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Female Parity, Maternal Kinship, Infant Age and Sex Influence Natal Attraction and Infant Handling in a Wild Colobine (*Colobus vellerosus*)

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Primate females often inspect, touch and groom others' infants (*natal attraction*) and they may hold and carry these infants in a manner resembling maternal care (*infant handling*). While natal attraction and infant handling occur in most wild colobines, little is known about the factors influencing the expression of these behaviors. We examined the effects of female parity, kinship, and dominance rank, as well as infant age and sex in wild *Colobus vellerosus* at Boabeng-Fiema Monkey Sanctuary, Ghana. We collected data via focal sampling of females in 2008 and 2009 ($N = 61$) and of infants in 2010 ($N = 12$). Accounting for the individuals who interacted with our focal subjects, this study includes 74 females and 66 infants in 8 groups. We recorded female agonistic interactions *ad libitum* to determine dominance ranks. We used partial pedigree information and genotypes at 17 short tandem repeat loci to determine kinship. We knew female parity, infant age and sex from demographic records. Nulliparous females showed more natal attraction and infant handling than parous females, which may suggest that interactions with infants are more adaptive for nulliparous females because they learn mothering skills through these behaviors. Compared to non-kin, maternal kin were more likely to handle infants. Maternal kin may be permitted greater access to infants because mothers are most familiar with them. Handlers may incur inclusive fitness benefits from infant handling. Dominance rank did not affect female interactions with infants. The youngest infants received the most natal attraction and infant handling, and male infants were handled more than female infants. The potential benefits of learning to mother and inclusive fitness, in combination with the relatively low costs of natal attraction and infant handling, may explain the high rates of these behaviors in many colobines. Am. J. Primatol.

Key words: colobine; natal attraction; infant handling; parity; kinship; dominance

INTRODUCTION

In most primate species, females inspect, touch, and groom others' infants (*natal attraction*), which can lead to holding and carrying of these infants in a manner that resembles maternal care (*infant handling*) [Hrdy, 2009]. While natal attraction shows an individual's interest in an infant, infant handling also depends on whether the mother is willing to allow independent interactions between her infant and the handler [Hrdy, 2009; Maestripieri, 1994]. Hence, the females who show the most natal attraction are not necessarily the ones who most often get to handle infants [Maestripieri, 1994].

Natal attraction and infant handling are documented in many primate species but relatively little is known about the factors influencing the expression of these behaviors [MacKinnon, 2011; Ross & MacLarnon, 2000]. In the following paragraphs, we discuss key factors shaping natal attraction and infant handling in primates, including female parity, kinship and dominance, as well as infant age and sex.

Female Parity

Nulliparous, immature females show higher rates of natal attraction and infant handling than parous females in most primate species [e.g. *Cercopithecus*

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mitis stuhlmanni: Förster & Cords, 2005; *Colobus vellerosus*: Brent et al., 2008; *Macaca mulatta*: Ross & MacLarnon, 2000; *M. fuscata*: Kurland, 1977; *Semnopithecus entellus*: Scollay & DeBold, 1980]. Nulliparous females may show high rates of handling because practicing their mothering skills on other females' infants may later improve the survivorship of their own infants, and hence their future reproductive success ["learning-to-mother" hypothesis: Lancaster, 1971; van Noordwijk, 2012].

Parous females show the highest rates of natal attraction and infant handling in some species [e.g. *Cercocebus atys*: Fruteau et al., 2011; *C. polykomos*: Horwich & Manski, 1975; *Erythrocebus patas:* Muroyama, 1994; *Lemur catta*: Gould, 1992; *Trachypithecus johnii*: Poirier, 1970; *T pileatus:* Stanford, 1992]. Natal attraction and infant handling by parous females can reflect a general interest in infants that is a by-product of selection for maternal behavior [Maestripieri, 1994]. They may also promote the possibility of adoption if the infant's mother dies or create favorable social bonds with higher-ranking animals [Maestripieri, 1994].

Female Kinship

Females often interact most with related infants [e.g. *Cebus olivaceus*: O'Brien & Robinson, 1991; *Chlorocebus aethiops*, several *Macaca spp.*: Kapsalis, 2004; *Papio cynocephalus*: Silk et al., 2003a,b]. Kin biases in natal attraction and infant handling are often explained by Hamilton's [1964] "kin selection" theory. Handlers may gain inclusive fitness benefits from promoting the survival of related infants, or from contributing to earlier weaning and reduced inter-birth intervals of related females [Hrdy, 2009]. Handlers can also gain inclusive fitness benefits when they enable related mothers to spend more time feeding and grooming unencumbered by their infants [Hrdy, 2009]. Natal attraction and infant handling also occur between unrelated individuals [e.g. *C. m, stuhlmanni*: Förster & Cords, 2005; *E. patas*: Muroyama, 1994; *M. fuscata*: Ross & MacLarnon, 2000; *T. pileatus*: Stanford, 1992] but mothers are generally more protective of their infants when approached by non-kin [Hrdy, 2009].

