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Evidence for paternal kin bias in the social affiliation of adult female blue monkeys

Marina Cords^{1,2}  | Taylor Minich¹ | Su-Jen Roberts^{1,2,3} | Clio Sleator⁴

¹ Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, New York

² New York Consortium in Evolutionary Primatology, New York, New York

³ Department of Education, Wildlife Conservation Society, Bronx, New York

⁴ Department of Physics, University of California, Berkeley, California

Correspondence

Marina Cords, Department of Ecology, Evolution and Environmental Biology, Columbia University, 10th Floor Schermerhorn Extension, 1200 Amsterdam Avenue, New York, NY 10027.
Email: mc51@columbia.edu

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If animals increase inclusive fitness by cooperating with relatives, nepotism should involve maternal and paternal kin equally, all else being equal. Evidence of a behavioral bias toward paternal half-siblings in primates is both limited and mixed, with most positive reports from papionins. To expand knowledge of paternal kin recognition, particularly in cercopithecine monkeys, we examined evidence for paternal kin bias in wild blue monkeys (*Cercopithecus mitis*), a species living mostly in one-male groups. Seasonal breeding and the amount of male reproductive skew in blue monkeys suggests that opportunities to distinguish paternal kin are plentiful, and their social system would make such discrimination beneficial. We compared spatial association and social contact (grooming and contact-sitting) of 20 adult females with at least one paternal half-sibling and at least one non-relative that were present at the same time. We used two data sets, one in which social partners were other parous females, the other in which they were juveniles. Data came from a 7-year period. When interacting with other adult females, subjects groomed and sat in contact with paternal half-siblings significantly more than with known non-kin, and there was a similar trend for spatial association. We detected no paternal kin bias in interactions with juvenile partners. Kin-biased affiliative contact with adult female partners did not appear to be based on age proximity, measured by birth cohort. The study species' social system suggests phenotype matching as the most likely alternative mechanism, though we could not test it directly. Across both behaviors, there was no significant relationship between the number of matrilineal kin a subject had and the degree to which she preferred paternal half-siblings over non-kin as affiliative partners. These findings contribute to a comparative understanding of paternal kin recognition in primates.

KEYWORDS

kin discrimination, kin selection, kinship, nepotism, social behavior

1 | INTRODUCTION

In many animals including primates, cooperative acts, which benefit others, are biased toward kin. If actors increase their inclusive fitness by cooperating with relatives, such nepotism should involve maternal and paternal kin equally, all else being equal. All else may not be equal, however, if maternal versus paternal kin are not equally available or

distinguishable, or if their presence or behavior as social partners benefits the cooperative actor differentially (Berman, 2011; Chapais & Belisle, 2004). The importance of partner availability is implicit in the common observation that sex-biased natal dispersal correlates with sex-biased nepotism (Langergraber, 2012). When females are philopatric, as in most cercopithecine monkeys, groups comprise one or more matrilineal lines, with many opportunities for cooperative

interactions among maternal kin; and indeed, affiliative behavior is well known to correlate with maternal kinship in these monkeys (Cords, 2012a), as well as in other primates with similar social organization (Perry, Manson, Muniz, Gros-Louis, & Vigilant, 2008). However, individuals in these societies may also have paternal kin available as social partners, and might therefore be expected to act nepotistically toward paternal relatives too (Widdig, 2007).

While there are reports of enhanced nepotism to paternal siblings in rodents and hyenas (reviewed in Widdig, 2007), evidence that female-philopatric primates bias behavior toward paternal kin is both limited and mixed. A key issue is the mechanism of paternal kin recognition. Langergraber (2012) recent review emphasized age proximity as one, though not the only, potential cue for paternal sibship, especially when male reproductive skew is high. Age proximity is not always a reliable cue, however, especially if certain males dominate paternity over multiple cohorts of infants, fathering siblings that differ substantially in age. Langergraber also raised the issue of breeding seasonality as a potential influence on paternal kin recognition through age proximity: in seasonally breeding species, close-aged siblings would grow up together, forming the early and enduring social bonds that function as a kin recognition mechanism. At the same time, however, when mating is seasonal, reproductive skew among males is expected to decrease because of lower monopolization potential, thus reducing the chance that two like-aged offspring are paternal siblings. Examining taxa with various mating systems and degrees of reproductive seasonality is key to differentiating the relative importance of these effects, and the role of age similarity as a cue of paternal sibship more generally.

