Cues to kinship and close relatedness during infancy in *Cebus capucinus*

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Abstract

The ability to recognize kin has important impacts on fitness because it can allow for kin-biased affiliative behaviors and for avoidance of mating with close kin. While the presence and effects of kin biases have been widely studied, less is known about the process by which animals recognize close kin. Here we investigate potential cues that white-faced capuchin monkeys (*Cebus capucinus*) may use to detect half-siblings and closer kin. We focus on the first year of life in a sample of 130 infant (n=65 infant females) wild capuchins from the Lomas Barbudal population in Costa Rica. We show that (1) infant relatedness to juvenile and adult males at the level of half-sibling and higher can be predicted by male alpha status, spatial proximity, and age proximity, and that (2) infant relatedness to juvenile and adult females at the level of half-sibling or higher can be predicted by spatial proximity (but not age proximity). Furthermore, (1) the identities of infants' fathers can also be predicted by male alpha status and the spatial proximity between infants and adult males, and (2) age proximity (but not spatial proximity) is predictive of paternal sibship. These results suggest that infant capuchins have access to multiple cues to close relatedness and paternal kinship, though whether infants use these cues later in life remains to be explored in future research.

Keywords: kin recognition, age proximity, early social familiarity, male dominance, capuchins

The ability to recognize kin has many adaptive benefits. It can help organisms increase their inclusive fitness by allowing them to allot a disproportionate amount of affiliative behaviors and coalitionary support toward individuals with which they share a larger proportion of their genes (Hamilton, 1964). Furthermore, by allowing individuals to recognize kin and discriminate against them in a mating context, kin recognition mechanisms can facilitate avoidance of the deleterious effects of close inbreeding (Charlesworth & Charlesworth, 1987).

We define *kin recognition* as the ability to identify and distinguish kin from non-kin, or more closely related kin from more distant kin, regardless of the mechanism or mechanisms through which it is accomplished, and regardless of whether it actually leads to differential treatment of individuals (i.e. *kin discrimination*). In this sense, we take on a broad as opposed to narrow definition of kin recognition (see Penn & Frommen, 2010). We consider the related term *kin bias* to be the differential treatment of kin versus non-kin (or close kin from distant kin), though not exclusively as the result of kin recognition.

Kin recognition has been documented in a wide array of animal taxa, including, to name only a few: Artic charr (*Salvelinus alpinus*) (Winberg & Olsén, 1992; Olsén & Winberg, 1996), spadefoot toads (*Scaphiopus bombifrons*) (Pfennig et al., 1993), Golden hamsters (*Mesocricetus auratus*) (Mateo & Johnston, 2000), and Belding's ground squirrels (*Spermophilus beldingi*) and Arctic ground squirrels (*Spermophilus parryii*) (Holmes & Sherman, 1982). While there is also ample evidence of kin discrimination or kin bias in numerous primate species, particularly among maternal kin (Kapsalis, 2004; Silk, 2002, 2009), less is known about the mechanisms by which organisms come to treat closely related individuals differently from more distantly related kin and non-kin. Mammalian infants rely on milk produced by their mothers for nutrition, and as a result, primates form early bonds with their mothers, which can continue throughout their lives depending on dispersal patterns. While well-maintained mother-offspring bonds likely explain patterns of maternal kin-biases in female philopatric species (Chapais, 2001; Chapais & Bélisle, 2004; Rendall, 2004), the mechanisms by which paternal kin recognition is possible remain less understood (Widdig, 2007).

Whereas primate studies commonly cite early social familiarity as the probable mechanism for kin discrimination in primates (Rendall, 2004; Berman, 2004), few studies quantify the usefulness of such a mechanism for accurately identifying different types of kin, as compared with other possible cues to relatedness such as age proximity for paternal sibship and adult male rank for paternity. Such quantification is critical, however, because the effectiveness of mechanisms determine the degree to which kin discrimination can occur in different species. For example, if early social familiarity because of maintained mother-offspring bonds is the mechanism for kin discrimination, then one can expect mother-offspring and maternal siblings to show patterns of kin recognition across their lifespan. However, if the fathers of infants do not preferentially associate with their own offspring, then early social familiarity is not likely to facilitate 1) offspring-father recognition unless in one-male units, or 2) paternal sibling recognition unless paternal siblings are concentrated into groups of similarly-aged peers.

