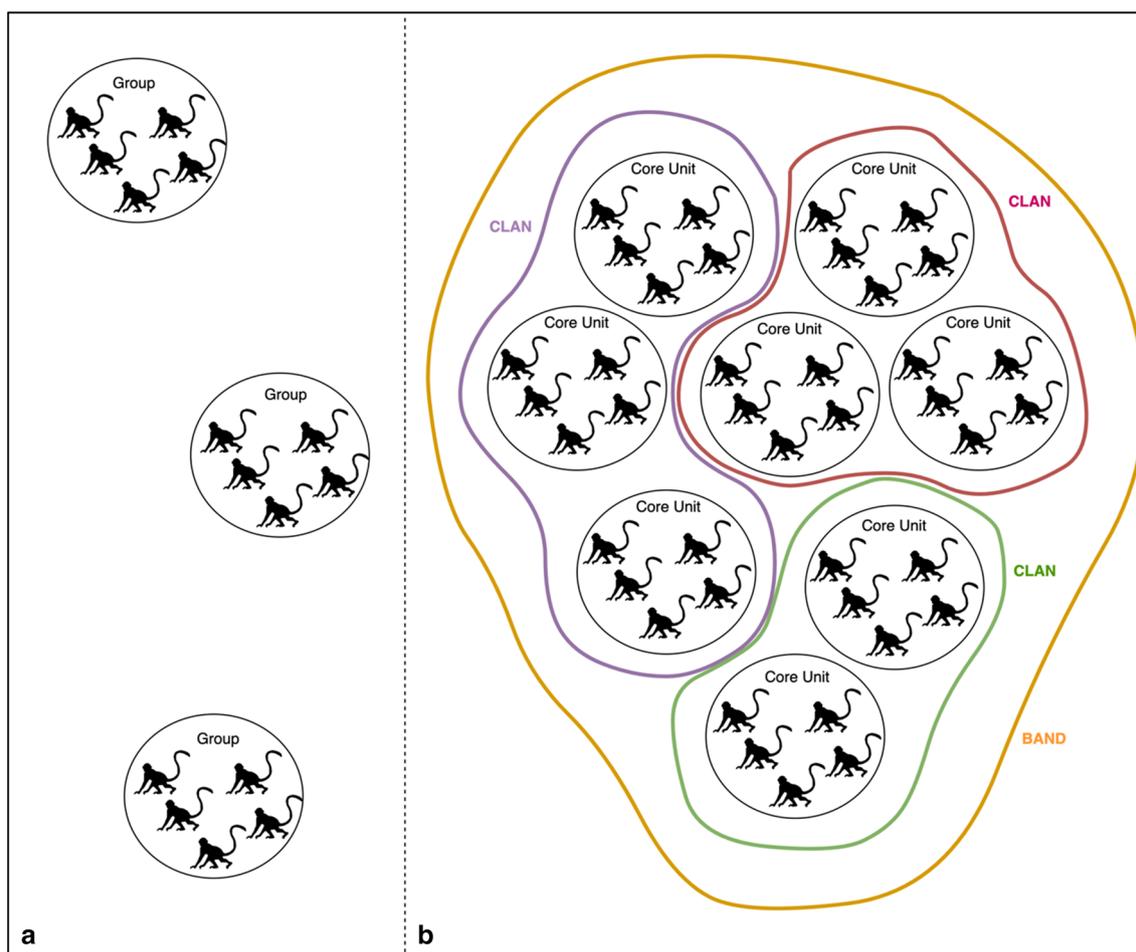


Fig. 1 Depiction of the social organizations of **(a)** *C. vellerosus*, *C. guereza* (relatively low levels of infant handling by adult males), and **(b)** *C. angolensis ruwenzorii* (relatively high levels of infant handling by adult males). The former two live in distinct groups that are cohesive and relatively intolerant of one another. The latter lives in a

multi-level society comprising distinct core units that travel together 75% of the time and make up a 'band'. Within a 'band', core units that associate preferentially make up a 'clan'. Figure created using diagrams.net

displays with other males. Given the dispersal patterns of all three species, adult males were in breeding groups and were unlikely to be natal to the study group (Harris et al. 2009; Stead and Teichroeb 2019; Teichroeb et al. 2011). Genetic paternity was not known for the study infants, and so we could not distinguish between sires and non-sires. For *C. vellerosus* and *C. a. ruwenzorii*, the initiator of the infant handling bout (whether it was the male or the infant) was recorded when possible. A bout could begin when (1) an infant moved into a male's lap and the male then began handling (actively supporting the infant with his arms and/or legs); (2) a male pulled an infant into his lap and began handling; or (3) a male took an infant from another handler and began handling. Infants were sampled opportunistically, rotating between individuals when possible and with priority given to infants with fewer data. If an infant moved into a male's lap and the male did not respond by actively

supporting the infant with his arms and/or legs, we did not consider this to be a handling bout. Because some infants were easier to locate than others and infants were born at different times during the study periods, it was not possible to obtain equal focal times for every infant.