Female Dominance

In species with despotic dominance relationships, high-ranking females often have priority of access to infants [e.g. *C. olivaceus*: O'Brien & Robinson, 1991; *M. radiata*: Silk, 1999; *C. atys*, *C. aethiops*: Fruteau et al., 2011; *P. cynocephalus*: Altmann, 1980; Henzi & Barrett, 2002; but see Bentley-Condit et al., 2001]. Furthermore, subordinate females may resist infant handling attempts directed at their infants, probably for fear of not being able to retrieve them from dominant females [e.g. *M. fuscata*, *M. mulatta*: Chism, 2000; but see Bentley-Condit et al., 2001]. In a few species, subordinate females often handle the infants of dominant mothers, and later benefit from this service through received grooming, tolerance from the mother while feeding and coalitionary support [e.g. *M. sylvanus*: Paul & Kuester, 1996; *P. c. ursinus*: Cheney, 1978].

Investigations of the effects of dominance on infant handling have focused on a limited number of despotic, female philopatric cercopithecines [Chism, 2000]. These primates usually display linear dominance hierarchies based on matrilineal inheritance of rank, which makes it difficult to tease apart the influences of maternal kinship and rank distance on behavior [Chapais, 2001; Kapsalis, 2004; Seyfarth, 1977]. The confounding effect of kinship and dominance on behavior is not an issue in species with individualistic dominance hierarchies (i.e. rank based on individual characteristics like body size or age). Because submissive and agonistic interactions are infrequent in these species, long-term observations are required to identify dominance hierarchies [e.g. *C. vellerosus*: Wikberg et al., 2013; *Gorilla beringei*: Robbins et al., 2005; *S. entellus*: Koenig, 2000; *T. phayrei*: Koenig et al., 2004]. It may consequently not be possible to determine the effects of dominance on natal attraction and infant handling during short-term studies of these species [e.g. Horwich & Manski, 1975; Jay, 1962]. However, a few studies report that access to infants is not affected by the handlers' relative dominance ranks in species where dominance interactions occur infrequently [e.g. *T. pileatus*: Stanford, 1992; *M. thibetana*: Berman et al., 2004].

Infant Influences on Natal Attraction and Infant Handling

In addition to female characteristics, infant age and sex may also influence natal attraction and infant handling. Primate females are generally most interested in the youngest infants [e.g. *C. vellerosus*: Brent et al., 2008; *M. radiata*: Silk, 1999; *P. c. ursinus*: Silk et al., 2003a] and natal attraction and infant handling tend to decrease or cease when infants become older and more independent [MacKinnon, 2011]. Mothers may allow extensive infant handling within the first few days of life [e.g. *Cercopithecus spp.*, *E. patas*: Chism, 2000; *T. leucocephalus*: Yao et al., 2012] but in other species, they may resist handling until infants are older [e.g. *M. fuscata*, *M. fascicularis*, *Papio spp*, *Theropithecus spp.*: Chism, 2000].

The frequent occurrence of natal attraction and infant handling in colobines relative to other primate taxa is perhaps associated with the contrasting natal coat color found in most colobine species [Hrdy, 1976; Treves, 1997]. Females show the most natal attraction and infant handling toward infants that display a natal coat and these behaviors decrease as infants get older and their natal coats disappear [Hrdy, 1976, 2009].

The sex of infants can also influence caregiving behaviors. Parental care can be biased toward male or female infants when investing in one sex over the other later leads to greater fitness outcomes for the caregiver [Bercovitch, 2002]. In female philopatric species for example, females may show greater interest and handling toward female infants because building these early relationships can later provide handlers with coalitionary partners once infants become adults. The early formation of social relationships among females may be the reason why *C. m. stuhlmanni* female infants spend more time than male infants in close proximity to adult females other than their mother [Förster & Cords, 2005]. Investigations of several other female philopatric primates however, report a lack of sex biases in natal attraction and infant handling [e.g. *M. radiata*: Silk, 1999; *M. fuscata*: Schino et al., 2003; *T. pileatus*: Stanford, 1992].

Research Objectives and Study Species

We know little about how social and demographic factors affect natal attraction and infant handling in colobines despite the fact that the occurrence of these behaviors is well-documented across species [Hrdy, 2009; Maestripieri, 1994; McKenna, 1979]. Here, we examine the influences of female parity, kinship and dominance, as well as infant age and sex on the expression of natal attraction and infant handling in a wild black-and-white colobus, *C. vellerosus* (ursine colobus or white-thighed colobus).

C. vellerosus is an arboreal, folivorous species [Saj & Sicotte, 2007] living in uni-male/multi-female and multi-male/multi-female groups [Wong & Sicotte, 2006]. Several characteristics make *C. vellerosus* an ideal species in which to investigate variation in the expression of natal attraction and infant handling. First, all females show natal attraction and infant handling, although rates of expression vary [Bădescu, 2011; Brent et al., 2008]. A preliminary study of six *C. vellerosus* infants showed that nulliparous females exhibited higher rates of natal attraction and infant handling than parous females [Brent et al., 2008]. We aimed to verify and expand on Brent et al.'s [2008] findings by using multivariate statistical tests on new behavioral data collected over three years from 66 infants, and with information on female parity, dominance rank [Wikberg et al., 2013], kinship [Wikberg et al., 2014a], infant age and sex.

Second, *C. vellerosus* females show facultative dispersal and the majority of females reside with both maternal kin and non-kin, which means that potential handlers have a choice between interacting with related and unrelated infants [Teichroeb et al., 2009; Wikberg et al., 2012, 2014a].

Third, females show individualistic dominance ranks based on individual characteristics. The potential effect of dominance in *C. vellerosus* is independent from kinship because females do not form nepotistic dominance hierarchies [Wikberg et al., 2013]. The dominance hierarchies are of intermediate strength, which means that females engage in submissive and agonistic dominance interactions less frequently than females in species with strict dominance hierarchies [Wikberg et al., 2013].