This research project seeks to assess social cues infants might use to recognize their close kin in primates living in groups containing multiple adult females and males. First, male dominance rank could cue infants to the identity of their father, if alpha males sire most infants. Numerous studies have shown that higher ranking males typically sire more offspring than lower ranking males in multi-male, multi-female primate groups (savannah baboons (Alberts et al., 2003, 2006; Altmann et al., 1996), macaques (de Ruiter, 1994; Widdig et al., 2004; Rodriquez-Llanes et al., 2009), chimpanzees (Constable et al., 2001; Boesch et al., 2006; Wroblewski et al., 2009), bonobos (Gerloff et al., 1999), mountain gorillas (Bradley et al., 2005), mandrills (Charpentier et al., 2005; Setchell et al., 2005), red howler monkeys (Pope, 1990), white-faced capuchins (Jack & Fedigan, 2006; Muniz et al., 2006, 2010), red-fronted lemurs (Kappeler & Port, 2008), and sifakas (Kappeler & Schäffler, 2008)). If male dominance rank and group membership can remain relatively stable for longer than the typical gestation length for their species, then male dominance rank can serve as a cue to paternity for infants.

Second, individuals that spend more time near an infant may be more likely to be its kin. For example, if males have some degree of paternity certainty based on their mating history with females, then they may bias the amount of time that they spend with infants toward those that are more likely to be theirs. Thus, spatial proximity may also be a cue that infants use to detect which adult males are their fathers. Evidence for father-offspring kin recognition has been documented in savannah baboons (Buchan et al., 2003; Onyango et al., 2012), chacma baboons (Huchard et al., 2010, 2013), rhesus macaques (Langos et al., 2013), chimpanzees (Lehmann et al., 2006), and capuchin monkeys (Muniz et al., 2006, 2010). Additionally, paternal recognition and affiliative bias of fathers toward their own offspring may also lead paternal siblings to spend more time near each other because of mutual attraction to the same adult male. Thus, spatial proximity may also cue infants to paternal sibship with natal group members.

Third, if alpha males sire most offspring during short breeding tenures, individuals closer in age to an infant will be more likely to be its paternal siblings, compared to older individuals. Peer group membership can serve as a cue to paternal sibship in species in which one or a few males monopolize reproduction during short breeding tenures, since this concentrates paternal siblings into similarly aged cohorts (Altman, 1979; Widdig, 2007, 2013). Studies on baboons (Alberts, 1999; Silk et al., 2006; Smith et al., 2003), rhesus macaques (Widdig et al., 2001, 2002, 2006; Schülke et al., 2013), and mandrills (Charpentier et al., 2007) suggest that some primates recognize paternal siblings. Membership in an age-cohort and – more generally – age proximity, have been hypothesized as a means for achieving paternal sibling recognition.

In addition to social mechanisms, phenotype matching, a process by which "an individual learns its own phenotype or those of its familiar kin by association" (Holmes & Sherman, 1983) may also play a role in kin recognition. Phenotype matching via various means has been postulated to play a role in primates (acoustic: Phefferle et al., 2015, Levréro, 2015; personality: Widdig, 2001; visual: Bower et al., 2012, Kazem & Widdig, 2013), but it is not a focus of our study because of limitations in our ability to estimate precise coefficients of relatedness between individuals in our study population. We do, however, discuss its potential role.

Study species

White-faced capuchins are an interesting species in which to study the mechanisms of and limits to kin recognition, because individuals tend to have available to them many kin of varied relatedness, age, and familiarity. This is because alpha males sire a disproportionately large number of offspring (Jack & Fedigan, 2006; Muniz et al., 2006, 2010), generating a high frequency of paternal siblings within groups. For example, in the Lomas Barbudal population some 55% of capuchin dyads in the same cohort (less than two years apart in age) were paternal siblings (Perry et al., 2008) compared to 5% in Ngogo chimpanzees, 13% in Cayo rhesus monkeys, and 37% of Amboseli baboons (Langergraber et al., 2007). In addition, the Lomas Barbudal population is characterized by long male tenures, as several alpha males have been documented to hold their rank for more than six years and the longest alpha tenure has been estimated (through genetic paternity data) to be 17 years. With inter-birth intervals of approximately two years, long tenures theoretically also produce many co-resident full sibling dyads (Strier, 2004). The combination of high male reproductive skew and long alpha tenures in capuchins creates a social system in which individuals have more co-resident close kin than is found in most other primate species. Previous studies have detected father-daughter inbreeding avoidance (Muniz et al., 2006, 2010), but females fail to favor paternal half siblings for affiliative interactions in the same way that they favor maternal siblings (Perry et al., 2008).