Data analysis

We calculated the rate of infant handling by adult males for each infant by dividing the total number of infant handling bouts by the total number of focal observation hours for that infant. These values were then divided by the number of adult males in an infant's social group. Controlling for the number of adult males available to handle each infant provides a more valid comparison between infants. To compare rates for all three species, we used a nonparametric Kruskal–Wallis test followed by post hoc two-by-two

Mann–Whitney *U* tests. We examined species differences in the duration of infant handling bouts using a Cox mixed-effects model because many bouts for *C. a. ruwenzorii* were right-censored, continuing beyond the focal animal sampling period. The independent variable in this model was handling bout duration and the fixed effect was species, with infant ID included as a random factor. Due to the high prevalence of censored handling bouts in *C. a. ruwenzorii*, we also used Kaplan–Meier survival analysis to estimate the median duration of bouts. The frequency of handling bout initiations by males versus infants was compared for *C. vellerosus* and *C. a. ruwenzorii* using Fisher’s exact test. We ran tests in R version 3.5.1 (R Core Team 2018) and set an alpha level of 0.05 for significance. Kaplan–Meier survival analyses were run with the package ‘survival’ (Therneau 2015), and the Cox mixed-effects model was run with the package ‘coxme’ (Therneau 2020).

Results

Infant handling by males

Colobus vellerosus

Only three of the nine *C. vellerosus* infants were handled by an adult male(s). One of these infants (CO) was in a multi-male group and two of them (KT, NC) were in the same one-male group. The mean infant handling rate by males was 0.044 bouts/focal hour/adult male ($N=9$, $SD=0.10$). The mean duration of infant handling bouts by males was 17.1 (± 11.9 SD) seconds ($N=10$, range 6–39 s). Of the 10 male infant handling bouts observed, 9 were observed from the beginning. Out of these, two were initiated by the male handler and seven were initiated by the infant. No male-to-male transfers of infants were observed (Table 1).

Colobus guereza

Three of the four *C. guereza* infants were handled by adult male(s). Two of these infants (KYINF, KOINF) were in the same multi-male group and one (BYINF) was in a different one-male group. The mean infant handling rate by males was 0.083 bouts/focal hours/adult male ($N=4$, $SD=0.071$). The mean duration of bouts of infant handling by males was 19.8 (± 20.3 SD) seconds ($N=44$, range 2–75 s). No male-to-male transfers of infants were observed (Table 2).

Colobus angolensis ruwenzorii

All five *C. a. ruwenzorii* infants were handled by adult male(s). Two of these infants (TER, DOT) were in the same one-male unit, one (ADE) was in a different one-male unit, and two (ASH, ZAR) were in different multi-male units. Infants were only ever handled by males from their core unit and never by males of a different core unit. The mean infant handling rate by males was 1.274 bouts/focal hours/adult male ($N=5$, $SD=1.12$). The duration of handling bouts by males ranged from 2 to > 600 s (i.e., males handled infants for the entire 10-min focal animal sample) with a mean, including censored bouts, of at least 140.2 s ($N=152$). The Kaplan–Meier estimator gave a median handling bout duration of 117 s (95% confidence intervals of 100–180 s, $N=152$). Out of the 152 male infant handling bouts observed, 110 were observed from the beginning. Of these, 90 were initiated by the male handler and 20 were initiated by the infant. All infants in multi-male core units were handled by multiple males. Male-to-male transfers of infants were observed; of the 110 male handling bouts observed from the beginning, 21 were initiated by one male taking an infant from another male. These always occurred between males residing in the same core unit (Table 3).