Fourth, infants are born with a completely white natal coat that darkens to gray between 7 and 12 weeks of age, and that finally changes to the adult black-and-white coloring after 12 weeks [Brent et al., 2008]. The patterning of natal coat changes (i.e. order in which areas of the body change color) is consistent for all infants as they age, which makes it possible for different observers to establish the onset of each color stage [MacDonald, 2011]. Brent et al. [2008] found that contrary to most colobines, white and gray infants were not handled more than black-and-white infants even though they were more attractive. We aimed to verify this preliminary report and assess the importance of coat color in predicting natal attraction and infant handling relative to other factors.

Predictions

We expected that (a) nulliparous females would exhibit natal attraction and infant handling more than parous females [Maestripieri, 1994; Brent et al., 2008]; (b) kin would exhibit more natal attraction and infant handling than non-kin [Kapsalis, 2004]; and (c) female dominance would not influence natal attraction and infant handling, congruent with results from other egalitarian colobines [Hrdy, 1976; Scollay & DeBold, 1980; Stanford, 1992]. In addition, we expected (d) females would show equal rates of natal attraction and infant handling to both male and female infants, according to most investigations in other species [Schino et al., 2003; Silk, 1999; Stanford, 1992], and (e) the youngest, white and gray infants would receive more natal attraction and infant handling than older, black-and-white infants [Treves, 1997].

METHODS

Study Site and Subjects

We conducted this study at Boabeng-Fiema Monkey Sanctuary (BFMS) in central Ghana (7° 43'N and 1° 42'W). BFMS is a 1.92 km^2 forest fragment that is connected to smaller forest fragments. *C. vellerosus* group sizes at BFMS range from 9 to 38 individuals [Wong & Sicotte, 2006]. Infants are born throughout the year, and females give birth every 1.5–2 years [Teichroeb & Sicotte, 2008a]. Male takeovers and infanticide occur regularly at BFMS; observational and circumstantial evidence suggest that male infanticides accounted for 38.5% of the infant mortality between 2000 and 2005 [Saj & Sicotte, 2005; Teichroeb & Sicotte, 2008a; Teichroeb et al., 2012]. For more details on BFMS, see Wong and Sicotte [2006] and Teichroeb and Sicotte [2008b].

Our study subjects resided in eight habituated groups (Table I), and they were individually recognizable from distinguishing permanent physical characteristics. Experienced observers overlapped in the field every year to ensure consistency in animal identification and data collection. Our study groups contained a total of 66 infants (0–1 year old) and 77 females (>2 years old) across all of our data collection periods combined (Table I). We did not include males in this study. Allonursing is extremely rare in *C. vellerosus*, and mothers display the greatest attentiveness and most frequent proximity with their own infants [Bădescu, 2011; MacDonald, 2011]. Hence, we could easily identify mother-infant dyads from observational data because we observed most infants from birth.

Behavioral Data Collection

ECW, IB, and three trained research assistants collected data from May 2008 to June 2009, and May 2010 to November 2010. We followed one to several groups daily from 06:00–18:00, and distributed our observations of each animal evenly between mornings and afternoons. We collected data using 10-minute focal animal sampling [Altmann, 1974] with continuous recording. For the focal individual, we recorded all directed and received behaviors, along with the identity of the interactants. We terminated our focal follow if the subject was out of view for more than one minute. We did not include time out of view when calculating the total number of focal hours in our analyses. Each day, the order with which we initially sampled focal individuals in each group was typically random. If we had an uneven number of focal hours per individual in the same group because we could not find some individuals during the previous sampling day or because the samples were terminated early, we attempted to even out the focal time by sampling individuals with less time in the beginning of each round of focals. After the initial round of focal samples, we sampled individuals in the same order for the rest of the day. We re-sampled each individual at a minimum of 30-minute intervals.

In 2008 and 2009, we collected focal samples from all females older than three years ($N = 61$) in the eight study groups. We collected a mean of 16.7 focal hours per female (±SD: 3.1, range: 7.3–19.3; Table I), and a mean of 1.3 focal samples per female, per day (±SD: 0.4, range: 0.7–2.1). Most of the females with fewer focal hours than the mean reside in BO group, because we started to collect data from this previously unhabituated group five months after the start of the field season in 2008. In 2010, we sampled 12 infants in four study groups. We collected a mean of 19.7 focal hours per individual (±SD: 12.3, range: 4.7–42.5; Table I), and a mean of 4.0 focal samples per infant, per day (±SD: 2.3, range: 0.6–7.9). The focal data per infant differ markedly because some infants were present during the whole data collection period while others were born at the end of the data collection period. We excluded three females from the analyses because we did not obtain sufficient behavioral data from them. Accounting for the individuals who interacted with our focal animals, our data set in the two data collection periods actually includes 66 infants and 74 females, and a total of 643 female-infant dyads. The infants in the 2008–2009 data set ($N = 54$) are different from the infants in the 2010 data set ($N = 12$) because the infants in the first data collection period had become juveniles before the start of the second data collection period. Thus, the female-infant dyads were different in the two data collection periods.