Another factor that may influence whether paternal kin are treated specially is the demographic context, which likely drives differential motivation or opportunity to develop close bonds (Hill, 2004). Demographic effects on female social interaction with maternal kin have been documented in various primates, in which a bias toward maternal kin is stronger in larger groups because of constraints on time available for social exchange (Berman & Thierry, 2010). Demographic effects on social interaction with paternal kin, and particularly paternal half-sibs, are less well known, but some have been documented. In wild yellow baboons (*Papio hamadryas cynocephalus*), for example, the bonds of adult females to paternal sisters were stronger if fewer close maternal relatives were present (Silk, Altmann, & Alberts, 2006). In olive baboons (*P. anubis*), juveniles formed closer bonds with paternal half-sib peers when the common father was present in their group (Lynch, DiFiore, Lynch, & Palombit, 2017).

To expand knowledge of paternal kin recognition, particularly in cercopithecine monkeys, we studied a population of wild blue monkeys (*Cercopithecus mitis*). Blue monkeys are female-philopatric like nearly all other cercopithecines, but have a different mating system from baboons and macaques, in which paternal kin relations have been studied. Specifically, a given group of philopatric females and young typically contains just one adult male, and females therefore appear to have few options as mates. Resident male tenure is variable, and a given male may persist in a group for up to 7.5 years. In such a system, age proximity may be a cue of limited accuracy in assessing paternal sibship.

Blue monkeys are also known, however, for their dynamic breeding system. Like other guenons (Butynski, 1988), they are seasonal breeders, with 64% of births occurring over an annual 3-month span in our study population (Cords & Chowdhury, 2010). In some mating seasons, multiple males invade a group of females and mate with them (Cords, 2002a). Such influxes set the stage for non-resident paternity, and indeed, residents may fail to sire about 40% of the young born into their groups (Roberts, Nikitopoulos, & Cords, 2014). Multiple paternity within a single cohort of offspring is another reason why age proximity may provide an inaccurate cue of paternal sibship in this species. Other kin recognition mechanisms (such as phenotype matching, or developmental association) could be possible, however, at least in principle.

Our study aimed to evaluate whether adult female blue monkeys discriminate paternally related kin, specifically paternal half-siblings, from non-relatives by examining sociopositive behavior. To match the choices made by individuals, we used a within-subjects design, asking whether a given female interacted at higher rates with her paternal sib/s (unrelated maternally) versus group-mates that were known to be neither paternally nor maternally related, when both were simultaneously present in her group. Finding some evidence for such kin bias, we examined whether age similarity could be the proximate mechanism. We also compared across females to see if the degree to which they favored paternal kin partners was related to the size of the female's matriline.

2 | METHODS

2.1 | Study population and participants

The study population inhabits the Isecheno area of the Kakamega Forest, western Kenya (0°19'N, 34°52'E), a fairly high altitude (1,580 m) rain forest (ca. 2,000 mm annual rainfall) comprising various habitat types (Mitchell, Schaab, & Wägele, 2009). This population has been under study since 1979 (Cords, 2012b), with up to six groups monitored simultaneously over the 7-year period (2010–2016) relevant to this study. Blue monkey groups comprise one or several matriline and, as noted above, a single non-natal adult male for the most part.

Long-term study of the population provided us with (1) pedigrees that enabled identification of maternal kin relations above $r = 0.0625$ (half-first-cousins) at least; and (2) focal sample data from adult females (details below), who were our subjects. The analysis was necessarily limited to animals whose paternity was known. Paternity information (details below) was available from a previous study of male reproductive strategies, which included offspring born over 10 years in eight groups (Roberts & Cords, 2015; Roberts et al., 2014). Offspring from that previous study had now grown up, such that some were adult females and others were still pre-reproductive juveniles. Because adult females interact differently with their peers versus with juvenile partners (Cords & Chowdhury, 2010; Cords & Nikitopoulos, 2015), we created two datasets to evaluate whether adult female subjects favored paternal half-sibs over unrelated partners: one in which their partners were other adult (parous) females, and another in which partners were juveniles (pre-reproductive if female, pre-dispersal if male, all ≥ 3 years old).