In this study, we attempt to determine the usefulness of early social familiarity, age proximity, and male alpha status as cues for kin recognition in the Lomas Barbudal population of white-faced capuchin monkeys. We first reassess the evidence for high male reproductive skew and inbreeding avoidance in capuchins, since the breeding system in *Cebus capucinus* is integral to our understanding of typical kin availability in capuchin groups. We then test for cues to kinship and close relatedness that are potentially available to infants. Specifically, we ask four questions. Can infants potentially infer close relatedness to males (both juvenile and adult) by using male alpha status, age proximity, or spatial proximity as cues? Can infants potentially infer close relatedness to females (both juvenile and adult) by using age proximity or spatial proximity as cues? Can the identity of an infant's father be predicted by male alpha status or spatial proximity of infants to adult males? Can paternal sibship be inferred though age proximity or spatial proximity?

METHODS

Study Site and Subjects

Subjects in this study are members of nine habituated groups of wild, white-faced capuchin monkeys (*Cebus capucinus*) in the Lomas Barbudal Biological Reserve (10°29–32′N, 85°21–24′W) and adjacent public and private lands in the Guanacaste province of Costa Rica (hereafter referred to as 'Lomas'). *C. capucinus* is a New World monkey that lives in multi-male, multi-female groups and females are typically the philopatric sex (Perry, 2012). Groups at Lomas range in size from 5 to 40 individuals (Perry et al., 2012). The Lomas population has been observed since 1990, with continuous monitoring since January 2002 as part of an infant development project (see Perry, 2012 and Perry et al., 2012 for more detailed information). Behavioral data were collected using focal-animal, scan, and *ad libitum* sampling methods (Altmann, 1974). Scan and *ad libitum* data were collected on all members of the eleven study groups at Lomas. Focal-animal sampling was done on select individuals depending on which particular projects were ongoing. Data included in this study are from an eleven-year period from January 2002 to December 2012, when one to three groups were typically monitored each day for 25-26 days per month. We analyze data from capuchins' first year of life, the period when they are particularly vulnerable to infanticide and when their closest social partners tend to be their mothers (Perry, 2012, Perry et al., 2012). We obtained behavioral data on 140 infants (born to 60 mothers) who survived their first year of life; we limited analyses to a subset of 130 infants (n=65 females) for which we also had genetic paternity data. This research was performed in compliance with the laws of Costa Rica. The UCLA Institutional Animal Care and Use Committee (IACUC), known as the Chancellor's Animal Research Committee (ARC), approved the protocol (ARC # 2005-084).

Proximity

Proximity information was extracted from group scan data taken from infants born into regularly followed study groups. During a group scan, observers noted the activity of a monkey and the identity of any other monkey within ten capuchin body lengths of that focal individual. A body length was defined as that of an adult male, from nose to tail base (~40 cm). Monkeys were scanned at the moment in which they were first seen, and observers rotated through the group trying to scan as many monkeys as possible. Group scans included in this study were collected from over six dozen different researchers. Before collecting data, observers were required to routinely exhibit 100% accuracy in identifying monkeys, and to match at 97% with the behavioral coding of more experienced researchers. To assess inter-observer reliability, assistants were tested monthly for continued mastery of the code and syntax system used for data collection and if errors were detected the relevant data were either fixed or discarded. All data collected contained tags, which denote which observer collected the data (typist), and which other observers (spotters) were out with them in the field. Field assistants regularly rotated through field partners including senior staff (i.e. SEP, IG, and field site managers), and field assistants were trained to double-check each other's identification of monkeys. Focal-animal sampling in each study group was done according to a rotation plan to facilitate equal sampling of focal individuals, but group scans were taken opportunistically, and thus were not distributed evenly across the hours of the day, season, or age for each individual. Ten minutes or more separate group scans for any individual monkey. This source generated a total of 49 976 group scans for 130 infants (n=65 females) from nine social groups, with an average of 384 group scans per infant (range: 53 - 1 082).