Behavioral Definitions

We established that “infant handling” occurred when females other than the mother used their arms or legs to hold or carry infants in a physically

TABLE I. Study Groups, Subjects and Focal Sampling Hours

Group ID	Number of infants	Infant mean number of focal hours (SD)	Number of females	Female mean number of focal hours (SD)	Total number of focal hours
BO	8	0[a]	11	10.6 (1.6)	116
BS	9	16.0 (0.7)	9	18.0 (1.0)	158
DA	8	0[a]	9	18.1 (0.5)	163
NP	5	0[a]	6	18.2 (0.5)	91
OD	9	30.1 (17.7)	9	17.0 (0.7)	222
RT	10	0[a]	10	19.8 (0.6)	139
SP	6	15.7 (5.9)	8	17.8 (0.8)	121
WW	11	13.2 (2.5)	15	17.3 (0.8)	243
Total 8	66	19.7 (12.3)	77	16.7 (3.1)	1253

[a] Infants were not focal subjects in this group and data were obtained from females only.

supportive way [Bădescu, 2011; Brent et al., 2008; Ross & MacLarnon, 2000]. We established that "natal attraction" occurred when we observed the following behaviors: prolonged inspection of an infant from a close distance, licking, grooming, attempting to touch or actually touching, attempting to transfer or actually transferring an infant when it was alone or held by its mother, or grooming the mother while she held her infant [Brent et al., 2008; Meaney et al., 1990; Silk et al., 2003a]. Natal attraction often leads to infant handling, but not necessarily so. When natal attraction and infant handling occurred sequentially, we counted the event in each of the two behavioral categories. Infant handling sometimes occurred without being preceded by natal attraction when infants were the ones initiating contact (e.g. infant jumps in female's lap and female subsequently begins to handle infant). When a female held an infant while simultaneously grooming, touching, or inspecting it, we counted this as infant handling only. Infant handling and natal attraction could simultaneously occur if one female held or carried an infant while another female touched, groomed or inspected the same infant.

Fecal Sample Collection and Genetic Analyses

We collected at least two fecal samples from each female in the eight groups [e.g. Strier et al., 2011]. To avoid contamination, we wore hats, gloves, and protective cloths over the mouth and nose, and used sterile sticks when collecting the samples. For each sample, we stored 1–2 g of fecal matter in 6 ml RNAlater® solution inside a sterile vial that was sealed with a cap and Parafilm wrap to avoid leakage and contamination [Nechvatal et al., 2008]. We kept the samples in a refrigerator (4°C) for up to 12 months while in the field and in a deep freezer (−20°C) in the Ting Laboratory (before and after analysis). We extracted DNA and amplified the extracts at 17 short tandem repeat loci [see Wikberg et al., 2012 for details regarding the laboratory protocol]. All animals included in the analyses below have at least 12 loci with confirmed genotypes. We used CERVUS [Kalinowski et al., 2007; Marshall et al., 1998] to determine the maternity and/or paternity of individuals whenever possible [see Wikberg et al., 2012 for details]. We determine the kinship of 374 mother-handler dyads from demographic records or assigned parentage analyses, and for 269 dyads whose kinship could not be determined in this way, we estimated their kinship using R values (i.e. dyadic estimated relatedness values). We calculated R using Milligan's [2003] dyadic likelihood estimator in the software COANCESTRY [Wang, 2010; see Wikberg et al., 2012 for details]. Because inferring kinship solely from R values may not be reliable [Csilléry et al., 2006; Robinson et al., 2013; van Horn et al., 2008; but see and Wikberg et al., 2014b], we used known kin dyads to determine the observed range of R for kin and non-kin [Wikberg et al., 2014a]. We used the lower 99% confidence interval of known half-siblings and grandparent-grandoffspring dyads to distinguish kin ($R \geq 0.28$) from non-kin ($R < 0.28$) [see Wikberg et al., 2014a for details].

Ethical Note

These methods were approved by the University of Calgary's Animal Care Committee, Ghana Wildlife Division, and management committee of Boabeng-Fiema Monkey Sanctuary. This research also adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Non Human Primates.

Data Analyses

Because some females did not interact with every infant in the group, many female-infant dyads had natal attraction and infant handling rates of zero. Of the total 643 female-infant dyads that could possibly interact, 269 of these dyads showed natal attraction and 137 dyads showed infant handling. Most multivariate statistical tests do not provide an appropriate error structure to deal with continuous response variables that have excess zero values [e.g. Gomes & Boesch, 2011]. To mitigate this problem, we analyzed how female kinship, dominance and parity, and infant age and sex influenced the 1) presence or absence of natal attraction and infant handling as binary response variables (i.e. who is most likely to show these behaviors), and 2) rates of natal attraction and infant handling as continuous response variables that exclude all female-infant dyads that never interacted (i.e. among females that show these behaviors, who does so most often) [e.g. Gomes & Boesch, 2011].

Natal attraction and infant handling

For each female-infant dyad, we first determined whether natal attraction or infant handling occurred (presence/absence). Second, we divided the frequency of natal attraction or infant handling bouts by the total number of focal hours for the handler or the infant to get hourly rates of behaviors per infant, by coat color. We counted natal attraction or infant handling as distinct bouts when behaviors were separated by at least 30 seconds. We used the focal hours for female handlers during the 2008–2009 study period and the focal hours for infants during the 2010 study period. We calculated behavioral rates using focal rather than dyadic hours because we did not collect focal samples of handlers and infants during the same data collection period.