For both datasets, we identified paternal siblings based on Roberts et al.'s (2014) microsatellite analysis, which used fecal DNA from offspring, mothers, and candidate fathers, and likelihood-based methods (Cervus 3.0, Kalinowski, Taper, & Marshall, 2007). Cervus requires the user to input a value for the proportion of males in the population that were sampled. As explained in the previous study, estimates of this proportion varied from year to year (Roberts et al., 2014, Table S3), so the authors examined how the observed range of values affected paternity assignments, finding that while the confidence of some assignments was sensitive to this value, the identity of the most likely father was always consistent. The present analysis included only individuals who were consistently assigned to one particular male with confidence levels of 95% throughout (87% of 68 individuals) or a with confidence levels of 95% or 80% (13% of individuals) depending on the value input for the proportion of males sampled. PHS shared the same assigned father, but were unrelated maternally. MNK were neither paternal siblings, nor related maternally.

Our analysis was based on a within-subjects comparisons (see Data Analysis), so we included adult female as subjects only if they had at least one PHS and at least one MNK available at the same time. All such females were included in the final dataset, as long as they were present along with their PHS and MNK for ≥ 50 days; we chose this cut-off so that data on a subject's social affiliation derived from a reasonable observational sample. The final set of animals in the analysis included 20 adult female subjects (18 in the adult partner dataset, 14 in the juvenile partner dataset, 12 of whom were in both), belonging to three social groups (mean adult group sizes over study period: 18.4/1.6 females/males, 17.9/1.1 females/males, 9.2/1.0 females/males) and 15 individuals who were adult social partners, 38 who were juvenile social partners (with 13 in both sets). Some partners served as a paternally related partner for one (or more) subjects but an unrelated partner for other subjects. The adult female subjects had 1–7 PHS (mean \pm SD: 3.5 ± 2.5) and 1–7 MNK (mean \pm SD: 3.3 ± 2.4) that were also adult females, and 1–20 PHS (mean \pm SD: 9.5 ± 7.4) and 1–22 MNK (mean \pm SD: 8.0 ± 7.2) that were juveniles.

2.2 | Behavioral data collection

Behavioral data came from long-term monitoring (Cords, 2012b), in which a team of trained observers followed each study group on a near daily basis, collecting focal animal samples (Altmann, 1974) of the behavior of all adult females while ensuring similar observation rates across individuals and across the morning, midday, and afternoon hours. During each 30-min sample, observers made instantaneous records at 1-min intervals of the subject's activity and social/proximity partners. Activities included grooming/being groomed, sitting in bodily contact (without grooming), feeding, moving, and resting. In addition, observers noted the identity of grooming and contact-sit partners, and which group-mates were "neighbors." Neighbors included all individuals within 7 m when the subject was feeding, and all individuals within 1 m if she was grooming or resting (i.e., not feeding or moving). We used larger proximity thresholds for feeding than for grooming/resting because group members are typically more dispersed while

feeding (Cords, 2002b); the 7 m criterion captured neighbors that could approach quickly, in just one or two leaps, and was also feasible in the forested environment. Observers could not score neighbors accurately if the subject was moving.

We used data from this database to represent the social activity of our female subjects. The mean number of observation hours used to assess each subject's social interactions with other adult females was $149.3 \pm \text{SD } 85.4$ hr collected over $744 \pm \text{SD } 420$ days ($N = 136$ triads of subject, PHS and MNK); in the dataset assessing interactions with juvenile partners, each subject averaged $119.3 \pm \text{SD } 64.3$ hr collected over $607 \pm \text{SD } 322$ days ($N = 507$ triads).

Our research complied with protocols approved by the Columbia University IACUC, and adhered to the legal requirements of Kenya and to the ASP Principles for the Ethical Treatment of Primates.

2.3 | Data analysis

As noted above, our analysis aimed to assess choices made by adult female subjects who had at least one PHS and one MNK simultaneously available as a social partner. Many subjects had more than one of each type of partner (see Results), allowing us to include multiple comparisons of related versus unrelated partners for each subject. Keeping the comparison within individual adult females minimized the potential effect of unmeasured (and perhaps unknown) factors that could influence social affiliation.

We used two measures of social affiliation to compare how subjects interacted with PHS versus MNK. The first was the proportion of time (i.e., proportion of activity records), excluding feeding and moving, in which the subject was in affiliative physical contact (grooming with or simply sitting in contact) with her partner. Previous study of this population showed that grooming is clearly biased toward maternal kin (Cords & Nikitopoulos, 2015). The second measure incorporated information on spatial association in various situations, particularly who was within 1 m when a subject was engaged in any activity other than moving or feeding, and who was within 7 m when she was feeding. Here, a female's total score was weighted according to how much time she spent in the different activities where spatial association was monitored in the field. Thus this measure represented overall spatial association across all activities, rather than the first more exclusive physical contact measure.