We calculated the percentage of group scans in which group members were within ten body lengths (~4 meters) of the focal infants during their first year of life. This provides a general proxy for the amount of time members of a dyad spent around each other over a given time period. We use these percentage scores as our measure of spatial proximity.

During the first few months of a capuchin's life, it is predominantly in physical contact with its mother with a shift toward both reliance on allo-parents and infant spatial independence somewhere between 4-6 months of age (Perry, 2012). Therefore, throughout the first few months, an infant's proximity to group members is a function of 1) its mother's interest in other group members and 2) the interest of other group members in either the infant or the mother. For this reason, we also analyze the proximity data from the first four months of an infant's life separately, since later periods will additionally be a function of the infant's own willingness to be in proximity of other monkeys.

Age approximation and classification

All infants in this study were either seen on the day of their birth (33.6%) or given birth date estimates based on the size, coloration, and activity level of the infant. The majority of births in this study (77.9%) were known to be accurate to within 14 days. For individuals not seen as neonates but first observed as juveniles, age was approximated using physical and behavioral characteristics (MacKinnon, 2002; Fragaszy et al., 2004) and assumed to be accurate by plus or minus two years (Table 2). Males first observed as adults were more difficult to assign age to, especially when the males were of full adult size (~10 years of age or older), but best estimates were used based on the years of experience of field researchers at Lomas. The ages of full-sized adult immigrant males from unknown natal groups and older females born prior to group habituation were assumed to be accurate to a margin of plus or minus five years. Males were classified as adults once they reached six years of age. All adult males were considered potential sires of the infants in their groups.

Table 1: Age accuracies of infants' social partners in this study.

Age accuracy	Female social partners (N=127)	Male social partners (N=137)
0-4 weeks	78 (61.4%)	76 (55.5%)
1-6 months	16 (12.6%)	17 (12.4%)
7-12 months	13 (10.2%)	10 (7.3%)
1-2 years	7 (5.5%)	19 (13.9%)
2-5 years	13 (10.2%)	15 (10.9%)

Male alpha status determination for paternity analyses

Alpha males are typically easy to identify by the use of particular vocalizations and the direction of dyadic submissive behaviors (Perry, 1998). The rank relations between subordinate males, however, are much more difficult to determine and cannot always be detected (Perry, 1998; Schoof & Jack, 2014).

Consistent with the range of known gestation lengths in *Cebus capucinus* (Carnegie et al., 2011), we generated conception windows beginning 145 and ending 166 days prior to the known or estimated date of birth for an infant. We used these windows to exclude infants (n=11 out of 130) conceived during periods for which we could not be certain of the alpha status of their fathers.

Genetic Sample Collection and Analysis

Faecal samples analyzed in this study were collected between 2004 and 2012. Approximately 5 g of faecal samples were collected and then stored according to one of three storage methods described in Nsubuga et al. (2004). Briefly, samples were placed into either (1) 50 ml conical tubes containing 20 g of silica gel beads, (2) tubes containing 10 ml of an RNAlater preservation solution from Ambion, or (3) 50 ml conical tubes containing 30 ml of 97% ethanol. Samples placed in ethanol were stored for at least 24 hours before the solid matter was transferred onto 50 ml conical tubes containing 20 g of silica beads (Roeder et al., 2004).

IG extracted DNA from the fecal samples of 161 individuals using the QIAmp DNA Stool Mini Kit from Qiagen, with modifications of the manufacturer's protocol. Approximately 100 mg of faecal matter per sample was used following Morin et al. (2001). RNAlater samples were extracted as described in Nsubuga et al. (2004), starting from 2 mL of the sample mixture. DNA was eluted with AE buffer to a final volume of 200 uL. DNA was extracted from one tissue sample from an infant that fell victim to infanticide. For this sample, IG used the DNeasy Blood &Tissue Kit from Qiagen and followed the manufacturer's instructions. 134 of the individuals sampled were born into one of the 11 study groups, 12 samples came from adult and subadult males that migrated into the study population, and 14 were unhabituated monkeys from non-study groups for which we opportunistically collected samples.