Female kinship

We analyzed how kinship between the female handler and the mother affected natal attraction and infant handling using two ways of recognizing kinship: "overall kinship" that included both maternal and paternal kin, and "maternal kinship" that included only maternal kin (see below). First, we analyzed differences in interactions between overall kin and non-kin. We established these kinship categories using ranges of dyadic *R* values. The overall kin category corresponds to mother-daughter, full sister, half sister, full aunt-niece, and grandmother-granddaughter dyads. The non-kin category corresponds to more distantly related and unrelated dyads. All females in our study groups had access to infants of both overall kin and non-kin, and we analyzed the effect of overall kinship in our full data set of female-infant dyads.

Second, we analyzed differences in interactions between maternal kin and non-kin in a subset of females for which we could determine maternal kinship from the demographic records or the parentage analysis. This smaller subset included 57 infants and 31 females (15 parous and 16 nulliparous) in 7 groups, resulting in 261 female-infant dyads. Maternal kin included mother- daughter and maternal sister dyads, while all other dyads were classified as non-kin. We excluded all possible grandmother-granddaughter dyads from this subset because this type of kin relationship remained unknown in the majority of dyads. We included only those handlers who had access to infants of both maternal kin and non-kin females. We analyzed only the presence or absence of natal attraction and infant handling because we did not have a sufficient number of handlers that interacted with infants of maternal kin and of non-kin at rates greater than zero.

Female dominance

We used submissive behaviors to compute females' elo-ratings [Neumann et al., 2011; Wikberg et al., 2013]. We standardized the probabilistic dominance ranks at the end of each field season (June 2009 and October 2010) by dividing the probabilistic rank number (range: 1,587–3,970) of each female by the highest rank in the group, which yielded numbers from 0.25 (lowest ranking) to 1 (highest ranking). We calculated the difference in standardized dominance ranks between the mother and the handler, with positive differences indicating that the mother is higher-ranking than the handler. The dominance ranks of 10 nulliparous females remained unknown because of few or no observed dominance interactions. Since we could not calculate the relative dominance rank for these females, we excluded them from our analyses.

Parity of female handlers

We distinguished parous from nulliparous females according to whether they had visible, elongated nipples from nursing infants, a larger body size that also appears more filled out, and a long, sleek pelage. Parous females include adult females that have given birth once (primiparous) or multiple times (multiparous). We observed around 82% of nulliparous females, and 8% of parous females, since infancy.

Infant coat color

We identified whether infants had a white, gray or black-and-white coat color, visually on each observation day. For the analyses, we lumped the youngest white and gray infants together in one category (white/gray) because these infants displayed a natal coat that stood out to handlers, whereas the hair of black-and-white infants looked identical to the adult pelage. To assess the effect of coat color, we calculated the variables separately for each infant when it had a white/gray coat and when it had a black-and-white coat.

Infant sex

We identified the sex of infants based on observations of their genitalia. Of our study infants, 42% were females, 52% were males and 6% were unknown. The infants with unknown sex were excluded from our analyses.

Random effects and covariates

We used infant and handler identities as random effects to control for repeated measurements of the same individuals. We included study period (2008–2009, 2010), the number of available handlers, and the number of white/gray infant months as covariates in the analyses. We used the number of available handlers as a covariate if the number remained the same throughout the study. If the number of available handlers changed partway through the data collection period, we used the weighted average of available handlers, which takes into account proportions of time with different numbers of available handlers. We calculated the number of white/gray infant months as the average number of other white/gray infants during each month in each group. This measure allowed us to account for the number of attractive white/gray infants that may influence rates of natal attraction and infant handling towards a specific infant.

Statistical test

We created Generalized Linear Mixed Models to assess the influence of the fixed effects (female parity, kinship, dominance, infant coat color, and sex) on natal attraction and infant handling as binary response variables and continuous response variables. We never included female parity and dominance in the same model because these variables were collinear, as all but two nulliparous handlers were lower ranking than the mothers. We used an information-theoretic approach [Burnham & Anderson, 2002] to select between candidate models that each investigated one or more of the hypotheses

TABLE II. Models Predicting the Presence (Binary) and Variation in Rates (Continuous) of Natal Attraction, the Fixed Effects Included in Each Model, and Each Model's AIC Corrected for Small Samples Sizes (AICc), Delta (i.e. Difference in AICc Between Each Model and the Best Fitting Model), and Akaike Weight (i.e. the Normalized Model Likelihoods). All Models Included Infant and Handler Identities as Random Effects

		Presence/absence			Presence/absence maternal kin			Rates		
Model	Fixed effects	AICc	Delta	Weight	AICc	Delta	Weight	AICc	Delta	Weight
Null	–	734.67	51.90	0.00	295.12	21.86	0.00	687.72	25.89	0.00
Covariates	Study period + # white/gray (WG) infant months + # handlers	709.08	26.31	0.00	286.97	13.72	0.00	686.42	24.60	0.00
Parity	Parity + study period + # WG infant months + # handlers	**685.34**	**2.57**	**0.22**	**273.25**	**0.00**	**0.70**	**663.30**	**1.47**	**0.32**
Kinship	Kinship + study period + # WG infant months + # handlers	710.58	27.82	0.00	289.06	15.80	0.00	687.33	25.50	0.00
Dominance	Dominance rank + study period + # WG infant months + # handlers	703.78	21.01	0.00	284.08	10.83	0.00	677.03	15.21	0.00
Coat color	Coat color + study period + # WG infant months + # handlers	708.17	25.40	0.00	286.88	13.63	0.00	683.85	22.03	0.00
Infant sex	Sex + study period + # WG infant months + # handlers	710.40	27.64	0.00	289.08	15.82	0.00	687.43	25.61	0.00
Combined model with parity	Parity + kinship + sex + coat color + study period + # WG infant months + # handlers	**682.77**	**0.00**	**0.78**	**275.03**	**1.78**	**0.29**	**661.82**	**0.00**	**0.68**
Combined model with dominance	Dominance rank + kinship + sex + coat color + study period + # WG infant months + # handlers	702.81	20.04	0.00	286.62	13.37	0.00	676.70	14.87	0.00