Table 1 Data on infant handling by adult male *C. vellerosus*

Infant ID	Group ID	Group size	# of adult males in group	Focal hours	# of handling bouts	Infant handling rates (# handling bouts/focal hours/# adult males in group)	% of handling bouts initiated by adult male(s) (number of bouts with known initiator)
OB	BS	25	2	13.34	0	0.000	–
RE	BS	25	2	13.54	0	0.000	–
KT	OD	20	1	25.62	1	0.039	0.000 (1)
NC	OD	20	1	25.03	8	0.320	28.571 (7)
TE	OD	20	1	28.43	0	0.000	–
FO	OD	20	1	4.05	0	0.000	–
CO	WW	25–27	2	13.78	1	0.036	0.000 (1)
SC	SP	19	1	18.78	0	0.000	–
XV	SP	19	1	10.33	0	0.000	–

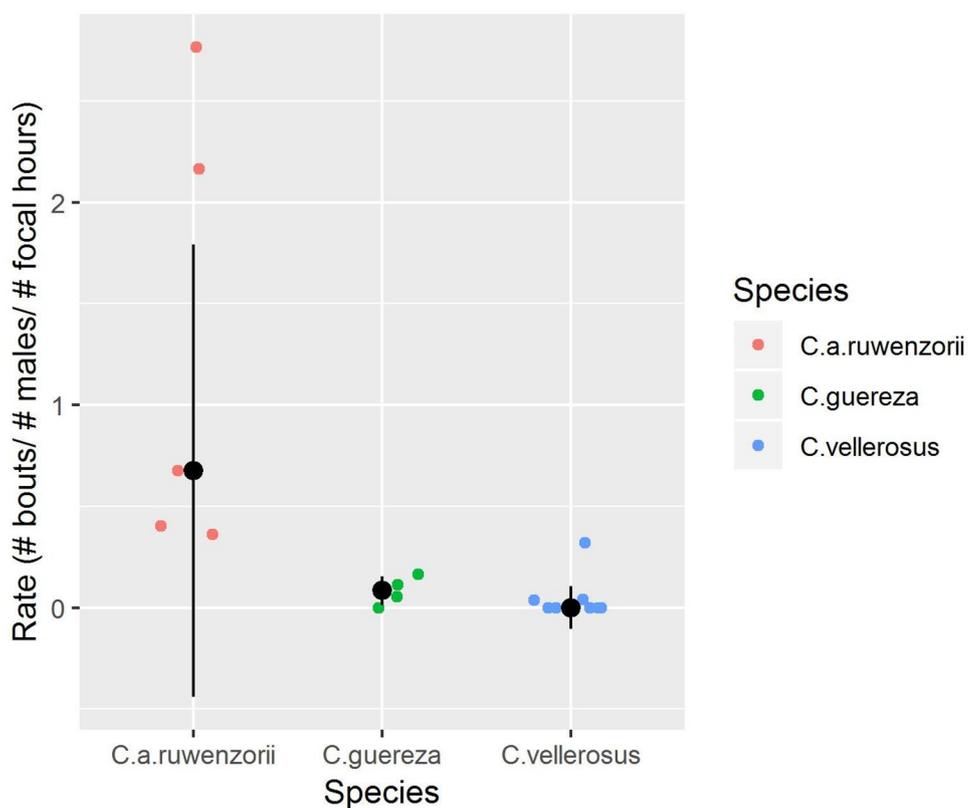
Table 2 Data on infant handling by adult male *C. guereza*

Infant ID	Group ID	Group size	# of adult males in group	Focal hours	# of handling bouts	Infant handling rates (# handling bouts/focal hours/# adult males in group)
KYINF	Kasembo	10	4	37.65	25	0.166
KOINF	Kasembo	10	4	37.4	17	0.114
BYINF	Bingi	11	1	36.3	2	0.055
TYINF	Tail	10	1	16	0	0.000

Table 3 Data on infant handling by adult male *C. a. ruwenzorii*

Infant ID	Core unit ID	Core unit size ^a	# of adult males in core unit	Focal hours	# of handling bouts	Infant handling rates (# handling bouts/focal hours/# adult males in group)	% of handling bouts initiated by adult male(s) (number of bouts with known initiator)
ASH	ANT	6	3	11.69	97	2.766	79.452 (73)
ADE	MAE	11	1	11.55	25	2.165	82.353 (17)
DOT	FAG	9	1	8.89	6	0.675	100.000 (4)
TER	FAG	9	1	7.48	3	0.401	0.000 (2)
ZAR	NEW	14	6	9.71	21	0.361	100.000 (14)

^aInfant handling by males was only observed within core units and not between core units within the band

Fig. 2 Handling rates by adult males for individual infants in *C. a. ruwenzorii*, *C. guereza*, and *C. vellerosus*. Black dots show medians and error bars show standard deviation

Interspecies comparison

Infant handling rates differed significantly between species per focal hour per male (Kruskal–Wallis: $H = 11.29$,