For the analysis, we designated as "a triad" each unique combination of a subject, one PHS and one MNK. Most individuals were members of several triads (each subject averaged 7.3 ± 3.4 triads for contact and 7.6 ± 3.5 for association with adult partners, and 25.7 ± 17.3 for contact, 36.1 ± 19.5 for association with juvenile partners), sometimes both as subject and as partner. For each triad, we calculated the difference in the proportion of time the subject affiliated with the related versus the unrelated partner. We averaged these PHS-MNK differences across all triads in the data set to create a test statistic, the "mean K-NK difference." This statistic expresses the average degree to which affiliative scores are higher for PHS than MNK partners.

To test the significance of the test statistic, we used a randomization test, permuting paternities in each social group 10,000 times. For a

single permutation, we randomly assigned each paternity within a social group to a monkey in the same social group. The relative frequency of paternity assignments across males was unchanged by this procedure, which altered only which animals were assigned as offspring of a given male. After each permutation, we computed the mean K-NK difference across all triads. After 10,000 permutations, we had a distribution of estimates of our test statistic, the mean K-NK difference, based on randomly assigned paternity, and we could compare the observed value to this distribution.

After finding evidence that affiliation with PHS was stronger than with non-kin, we examined whether relative age proximity might explain this effect. We used linear mixed models to predict K-NK (the degree to which the subject interacted more with her PHS relative to MNK) as a function of relative age differences between herself and her two partners, including random effects of subject, kin partner and non-kin partner identity. We expressed age differences in terms of annual cohorts: a subject and her partner were in the same cohort (cohort difference = 0) if their birthdates were <1 year apart, in subsequent cohorts (cohort difference = 1) if ≥ 1 but <2 years apart (no matter which individual was older), and so forth. In one model, relative age difference was the subject's cohort difference with MNK minus the cohort difference with PHS: this difference should predict the strength of kin-biased social behavior if kin

recognition is based on relative age similarity to the subject. In a second model, we used a binary classification of how the subject's age related to that of her two partners: here, triads in which (i) the PHS was in the subject's cohort; and (ii) the MNK was in a different cohort were coded as kin bias "expected" and all other relative ages were coded as "not expected." "Not expected" included triads in which both PHS and MNK were in the subject's cohort, and triads in which neither partner was in the subject's cohort. If kin recognition was based on being in the same cohort, one would kin bias in social behavior to be stronger for triads with kin bias "expected" versus "not expected."

We also explored whether the number of matrilineal kin affected the degree of paternal kin-bias shown by our subjects toward adult female partners, using linear mixed models to see if a subject's matriline size predicted the difference between her average PHS versus average MNK score. We ran separate models for the two behavioral measures, and included matriline identity as a random effect as two matrilineal included two subjects each. We computed mean matriline size for each subject over the timespan between her earliest and latest focal observations that were part of our data set. Matrilineal included all animals known to be related maternally, though we also examined a set of closest relatives, that is, mother, offspring, and maternal sisters.