outlined in the introduction (Table II and Table III). We evaluated the support for each model based on Akaike Information Criterion (AIC) values [Akaike, 1974]. We ran the statistical analyses using the package lme4 [Bates et al., 2014] in R version 3.1.0. [R Core Team, 2014]. Because several models received similar support, we took model selection uncertainty into account by averaging coefficients across models [Burnham & Anderson, 2002] using R package MuMIn [Barton, 2013].

RESULTS

Presence and Absence of Natal Attraction

Of the models predicting rates of natal attraction, two of our alternative models (the parity model

TABLE III. Models Predicting the Presence (Binary) and Variation in Rates (Continuous) of Infant Handling, the Fixed Effects Included in Each Model, and Each Model's AIC Corrected for Small Samples Sizes (AICc), Delta (i.e. Difference in AICc Between Each Model and the Best Fitting Model), and Akaike Weight (i.e. the Normalized Model Likelihoods). All Models Included Infant and Handler Identities as Random Effects

		Presence/absence			Presence/absence maternal kin			Rates		
Model	Fixed effects	AICc	Delta	Weight	AICc	Delta	Weight	AICc	Delta	Weight
Null	–	501.31	37.96	0.00	242.60	30.01	0.00	378.22	17.21	0.00
Covariates	Study period + # white/gray (WG) infant months + # handlers	476.86	13.50	0.00	225.65	13.06	0.00	376.44	15.44	0.00
Parity	Parity + study period + # WG infant months + # handlers	471.66	8.30	0.01	221.44	8.85	0.01	**363.54**	**2.54**	**0.22**
Kinship	Kinship + study period + # WG infant months + # handlers	477.78	14.42	0.00	222.37	9.78	0.00	378.19	17.18	0.00
Dominance	Dominance rank + study period + # WG infant months + # handlers	472.83	9.47	0.00	220.73	8.14	0.01	376.51	15.51	0.00
Coat color	Coat color + study period + # WG infant months + # handlers	**465.67**	**2.32**	**0.16**	220.39	7.80	0.01	375.56	14.56	0.00
Infant sex	Sex + study period + # WG infant months + # handlers	478.84	15.48	0.00	227.75	15.16	0.00	375.44	14.44	0.00
Combined model with parity	Parity + kinship + sex + coat color + study period + # WG infant months + # handlers	**463.35**	**0.00**	**0.52**	**212.59**	**0.00**	**0.50**	**361.00**	**0.00**	**0.78**
Combined model with dominance	Dominance rank + kinship + sex + coat color + study period + # WG infant months + # handlers	**464.42**	**1.07**	**0.30**	**212.67**	**0.08**	**0.48**	376.15	15.14	0.00

and the combined model that also included parity) received greater support than the other models (Table II). Nulliparous females were more likely to engage in natal attraction than parous females (Fig. 1A), and this fixed effect had the highest variable importance (i.e. sum of the normalized model likelihood over all models including the fixed effect). Coat color had a high variable importance, and females were less likely to engage in natal attraction with black-and-white infants (Fig. 1A). Although there was a positive effect of the mother's relative dominance rank on natal attraction, this fixed effect had an extremely low variable importance (Fig. 1A). There was no consistent effect of kinship or infant sex on the likelihood of natal attraction.

When restricting the analysis to handlers that resided with infants of both maternal kin and non-kin, we also obtained the greatest support for the parity model and the combined model with parity (Table II). There was no consistent effect of maternal kinship on natal attraction (Fig. 1B). The effects of the other fixed effects were similar as in the analysis of the likelihood of natal attraction in our full dataset.

Rates of Natal Attraction

We obtained similar results as above when we investigated rates of natal attraction (Table II). Female parity had the greatest variable importance, and nulliparous females showed higher rates of natal attraction than parous females (Fig. 1C). Black-and-white infants received lower rates of natal attraction than white/gray infants, and this fixed effect had an intermediate variable importance (Fig. 1C). Infants received higher rates of natal attraction when their mother was higher ranking than the handler, but this fixed effect had an extremely low variable importance (Fig. 1C). There were no consistent effects of kinship or sex on rates of natal attraction.

Presence and Absence of Infant Handling

Three of the alternative models (the coat color model and the combined models with parity/dominance rank) received stronger support than the other models (Table III). Coat color had a high variable importance, and black-and-white infants had a lower probability of being handled (Fig. 2A). Nulliparous females were more likely to engage in infant handling than parous females, and this fixed effect had an intermediate variable importance (Fig. 2A). Although infants were more likely to be handled if their mothers were higher ranking than the handler, this fixed effect had lower variable importance than parity (Fig. 2A). There were no consistent effects of kinship or sex on the likelihood of handling.