$df = 2$, $P = 0.004$; Fig. 2). These differences were driven by significant differences in infant handling by males between *C. vellerosus* and *C. a. ruwenzorii* (Mann–Whitney U : $N_{vellerosus} = 9$, $N_{ruwenzorii} = 5$, $W = 45$, $P = 0.002$) and

between *C. guereza* and *C. a. ruwenzorii* ($N_{\text{vellerosus}} = 4$, $N_{\text{ruwenzorii}} = 5$, $W = 0$, $P = 0.016$). *Colobus vellerosus* and *C. guereza* ($N_{\text{vellerosus}} = 9$, $N_{\text{ruwenzorii}} = 4$, $W = 27$, $P = 0.131$) did not differ in their rates of infant handling by males (Fig. 2). The Cox mixed-effects model controlling for infant ID also showed a significant difference between species in male infant handling bout durations (Coef = -1.22 , $SE = 0.26$, $Z = -4.7$, $P < 0.0001$) (Fig. 3). The pattern of initiations of infant handling bouts differed significantly between *C. a. ruwenzorii*, where males initiated 81.8% of bouts, and *C. vellerosus*, where males initiated 22.2% of bouts (Fisher's exact test: $P = 0.0004$).

Discussion

Infant handling by adult males was observed in all three species of black-and-white colobus. *Colobus a. ruwenzorii* males handled infants significantly more often and for significantly longer periods of time than males in either of the other two species. Moreover, *C. a. ruwenzorii* males tended to initiate infant handling bouts more often (81.8%) than infants (18.2%) and were regularly observed to hold infants ventrally and carry them during group movements (Fig. 4). Conversely, *C. vellerosus* handling bouts were most often initiated by infants (77.8%), and males rarely supported infants ventrally or carried them during group movement. In *C. vellerosus*, infant handling by adult males occurred most often when the males were stationary and the infants

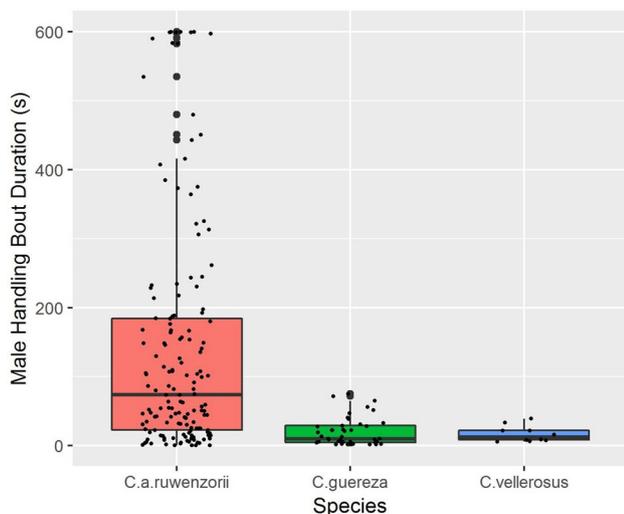


Fig. 3 Duration of observed bouts of infant handling by adult males in *C. vellerosus*, *C. guereza*, and *C. a. ruwenzorii*. Boxes show the upper and lower quartile, the line is the median (which does not consider that many bouts were right-censored in *C. a. ruwenzorii*), and the whiskers display the highest and lowest values excluding outliers, which are represented by the large dots



Fig. 4 Adult male *C. a. ruwenzorii* carrying an infant ventrally during group movement. Photo by Samantha Stead

were being supported in their lap. Though we did not obtain initiation data for *C. guereza*, handling was similar in nature to *C. vellerosus*.

Differences in infant handling by males between these species may stem from their markedly different social organizations. As mentioned, *C. a. ruwenzorii* females at Nabugabo tend to disperse outside of the band and males tend to disperse within the band (Stead and Teichroeb 2019; Fig. 1). Due to the highly connected nature of core units from the same band, it is likely that males will maintain some form of social contact with (especially male) infants for the remainder of their lives. Therefore, infant handling may serve as a way for males to begin forming social bonds with members of their social network (Dunayer and Berman 2017). *C. a. ruwenzorii* males may also be using infants as ‘props’ to bond with one another and manage social conflict, allowing them to live together despite high competition for females (‘agonistic buffering’ Deag and Crook 1971; ‘bridging’ Ogawa 1995; ‘triadic male–infant interactions’ Taub 1980; ‘male–infant–male interactions’ Zhao 1996; see above). Out of the 110 male *C. a. ruwenzorii* handling bouts observed from the beginning, 21 were initiated by a male taking an infant from another male. More research is needed to determine whether infant handling serves as a mechanism for males to facilitate bonding with infants and/or other males.