DNA was amplified at 18 tetranucleotide loci (Muniz & Vigilant 2008) (See **Appendices**, **Table S1**). Genetic information for 172 capuchins from the Lomas Barbudal population was available from previously published work (Muniz et al., 2006) and we reanalyzed DNAs from nine individuals from that study to ensure consistency in allele calling. The PCR protocol (Muniz & Vigilant, 2008) was adapted to allow for two-step multiplex PCR (Arandjelovic et al., 2009). Briefly, we added 5 uL of our DNA extract to a 15 uL master mix containing 16 of our 18 primers pairs. Two primer pairs (Ceb115, Ceb130) did not amplify well under the new multiplex protocol and were analyzed according to the original protocol. After the first round of multiplex PCR, 5 uL of a 1:100 dilution of each tube was added to 16 new tubes, each containing 15 uL of a new master mix with one of the 16 primer pairs. All DNA samples were run in triplicate. IG analyzed the PCR products with an ABI PRISM3100 automated sequencer and Genemapper software. PCR protocols for first and second round amplifications, plus detailed primer pair information is available in the Appendices (**Tables S1**, **S2**, and **S3**). As per Arandjelovic et al. (2009), genotypes were assigned as heterozygous when each allele was seen at least two times from independent PCRs, and genotypes were assigned as homozygous after a minimum of 3 independent PCRs.

In order to guard against sample mix up or animal misidentification, all migrant males and individuals born into one of our study groups but with unknown mothers were genotyped twice using DNA extracted from two independent faecal samples. All infants of known maternity had their genotypes compared for mismatches to their mother's in order to guard against possible sample mix up. We used identity analysis to check for the same genotype appearing under different names, and compared genotypes between the Muniz dataset and the new one.

By including three standard deviations outside the estimated gestation length of wild capuchins (157.83±8.13 days, Carnegie et al., 2011) we obtained a conception window of 49 days between 183 and 133 days prior to the estimated birth date of each infant. We had census information for the conception window for 122 out of 134 (91%) genotyped individuals born into one of the 11 study groups. For these infants we included all group males older than 6 years of age around the time of an infant's conception as potential sires. Nine of the newly genotyped capuchins were born prior to the habituation of their natal group (NM group), but we assigned as candidate parents all adult males (i.e. 6 years or older) present in their group at the time of habituation, and all known habituated migrant males which were seen in the group during partial censuses after intergroup encounters and searches for other groups. The three other infants without census data were born into SP group, which was only sporadically monitored between 2004 and 2008. For those infants we widened their conception windows to 94 (n=2) and 182 days (n=1). The number of candidate fathers varied from 1 to 11 (median: 3, mean: 4.2, SD: 2.5). Males under six years of age would only be considered potential sires if we had good demographic records and, in using CERVUS we could not identify a sire with high statistical confidence. Such a case, however, did not arise (See **Appendices**, **Table S5**). In our previous genetic parentage analysis of infants that were conceived after habituation of their social groups, we have without exception been able to identify sires within the social group of the mother (Muniz et al. 2006, 2010), and the youngest age at which a male sired young was 7.72 years

(Perry, 2012). In one case in the Muniz dataset (2006, 2010), two males were each genetically compatible as the father of a particular offspring, but one of these males was the full-sibling of the offspring and paternity was assigned to the older male.

Likelihood-based paternity assignments were generated using the computational program CERVUS 3.0.7 (Kalinowski et al., 2007). Simulation settings in CERVUS were set to 10 000 offspring, 98% of loci typed, 1% of loci mistyped, 98% of candidate parents sampled, seven candidate fathers, and the minimum of 16 loci typed.