When restricting the analysis to females that resided with infants of maternal kin and non-kin, the two combined models (with parity versus dominance rank) received stronger support than the other models (Table III). Maternal kin were more likely to engage in infant handling than non-kin and this fixed effect had high variable importance (Fig. 2B). The effect of infant coat color and sex, female parity and relative dominance rank were similar as in the analysis of the presence and absence of infant handling in our full data set.

Rates of Infant Handling

When analyzing rates of infant handling, two of the alternative models (the parity model and the combined model with parity) received stronger

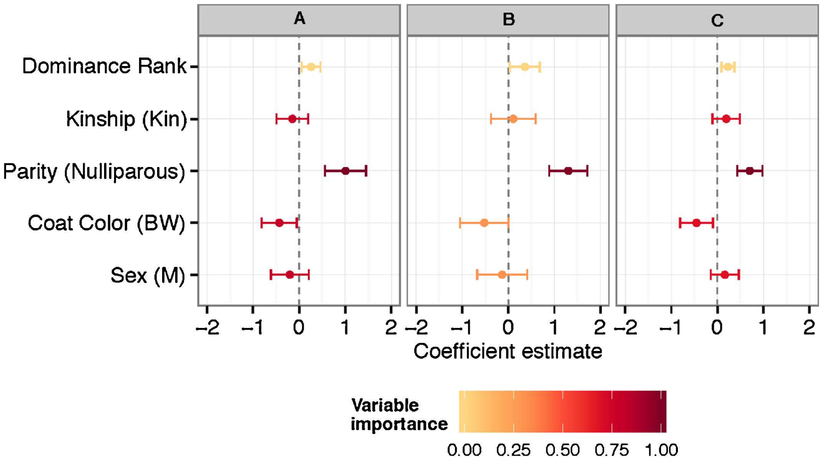

Fig. 1. Coefficient estimates and their 95% confidence intervals averaged across models investigating the presence/absence of natal attraction of all females (A), the presence/absence of natal attraction of maternal kin and non-kin only (B), and the variation in rates of females that showed natal attraction (C). The mother's relative dominance rank is a continuous fixed effect, and the remaining fixed effects are binary: kinship between the mother and the handler, handler parity, infant coat color (BW = black-and-white), and infant sex (M = male). The color represents variable importance (i.e. sum of the normalized model likelihood over all models including the fixed effect).

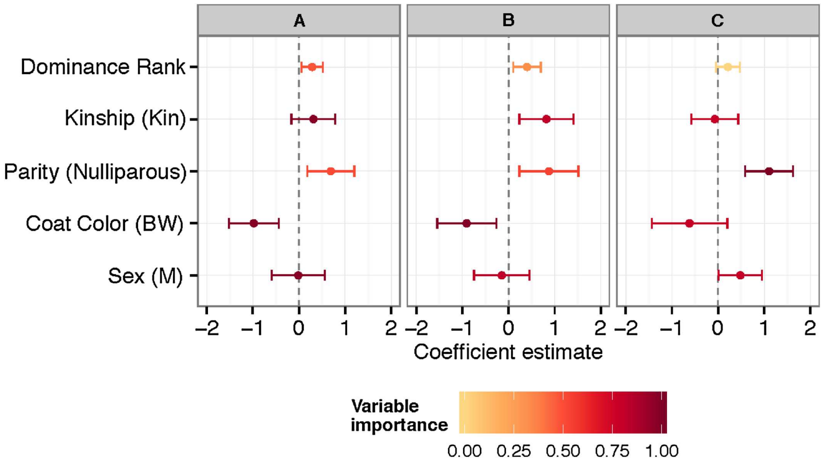

Fig. 2. Coefficient estimates and their 95% confidence intervals averaged across models investigating the presence/absence of infant handling of all females (A), the presence/absence of infant handling of maternal kin and non-kin only (B), and the variation in rates of females that showed infant handling (C). The mother's relative dominance rank is a continuous fixed effect, and the remaining fixed effects are binary: kinship between the mother and the handler, handler parity, infant coat color (BW = black-and-white), and infant sex (M = male). The color represents variable importance (i.e. sum of the normalized model likelihood over all models including the fixed effect).

support than the other models (Table III). Female parity had the greatest variable importance, and nulliparous females handled at higher rates than parous females (Fig. 2C). Infant sex also had relatively high variable importance, and male infants were handled at higher rates than female infants (Fig. 2C). There were no significant effects of kinship, coat color, and dominance rank on rates of infant handling.

DISCUSSION

Female Parity

We examined the effects of female kinship, dominance and parity, as well as infant age and sex on natal attraction and infant handling in a wild African colobine. Female parity had the greatest predictive power for both natal attraction and infant handling in *C. vellerosus*. Nulliparous females had higher rates, and were more likely to show natal attraction and infant handling than parous females. This finding is in line with with Brent et al.'s [2008] preliminary report from the same population, and it is also similar to other colobines [*T. johnii*: Poirier, 1968; *S. entellus*: Hrdy, 1976; Scollay & DeBold, 1980; *Trachypithecus leucocephalus*: Yao et al., 2012] and several cercopithecines [*C. aethiops*: Lancaster, 1971; Meaney et al., 1990; *C. m. stuhlmanni*: Förster & Cords, 2005; *M. fuscata*: Kurland, 1977; Schino et al., 2003]. These studies and our results are consistent with the notion that immature females may learn mothering skills through infant handling, which can be beneficial for their own offspring rearing and reproduction [e.g. *Callithrix jacchus*, *Saguinus Oedipus*: Tardif et al., 1984; *C. aethiops*: Fairbanks, 1990; Lancaster, 1971; MacKinnon, 2011].