There appears to be a stark difference in the occurrence of infanticide between the three species (Hrdy 1977; van Schaik and Janson 2000). Infanticide by males occurs frequently in *C. vellerosus* living at BFMS; 38.5% of infant mortality was due to confirmed or suspected infanticide by males from 2000 to 2005 (Teichroeb & Sicotte 2008). Infanticide by males often occurs in this population during or shortly after an extra-group male(s) ousts a group’s resident male(s), or co-resident male(s) try to evict one another, resulting in a

new alpha male (Teichroeb et al. 2011, 2012; Sicotte et al. 2017). Infanticide by males has also been reported in the population of *C. guereza* living at Kanyawara, with confirmed or suspected cases following takeover events (Oates 1977; Onderdonk 2000; JMR, personal observation) as well as during intergroup encounters (Harris and Monfort 2003). Conversely, infanticide has not been observed in the *C. a. ruwenzorii* living at Nabugabo after 7 years of intensive data collection. Eight males have transferred between core units within the study band, and no aggression between these males and infants in the new core units was ever observed. Infanticide has also never been observed by researchers studying *C. a. ruwenzorii* in the Nyungwe Forest in Rwanda (A. Miller, P. Fashing, A. Vedder, personal communications). We therefore suspect that *C. a. ruwenzorii* males do not rely on infanticide as a reproductive strategy to the same extent as males in the other two *Colobus* species. This may explain why mothers in this species are more permissive of interactions between their infants and adult males. *Colobus vellerosus* and *C. guereza* subadult males handle white and grey infants more often than adult males, which suggests that infant handling decreases in these species once males reach adulthood (Bădescu 2011; Fox 2015; Raboin et al. in press). It is likely that these subadult males are in their natal groups and are handling related or familiar infants, whereas once they become adults and transfer to a new group, they become an infanticide risk and so mothers are less tolerant of handling by these males. More data are needed to understand how infant handling by males impacts the fitness of the male, the offspring, and the mother, and to determine whether benefits align with the paternal care, mating effort, and/or maternal relief hypotheses in each of these *Colobus* species.

Our findings of variation in infant handling by adult males in three closely related species with markedly different social systems may point to the importance of the social environment in the expression of this behaviour. We urge primatologists at different research sites to design standardized data collection protocols such that more comparisons of this nature are possible. Long-term and detailed comparisons of infant handling by males across species and populations will shed light on how socio-ecology and phylogeny have shaped the evolution of male–infant interactions in the Primate order (Gettler et al. 2020).

Acknowledgements We thank Katie Carmichael, Robert Koranteng, Hillary Musinguzi, Moses Tumuhaise, Richard Komuhendo, Stella Kezabu, Edward Mujjuzi, Hannington Kakeeto, and Dennis Twinomugisha for their assistance and support during data collection. Funding for work on *C. vellerosus* was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), the University of Calgary, and Sigma Xi. Funding for work on *C. guereza* was provided by the ABC Grant for Thesis Research at Hunter College and by the National Science Foundation (1521528 to JMR). Funding for work on *C. a. ruwenzorii* was provided by NSERC and the University of

Toronto School of the Environment. Work in Ghana was approved by the Ghana Wildlife Division and the Management Committee of the Boabeng-Fiema Monkey Sanctuary. Work in Uganda was approved by the Uganda Wildlife Authority and the Uganda National Council of Science and Technology. Research on *C. vellerosus* was approved by the University of Calgary's Animal Care Committee. Research on *C. guereza* was approved by the Institutional Animal Care and Use Committee at Hunter College. Research on *C. a. ruwenzorii* was approved by the University of Toronto's Animal Care Committee.

Declarations

Conflict of interest The authors have declared that no competing interests exist.