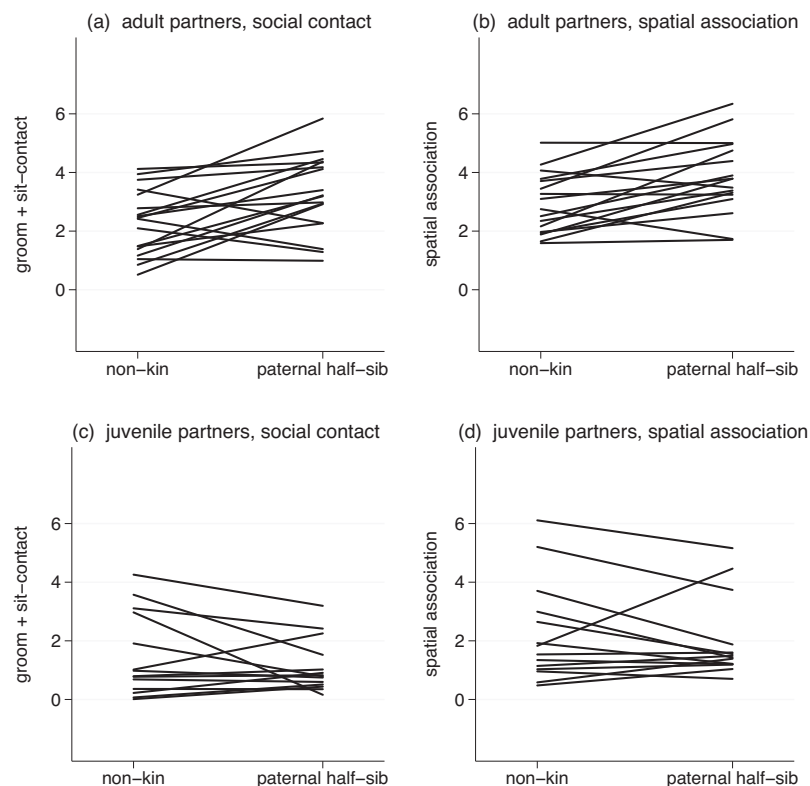


FIGURE 1 Affiliative social behavior (% of time) of adult female subjects with unrelated versus paternal half-sib partners. (a) Social contact (grooming or sitting in contact, as percentage of activity other than feeding or moving) with other adult females. (b) Spatial association across all activities other than moving (see text for details) with other adult females. (c) Social contact with juvenile partners. (d) Spatial association with juvenile partners. Each line represents one adult female subject ($N = 18$ for adult partners, $N = 14$ for juvenile partners), for whom social data were averaged for each partner type (paternal kin vs. non-kin) for illustrative purposes: actual statistical analysis used "triads" of subject, kin and non-kin partners, as described in the text. Averaged across subjects, values for kin peers exceeded those for non-kin peers by a factor of 1.8 for social contact, and 1.3 for spatial association

3 | RESULTS

3.1 | Kin bias in social affiliation

The 18 subjects for whom we could evaluate paternal kin-bias for adult female social partners averaged 3.3 ± 2.4 paternal half-sibs and 3.3 ± 2.4 non-kin partners. Six subjects had more kin than non-kin, nine had fewer kin than non-kin, and three had equal numbers (namely one) each. For adult female partners, the mean K-NK difference for affiliative contact was 0.42% ($N = 136$ triads, 18 subjects), a value falling at the 95th percentile of the simulated mean scores (i.e., one-tailed $p < 0.047$); thus overall, adult female subjects spent significantly more time in contact with peers that were paternal half-sibs versus those that were unrelated (Figure 1a). Results were similar but not quite significant (by conventional standards) when we compared spatial association: the mean K-NK difference was 0.77%, falling at the 92nd percentile (i.e., one-tailed $p < 0.082$; Figure 1b).

The 14 adult female subjects for whom we could evaluate preferences for juvenile social partners averaged 9.5 ± 7.4 paternal half-sibs and 7.9 ± 7.2 non-kin partners. Seven subjects had more known paternal kin than non-kin, and seven had fewer kin than non-kin. Adult females interacting with juvenile partners did not appear to favor paternal half-sibs over non-kin. The mean K-NK difference for affiliative contact was -0.15% ($N = 360$ triads, 14 subjects), falling at the 22nd percentile of simulated mean scores (i.e., $p < 0.783$; Figure 1c). The mean K-NK difference for spatial association was -0.23% , falling at the 31st percentile (i.e., $p < 0.690$; Figure 1d).

The absence of a kinship effect for juvenile partners did not appear to relate to the particular sex or age composition of triads in the dataset. That is, when we limited analysis to triads in which both juvenile partners were female (14 subjects, 129 triads) or both were male (10 subjects, 125 triads), there was still no kinship effect (contact: $p = 0.744$ for females, $p = 0.676$ for males; association $p = 0.497$ for females, $p = 0.840$ for males). Similarly, when we limited analysis to triads in which the juvenile half-sib was not more discrepant in age (i.e., annual cohorts) relative to the subject than was the unrelated juvenile partner—a situation that might obscure kin recognition based on age similarity—there was still no evidence that affiliation was stronger for PHS than for MNK (contact: $p = 0.534$, association $p = 0.417$, 14 subjects, 330 triads).

3.2 | Is kin discrimination based on age similarity?