Although CERVUS showed no evidence for null alleles, previous analyses had detected one at locus Ceb115, which was carried by at least 12 members of FF group (Muniz et al., 2006, 2010) and originated from the alpha male of FF group (FZ). One of those carriers (HE, a son of FZ) became alpha male of FL group and passed the null allele to one offspring there. Our current analysis has identified an additional 7 carriers of the null allele at Ceb115 (1 in FF group, 3 in FL group, and 4 in RF group), all of whom are descended (offspring or grandoffspring) from the former alpha male of FF group (FZ).

Pedigrees and coefficients of relatedness

It is notoriously difficult to use microsatellite genotyping data to determine the kinship category or reliably estimate the pairwise coefficient of relatedness for two individuals in the absence of pedigree information (Csilléry et al., 2006; Van Horn et al., 2008; Langergraber et al., 2007). We therefore used pedigrees established through maternity and paternity analyses to calculate pairwise coefficients of relatedness using Ed Hagen's DESCENT software (http://itb.biologie.hu-berlin.de/~hagen/Descent/). After we provided the identity of each capuchin, as well as the identity of each capuchin’s known mother and genetically assigned father, the DESCENT program generated estimated coefficients of relatedness for all possible dyads formed with each individual. Lack of complete pedigrees means that the estimated coefficients of relatedness generated by the software can be lower than their actual measure.

16 of 166 (9.6%) adult females in our study population (including females not in data analyses presented here) had mothers that were unknown to us because the females were born prior to group habituation and we had no genetic samples from their mothers. We lacked complete pedigree information for more adult males (68 of 246, 27.6%), because they were immigrants from unknown social groups. These migrant males, however, were assumed to be unrelated to monkeys in our study group unless they were later determined to be the fathers of infants. Since males of *Cebus capucinus* often emigrate with natal kin (Perry, 2012, Perry et al., 2008, 2012; Wikberg et al., 2014), it is likely some non-natal males that were assigned as non-kin of infants are actually the paternal uncles (or more distant kin) of infants. Of the 39 males known to have sired infants at Lomas Barbudal, 56.4% (n=22) had unknown parents.

For 50.8% of infants in this study and 26.9% of their available genotyped social partners, we could reconstruct full pedigrees two generations back (i.e. we identified the 4 grandparents) (**Table 1**). As a result of limited pedigrees for many of our dyads, we ran analyses considering close relatives defined as having a coefficient of r=0.25 or higher, because we could be more confident about relatedness at this level and not at more distantly related levels. For example, kinship categories at ≥ 0.25 for which we are confident include parents, full siblings, half siblings, full nephews/nieces, and grandparents of infants, while categories that may be under-sampled due to incomplete multi-generational pedigrees are full aunts/uncles and double full first cousins. However, there were no known double full first cousins in our dataset.

Table 2: Pedigree completeness for genotyped dyads in the dataset. The table shows data for 130 infants and their 265 social partners in the behavioral dataset.

No. of known grandparents	Infants	Social partners
0	8 (6.2 %)	75 (28.3 %)
1	12 (9.2 %)	35 (13.2 %)
2	29 (22.3 %)	63 (23.8 %)
3	15 (11.5 %)	20 (7.5 %)
4	66 (50.8 %)	72 (27.2 %)

Dyads in the datasets

Our sample of 130 infants and their 298 potential social partners corresponded to a total of 3 321 dyads; however, infant-mother dyads (n=130 dyads) were not included in any behavioral analysis. Infant-mother dyads were excluded because infant-mother relationships have the highest certainty, as mothers know which infants they give birth to. Furthermore, infants rely on their mothers to be their closest adult female associates during their first year of life barring such exceptions as being orphaned or abandoned.

We restricted our behavioral dataset to pairs where both members of the dyad were genotyped. All adults and non-infant juveniles in the dataset were genotyped. The dyads excluded (n=66) were formed with 33 social partners, all of which were infants (i.e. less than one year of age) and 18 of which (55%) died before reaching one year of age.

We further restricted behavioral analyses to pairs with at least 30 group scans. The dyads excluded (n=71) were all formed with social partners that were present for less than a quarter of the days on which data were collected for the focal infants. 42.3% of the excluded dyads were formed with infants more than seven months younger than the focal infants, and which were thus not available as social partners for focal infants throughout their entire first year of life. An additional 19.7% of dyads were formed with social partners that died during the focal infants first year, and another 38% were formed with males that migrated out of the infants' social groups. Our behavioral dataset thus totaled 3 054 dyads formed between 130 infants and 265 social partners (Table 3).