References

- Achenbach GG, Snowdon CT (2006) Costs of caregiving: weight loss in captive adult male cotton-top tamarins (*Saguinus oedipus*) following the birth of infants. *Int J Primatol* 23:179–189
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–267
- Altmann J, Samuels A (1992) Costs of maternal care: infant-carrying in baboons. *Behav Ecol Sociobiol* 29(6):391–398
- Arseneau-Robar TJM, Joyce MM, Stead SM, Teichroeb JA (2018) Proximity and grooming patterns reveal opposite-sex bonding in Rwenzori Angolan colobus monkeys (*Colobus angolensis ruwenzorii*). *Primates* 59(3):267–279
- Bădescu I (2011) The effect of female kinship and relatedness on infant handling in ursine colobus. University of Calgary (Master's dissertation)
- Bădescu I, Sicotte P, Ting N, Wikberg EC (2015) Female parity, maternal kinship, infant age and sex influence natal attraction and infant handling in a wild colobine (*Colobus vellerosus*). *Am J Primatol* 77(4):376–387
- Bauer B, Sheeran LK, Matheson MD, Li JH, Wagner RS (2013) Male Tibetan macaques' (*Macaca thibetana*) choice of infant bridging partners. *Zool Res* 35:222–230
- Berghänel A, Ostner J, Schröder U, Schülke O (2011) Social bonds predict future cooperation in male Barbary macaques, *Macaca sylvanus*. *Anim Behav* 81:1109–1116
- Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P (1999) Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups—defence pattern, paternity and sexual behaviour. *Behav Ecol Sociobiol* 46(5):350–356
- Broekhuizen S, Bouman E, Went W (1986) Variation in timing of nursing in the brown hare (*Lepus europaeus*) and the European rabbit (*Oryctolagus cuniculus*). *Mam Rev* 16(3–4):139–144
- Buchan JC, Alberts SC, Silk JB, Altmann J (2003) True paternal care in a multi-male primate society. *Nature* 425(6954):179–181
- Busse C, Hamilton WD (1981) Infant carrying by male chacma baboons. *Science* 212:1281–1283
- Charpentier MJE, VanHorn R, Altmann J, Alberts SC (2008) Paternal effects on offspring fitness in a multimale primate society. *Proc Natl Acad Sci* 105:1988–1992
- Deag JM (1980) Interactions between males and unweaned Barbary macaques: testing the agonistic buffering hypothesis. *Behaviour* 75:54–81
- Deag JM, Crook JH (1971) Social behaviour and 'agonistic buffering' in the wild barbary macaque *Macaca sylvana* L. *Folia Primatol* 15:183–200