The paternal kin bias we observed in affiliative contact with adult female partners did not appear to reflect a subject's relative age similarity with her two matched partners. The degree to which nonkin partners were more discrepant in age than kin did not predict the amount of kin bias in affiliative contact ($\beta = -0.00023$, $p = 0.672$, 95% CI: -0.00130 – 0.00084). In addition, subjects "expected" to recognize kin from their own birth cohort relative to non-kin of different cohorts did not show a stronger kin bias than subjects "unexpected" to recognize kin based on such a comparison ($\beta = -0.00332$, $p = 0.121$, 95% CI: -0.00751 – 0.00087).

3.3 | Effects of matriline size

Subjects belonged to matrilineages that varied considerably in size (range: 1.9–27.2 members). However, matriline size was not significantly related to the difference between mean PHS versus MNK scores: in other words, subjects interacting with peers did not modify their bias toward paternal half-sibs versus non-kin as a function of the number of matrilineal kin available to them (contact $\beta = -0.00010$, $p = 0.614$, 95% CI: -0.00051 – 0.00030 , spatial association $\beta = -0.00003$, $p = 0.938$, 95% CI: -0.00084 – 0.00078). Assessing matriline size based only on close relatives (mother, offspring, maternal sisters, with numbers of such relatives ranging from 0.4–6.4 per subject) did not change these results (contact: $\beta = 0.00059$, $p = 0.424$, 95% CI: -0.00085 – 0.00203 , spatial association: $\beta = 0.00130$, $p = 0.348$, 95% CI: -0.00141 – 0.00400).

4 | DISCUSSION

4.1 | Recognition of paternal half-siblings in comparative context

When interacting with other adult females, adult female blue monkeys biased their sociopositive behavior, particularly affiliative physical contact, toward paternal half-siblings relative to unrelated individuals. A paternal kin bias for general spatial association was weaker, though evident. When interacting with juvenile partners, however, adult females showed no bias toward paternal half-sibs over non-kin, even when we separated juvenile partners by sex, or omitted cases in which the relative age discrepancy of kin versus non-kin might have obscured a kinship effect based on age similarity.

These results mirror a known maternal kin bias among adult female blue monkeys, and similarly show a stronger effect for more intimate affiliative contact compared to simple spatial association (Cords & Nikitopoulos, 2015). Our findings contrast, however, with those from the only other study of kin recognition in guenons (*C. solatus*, Charpentier, Deubel, & Peignot, 2008), which documented enhanced sociopositive behavior among maternal kin but no difference between paternal kin (i.e., half-siblings) and non-kin. It is possible that this short study of a small group of 10 captive animals of mixed ages did not have the power to detect paternal kin recognition, though it did reveal what appears to be a stronger pattern of maternal (vs. paternal) kin bias.

Our findings also agree with reports from other cercopithecines, namely captive or provisioned rhesus macaques and wild baboons, which showed that adult females were more affiliative toward paternal half-sisters than toward non-kin (Schülke, Wenzel, & Ostner, 2013; Silk et al., 2006; Smith, Alberts, & Altmann, 2003; Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2001; see also similar results for juvenile macaque and mandrill subjects, Charpentier, Peignot, Hossaert-McKey, & Wickings, 2007; Widdig, Langos, & Kulik, 2016). Outside the cercopithecines, researchers have looked for evidence of paternal kin discrimination in white-faced capuchins (Perry et al., 2008; Sargeant, Wikberg, Kawamura, Jack, & Fedigan, 2016), ursine colobus monkeys (Wikberg, Ting, & Sicotte, 2014), and infant chimpanzees

(Lehmann, Fickenscher, & Boesch, 2006), and failed to find clear behavioral discrimination of these paternal relatives. It is unclear if others may have looked and failed to report negative results. Unfortunately, published results are still too few to conduct a rigorous comparative analysis to evaluate the importance of factors that could explain the apparent variation across species. Those factors might include the value of different cues in signaling relatedness of paternal half-siblings (e.g., Godoy, Vigilant, & Perry, 2016), as well as the degree of paternity concentration and breeding seasonality that are likely to underlie variation in the value of such cues. In addition, there could be cognitive or perceptual differences across species or clades. We also encourage studies that set up a within-subject data analysis, as this most closely mimics the discriminations that animals must make. Clearly both positive and negative results will be relevant to building up a database that could allow comparative tests.