Female Kinship

Female *C. vellerosus* bias affiliation to long-term co-resident female kin [Wikberg et al., 2014a,b], and our study further shows that females are more likely to handle the infants of their maternal kin. Similarly, several nepotistic and philopatric cercopithecines also exhibit kin-biased infant handling [*C. aethiops*: Fairbanks, 1988, 1990; several *Macaca spp.*: Chism, 2000; Kapsalis, 2004; *P. cynocephalus*: Altmann, 1980; Silk et al., 2003a,b; Sterck et al., 1997]. Most studies of colobines could not evaluate the effects of kinship on infant handling due to insufficient genealogical data [e.g. *Colobus guereza*, *C. polykomos*, *Procolobus badius*: Horwich & Manski, 1975; Korstjens et al., 2002; *T. johnii*: Poirier, 1968; *T. pileatus*: Stanford, 1992]. However, our results are analogous to the kin-biased infant handling of *S. entellus* [Borries, 1988; Sommer, 1989; Hrdy, 2009], a colobine for which genealogical data are available [Borries et al., 1991; Hrdy & Hrdy, 1976; Koenig, 2000].

In contrast to maternal kinship, overall kinship that includes both maternal and paternal kinship did not influence the expression of infant handling in *C. vellerosus*. This disparity may be due to methodological differences in determining maternal kin versus combined kin. Maternal kinship was based on demographic information or parentage analyses, which are considered robust estimates of kinship. In contrast, the combined kin category was based on *R* values, and even though *R* is relatively accurate in our study population [Wikberg et al., 2014b], it is possible that this kin category contains a small proportion of non-kin. Alternatively, these findings may indicate that females are unable to distinguish paternal kin from non-kin or that they do not benefit from biasing their behaviors toward paternal kin [also see Wikberg et al., 2014b]. It is therefore plausible that females show maternal kin bias in infant handling based on their greater familiarity rather than kinship [Chapais, 2001]. A lack of paternal kin bias is consistent with many species of primates, with the exception of a few cercopithecines [Rendall, 2004]. Consequently, it may only be maternal kin who can incur inclusive fitness benefits from infant handling [Hamilton, 1964; Maestripieri, 1994].

Female Dominance

Female *C. vellerosus* biased natal attraction and infant handling to infants whose mothers were higher ranking. Dominance rank however, always had lower variable importance than parity, and we suspect that the significant effect of dominance is a by-product of parity because these two variables are collinear (i.e. nulliparous females are almost always lower ranking than the mothers). This is in line with a lack of an effect of dominance on affiliative and coalitionary behaviors between females in our population [Wikberg et al., 2014a]. Thus, we conclude that dominance rank is not important in shaping natal attraction and infant handling, which is similar to other primate species with individualistic and/or relatively egalitarian dominance hierarchies [e.g. *E. patas*, *T. pileatus*: Maestripieri, 1994; *Macaca thibetana*: Berman et al., 2004].

Infant Age and Sex

The youngest *C. vellerosus* infants received the greatest interest and females handled them most. These results differ from Brent et al.'s [2008] preliminary report on this species, which found that the youngest infants were not handled most, but they are analogous to the trend documented for most primates [MacKinnon, 2011; Maestripieri, 1994]. Our results suggest that natal coats in *C. vellerosus* may have evolved to attract attention and induce handling from females during the most vulnerable time in infants' lives, when they need the most care [Hrdy, 2009; Treves, 1997].

Contrary to our predictions, male infants received higher rates of infant handling than female infants. Most species in which sex-biased female infant handling has been investigated do not show a sex bias [Schino et al., 2003; Silk, 1999; Stanford, 1992], possibly because building relationships early is not useful when infant mortality is high [van Noordwijk, 2012]. Our results are puzzling and this trend should be examined more closely. Infanticidal males in our population attack male infants more often than female infants [Teichroeb & Sicotte, 2008a]. Male-biased infant handling may therefore reflect a greater need to protect male infants because of a higher infanticide risk.

CONCLUSION

Our findings provide some support for the learning-to-mother and kin selection hypotheses. To fully investigate the learning-to-mother hypothesis, we need to compare the future rearing success of females that were frequent versus infrequent infant handlers [e.g. Paul & Kuester, 1996; Silk, 1999]. To test whether maternal kin gain inclusive fitness benefits from handling, we should measure possible fitness benefits that related mothers gain from this interaction, such as increased fecundity, foraging efficiency and infant survival [e.g. Paul & Kuester, 1996].

Similar factors shaped both natal attraction and infant handling in this study, which suggests that mothers permit handling on demand by the females that show natal attraction. Given that infant handling is seldom costly for *C. vellerosus* mothers [i.e. infants are rarely dropped or roughly handled: Bădescu, 2011; Brent et al., 2008] and because inexperienced, nulliparous females are most often allowed to interact with infants regardless of their dominance rank, it is likely that mothers incur greater benefits than costs when other females handle their infants. This is probably the case for most colobine species [Maestripieri, 1994; McKenna 1979]. Even though further studies of the fitness benefits of natal attraction and infant handling are required [MacKinnon, 2011; Maestripieri, 1994], our findings suggest that there may be multiple potential benefits, which in combination with relatively low costs, contribute to explaining the high rates of natal attraction and infant handling in *C. vellerosus* and other colobines.

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