- Dunayer ES, Berman CM (2017) Infant handling enhances social bonds in free-ranging rhesus macaques (*Macaca mulatta*). *Behaviour* 154:875–907
- Dunbar RIM (1984) Infant-use by male gelada in agonistic contexts: agonistic buffering, progeny protection or soliciting support? *Primates* 25:28–35
- Fashing PJ (2001) Feeding ecology of guerezas in the Kakamega Forest, Kenya: the importance of Moraceae fruit in their diet. *Int J Primatol* 22(4):579–609
- Fashing PJ (2011) African colobine monkeys: their behavior, ecology and conservation. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (eds) *Primates in perspectives*, 2nd edn. Oxford University Press, New York, pp 203–229
- Fernandez-Duque E, Valeggia CR, Mendoza SP (2009) The biology of paternal care in human and nonhuman primates. *Ann Rev Anthropol* 38(1):115–130
- Fox SA (2015) The effect of potential and actual paternity on positive male-infant behaviour in ursine colobus. University of Calgary (Master's dissertation)
- Fragaszy DM (1982) Longitudinal observations of care and development of infant titi monkeys (*Callicebus moloch*). *Am J Primatol* 2:191–200
- Gettler LT, Boyette AH, Rosenbaum S (2020) Broadening perspectives on the evolution of human paternal care and fathers' effects on children. *Ann Rev Anthropol* 49(1):141–160
- Gogarten JF, Jacob AL, Ghai RR, Rothman JM, Twinomugisha D, Wasserman MD, Chapman CA (2014) Group size dynamics over 15+ years in an African forest primate community. *Biotropica* 47(1):101–112
- Harris TR (2006) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). *Behav Ecol Sociobiol* 61(2):317–329
- Harris TR, Monfort SL (2003) Behavioral and endocrine dynamics associated with infanticide in a black and white colobus monkey (*Colobus guereza*). *Am J Primatol* 61(3):135–142
- Harris TR, Caillaud D, Chapman CA, Vigilant L (2009) Neither genetic nor observational data alone are sufficient for understanding sex-biased dispersal in a social-group-living species. *Mol Ecol* 18(8):1777–1790
- Hatchwell BJ (1999) Investment strategies of breeders in avian cooperative breeding systems. *Am Nat* 154:205–219
- Haunhorst CB, Heesen M, Ostner J, Schülke O (2017) Social bonds with males lower the costs of competition for wild female Assamese macaques. *Anim Behav* 125:51–60
- Heinsohn RG (2004) Parental care, load-lightening, and costs. In: Koenig WD, Dickinson JL (eds) *Ecology and evolution of cooperative breeding in birds*. Cambridge University Press, Cambridge, pp 67–80
- Hrdy SB (1977) Infanticide as a primate reproductive strategy. *Am Sci* 65:40–49
- Huchard E, Charpentier MJ, Marshall H, King AJ, Knapp LA, Cowlshaw G (2012) Paternal effects on access to resources in a promiscuous primate society. *Behav Ecol* 24:229–236
- Huck M, Fernandez-Duque E (2013) When dads help: male behavioral care during primate infant development. In: Clancy KBH, Hinde K, Rutherford JN (eds) *Building babies*. Springer New York, New York, pp 361–385
- Kalbitz J, Schülke O, Ostner J (2017) Triadic male-infant-male interaction serves in bond maintenance in male Assamese macaques. *PLoS ONE* 12(10):e0183981
- Kerhoas D, Kulik L, Perwitasari-Farajallah D, Agil M, Engelhardt A, Widdig A (2016) Mother-male bond, but not paternity, influences male-infant affiliation in wild crested macaques. *Behav Ecol Sociobiol* 70(8):1117–1130
- Langos D, Kulik L, Mundry R, Widdig A (2013) The impact of paternity on male-infant association in a primate with low paternity certainty. *Mol Ecol* 22:3638–3651
- Langos D, Kulik L, Ruiz-Lambides A, Widdig A (2015) Does male care, provided to immature individuals, influence immature fitness in rhesus macaques? *PLoS ONE* 10(9):e0137841
- Lappan S (2008) Male care of infants in a siamang (*Symphalangus syndactylus*) population including socially monogamous and polyandrous groups. *Behav Ecol Sociobiol* 62(8):1307–1317
- Ménard N, von Segesser F, Scheffrahn W, Pastorini J, Vallet D, Gaci B, Martin RD, Gautier-Hion A (2001) Is male-infant caretaking related to paternity and/or mating activities in wild Barbary macaques (*Macaca sylvanus*)? *C R Acad Sci* 324:601–610
- Mendoza SP, Mason WA (1986) Parental division of labour and differentiation of attachments in a monogamous primate (*Callicebus moloch*). *Anim Behav* 34:1336–1347
- Miller A, Uddin S, Judge DS, Kaplin BA, Ndayishimiye D, Uwingeneye G, Grueter CC (2020) Spatiotemporal association patterns in a supergroup of Rwenzori black-and-white colobus (*Colobus angolensis ruwenzorii*) are consistent with a multilevel society. *Am J Primatol* 82:e23127
- Minge C, Berghänel A, Schülke O, Ostner J (2016) Patterns and consequences of male-infant relationships in wild Assamese macaques (*Macaca assamensis*). *Int J Primatol* 37(3):350–370
- Murray CM, Stanton MA, Lonsdorf EV, Wroblewski EE, Pusey AE (2016) Chimpanzee fathers bias their behaviour towards their offspring. *R Soc Open Sci* 3(11):160441
- Oates JF (1977) The social life of a black-and-white colobus monkey, *Colobus guereza*. *Z Tierpsychol* 45:1–60
- Ogawa H (1995) Bridging behavior and other affiliative interactions among male Tibetan macaques (*Macaca thibetana*). *Int J Primatol* 16(5):707–729
- Onderdonk DA (2000) Infanticide of a newborn black and white colobus monkey (*Colobus guereza*) in Kibale National Park, Uganda. *Primates* 41:209–212
- Ostner J, Schülke O (2014) The evolution of social bonds in primate males. *Behaviour* 151:871–906
- Paul A, Preuschoft S, van Schaik CP (2000) The other side of the coin: infanticide and the evolution of affiliative male-infant interactions in Old World primates. In: van Schaik CP, Janson CH (eds) *Infanticide by males and its implications*. Cambridge University Press, Cambridge, pp 269–292
- Price EC (1990) Infant carrying as a courtship strategy of breeding male cotton-top tamarins. *Anim Behav* 40(4):784–786
- R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>
- Raboin DL, Baden AL, Rothman JM (in press) Maternal feeding benefits of allomaternal care in black-and-white colobus (*Colobus guereza*). *Am J Primatol*
- Ransom TW, Ransom BS (1971) Adult male-infant relations among baboons (*Papio anubis*). *Folia Primatol* 16:179–195
- Rosenbaum S, Gettler LT (2018) With a little help from her friends (and family) part I: the ecology and evolution of non-maternal care in mammals. *Physiol Behav* 193:1–11
- Rosenbaum S, Vigilant L, Kuzawa CW, Stoinski TS (2018) Caring for infants is associated with increased reproductive success for male mountain gorillas. *Sci Rep* 8(1):15223
- Ross C (2001) Park or ride? Evolution of infant carrying in primates. *Int J Primatol* 22(5):749–771
- Saj T, Teichroeb JA, Sicotte P (2005) The population status of *Colobus vellerosus* at Boabeng-Fiema sacred grove, Ghana. In: Paterson JD, Wallis J (eds) *Commensalism and conflict: human-primate interface*. American Society of Primatology, Oklahoma, pp 350–375