Given that nearly all guenons live in one-male groups, one would expect paternal sibs to be commonly available as partners, and indeed, adult females in our study groups commonly had paternal siblings, both as peers and as juvenile group-mates. The fact that resident males do not entirely monopolize paternity (Roberts et al., 2014), which may relate to the seasonal breeding that characterizes these monkeys (Cords, 2000), nevertheless means that not all members of a single cohort, or of successive cohorts, share a father. Specifically, if resident males sire 61% of offspring at most (Roberts et al., 2014), then one can estimate the chance that two offspring are paternal siblings as approximately 37–52% (37% if each offspring sired by a non-resident male had a different father, 52% if all offspring not sired by the resident male had the same father). Thus group members seeking to associate or affiliate with others, even peers, would have a significant opportunity to choose between maternal and paternal sibs, as well as non-relatives. It seems it would be advantageous for these monkeys to be able to distinguish paternal half-siblings from non-kin, just as they distinguish maternal half-siblings: to the extent that social contact benefits both parties through pathways like stress reduction or thermoregulation, and that tolerant spatial association enables more efficient or safer foraging, a bias toward interacting with kin generally should enhance fitness (Cords & Thompson, 2017).

It remains unclear why females had differentiated relationships with paternal half-sibs versus non-relatives when social partners were adult females but not when they were juveniles. This difference may reflect generally higher rates of social interaction with adult versus juvenile partners. (In our data set, rates of affiliative contact were 3.9 times higher for adult vs. juvenile kin partners, and 1.7 times higher for adult vs. juvenile non-kin partners; for spatial association, these figures were 2.2 and 1.5, respectively.) Higher rates of interaction or association may make it easier to discern differences between kinship classes. Age-based differences in distinctions between paternal half-sibs and non-kin merit further study.

4.2 | Paternal kin recognition mechanisms

Age similarity does not appear to be the mechanism of kin recognition in blue monkeys. This finding is perhaps not surprising, as the character-

istics of the breeding system, described above, would limit the accuracy of age similarity as a cue. Our study has not resolved what the mechanism actually is. Possibilities that remain are phenotype matching and social familiarity mediated through means other than age similarity.

It seems that a mechanism like phenotype matching would be required for paternal kin recognition in a matrilineal species like blue monkeys, where mothers act as the social nucleus, males are socially peripheral (especially in interacting with immatures), and age proximity is an unreliable cue of paternal sibship. Data on phenotype matching in primates are still somewhat limited, especially for recognition of paternal siblings (Langergraber, 2012; Widdig, 2007), but results of several recent studies have supported this kin recognition mechanism based on acoustic or visual cues (Charpentier, Harte, Ngoubangoye, Herbert, & Kappeler, 2017; Levréro et al., 2015; Pfefferle, Kazem, Brockhausen, Ruiz-Lambides, & Widdig, 2014; Pfefferle, Ruiz-Lambides, & Widdig, 2014).

4.3 | Demographic factors affecting paternal sibling recognition

Previous research on cercopithecines has shown that preferential treatment of paternal half-sibs depends on the availability of or interaction with maternal kin (Charpentier et al., 2012; Silk et al., 2006). We did not corroborate such an effect in blue monkeys, however; across subjects, the degree to which social contact with peers occurred more with PHS than with MNK was unrelated to overall matriline size or the number of the most closely related matriline members. All of our subjects had at least one adult maternal sister and/or their mother/daughter present, so if just one particularly close maternal relative is what counts (Silk et al., 2006), this fact may explain why matriline size was irrelevant. However, we emphasize that blue monkeys females generally have particularly amicable relations not only with their mothers/daughters and sisters, but with more distant matrilineal kin as well; in addition, they generally groom with all their kin (Cords & Nikitopoulos, 2015). This is why we chose to examine effects of total matriline size, as well as the number of close maternal kin. It is possible that matriline size is normally small enough that blue monkeys do not “saturate” their social time with maternal kin; that is, even if females were to groom and sit in contact with maternal kin preferentially, they could still have time to interact with paternal kin as well. More comparative data are needed to evaluate comprehensively how the presence of and bonds with maternal kin influence paternal kin discrimination. Other demographic effects, such as the presence of fathers, may also be important in explaining variation in paternal kin bias (Lynch et al., 2017), although we were not able to address them with our dataset.

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ORCID

Marina Cords  <http://orcid.org/0000-0001-7416-0603>

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