- Schradin C, Anzenberger G (2001) Costs of infant carrying in common marmosets, *Callithrix jacchus*: an experimental analysis. *Anim Behav* 62(2):289–295
- Schülke O, Bhagavatula J, Vigilant L, Ostner J (2010) Social bonds enhance reproductive success in male macaques. *Curr Biol* 20:2207–2210
- Sharp JA, Cane KN, Lefevre C, Arnould JPY, Nicholas KR (2006) Fur seal adaptations to lactation: insights into mammary gland function. *Curr Top Dev Biol* 72:275–308
- Sicotte P, Macintosh A (2004) Inter-group encounters and male incursions in *Colobus vellerosus* in Central Ghana. *Behaviour* 141(5):533–553
- Sicotte P, Teichroeb JA, Vayro JV, Fox SA, Bădescu I, Wikberg EC (2017) The influence of male takeovers on female dispersal in *Colobus vellerosus*. *Am J Primatol* 79:e22436
- Smuts B (1985) Sex and friendship in baboons. Cambridge University Press, Cambridge
- Städele V, Roberts ER, Barrett BJ, Strum SC, Vigilant L, Silk JB (2019) Male-female relationships in olive baboons (*Papio anubis*): parenting or mating effort? *J Hum Evol* 127:81–92
- Stead SM, Teichroeb JA (2019) A multi-level society comprised of one-male and multi-male core units in an African colobine (*Colobus angolensis ruwenzorii*). *PLoS ONE* 14(10):e0217666
- Taub DM (1980) Testing the “agonistic buffering” hypothesis: I. The dynamics of participation in the triadic interaction. *Behav Ecol Sociobiol* 6(3):187–197
- Teichroeb JA, Sicotte P (2008) Infanticide in ursine colobus monkeys (*Colobus vellerosus*) in Ghana: new cases and a test of the existing hypotheses. *Behaviour* 145:727–755
- Teichroeb JA, Wikberg EC, Sicotte P (2009) Female dispersal patterns in six groups of ursine colobus (*Colobus vellerosus*): infanticide avoidance is important. *Behaviour* 146:551–582
- Teichroeb JA, Sicotte P, Wikberg EC (2011) Dispersal in male ursine colobus monkeys (*Colobus vellerosus*): influence of age, rank and contact with other groups on dispersal decisions. *Behaviour* 148(7):765–793
- Teichroeb JA, Wikberg EC, Bădescu I, Macdonald LJ, Sicotte P (2012) Infanticide risk and male quality influence optimal group composition for *Colobus vellerosus*. *Behav Ecol* 23:1348–1359
- Therneau T (2015) Package ‘Survival’: a package for survival analyses in R.
- Therneau T (2020) Package ‘coxme’: mixed effects cox models.
- van Schaik CP, Janson CH (2000) Infanticide by males and its implications. Cambridge University Press, Cambridge
- Whitten P (1987) Infants and adult males. In: Smuts B, Cheney D, Seyfarth R, Wrangham R, Struhsaker T (eds) *Primate societies*. University of Chicago Press, Chicago, pp 343–357
- Wikberg EC, Sicotte P, Campos FA, Ting N (2012) Between-group variation in female dispersal, kin composition of groups, and proximity patterns in a black-and-white colobus monkey (*Colobus vellerosus*). *PLoS ONE* 7(11):e48740
- Wong SNP, Sicotte P (2006) Population size and density of *Colobus vellerosus* at the Boabeng-Fiema Monkey Sanctuary and surrounding forest fragments in Ghana. *Am J Primatol* 68(5):465–476
- Wright P (1984) Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In: Small M (ed) *Female primates: studies by women primatologists*. Alan R, Liss, New York, pp 59–75
- Xiang Z-F, Sayers K, Grueter CC (2009) Direct paternal care in black-and-white snub-nosed monkeys. *J Zool* 278(2):157–162
- Young C, Majolo B, Heistermann M, Schülke O, Ostner J (2014) Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. *Proc Natl Acad Sci USA* 111:18195–18200
- Zhao Q-K (1996) Male-infant-male interactions in Tibetan macaques. *Primates* 37(2):135–143

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.