In our models that include male alpha status as a test predictor, we dropped an additional 50 dyads that were formed between infants (n=20) and alpha males (n=18) during unstable years when there were rank reversals in the alpha male position. Including these dyads in analyses did not change whether or not any of our predictor variables were significant or not, nor the direction of their effects.

Table 3: Study subjects and study group information. This table shows the number of study infants per group, their female and male social partners, as well as the range of group sizes per study group. Female and male social partners can appear in more than one study group as a result of migrations or group fissions. Only genotyped social partners are included in this table and in our analyses.

Study group	Years of observation	Group size	No. of study infants	No. of female social partners	No. of male social partners
RR	2002-2012	26-42	27	31	38
FF	2002-2012	20-39	26	28	31
AA	2004-2012	20-35	25	23	24
FL[a]	2004-2012	14-20	15	12	15
MK[b]	2004-2010	15-21	10	27	27
RF[c]	2007-2012	18-27	9	26	19
SP[b]	2008-2012	21-29	8	14	20
CU[d]	2008-2012	5-10	6	4	8
NM	2009-2010	14	4	7	8

[a] Fission product of AA
[b] Fission product of RR
[c] Fission product of FF
[d] Fission product of MK

Statistics and Data Analysis

Statistical analyses were run in R v.3.2.2 (R Core Team, 2015) using the glmer or lmer function from the lme4 package (Bates et al., 2015). We ran Generalized Linear Mixed Models (GLMM, Baayen, 2008) with binomial error structure and logit link function to assess the significance of our predictor variables for detecting close kin during infancy.

For all models, we included random intercepts for infant identities, partner identities, and primary group of residence as well as random slopes where possible. We confirmed model stability by excluding all levels of all random effects one by one and comparing the estimates with estimates derived from the model based on the full data set. We assessed collinearity – excessive correlation among our explanatory variables – by calculating Variance Inflation Factors (Field, 2005) using the function "vif" of the "car" package (Fox and Weisberg, 2011). The highest Variance Inflation Factor in any model was 2.04 suggesting no collinearity problems. In order to establish the significance of the test predictors, we conducted a full versus null model comparison (Forstmeier & Schielzeth, 2011) using a likelihood ratio test (Dobson & Barnett, 2008). The null model comprised all terms in the full model except the test predictors. P-values for individual predictors were also obtained using likelihood ratio tests via the "drop1" function in R. We z-transformed all quantitative fixed effects to a mean of 0 and standard deviation of 1.

Since the number of adult females and the number of adult males can limit the ability of dominant males to monopolize reproduction (Cowlishaw & Dunbar, 1991) - in turn impacting the probability of certain kin types and relatedness within groups - we include both as control predictors for all of our GLMMs.

Our models were all stable, meaning that no one infant, social partner, or group of residence drove the results that are shown in these analyses.

RESULTS

Reproductive Skew

We genotyped 162 monkeys at 18 loci and combined these data with published data for a total of 334 genotyped individuals. For all 129 newly genotyped individuals with known mothers, CERVUS assigned a single well-supported father (**Appendices**, **Table S5**). For 4 out of 5 individuals in NM group for which we did not know the identity of their mother, CERVUS also assigned only one well-supported father, while one older female had no assigned father. The youngest assigned father in dataset was 6.25 years old at the time of his infant's conception. There was one case of extra-group paternity. We included the male as a candidate father because the mother of the infant had previously been seen spending a night in that male's social group, after having been separated from her own group during an intergroup encounter. The sire in this case was a familiar male (i.e. he emigrated out from the female's natal group) and was alpha of a neighboring group. Thus, there is little evidence that females seek mates outside of their social group.

For 119 newly genotyped infants we knew the alpha male during the time of their conception and found that they sired the majority (83.2%, n=99) of infants. However, while alpha males sired 94.1% (n=96 of 102) of infants born to females that were not their daughters or granddaughters, they only sired 17.6% (n=3 of 17) of infants born to females that were their descendants, and this difference was significant (Fisher's Exact test: $P < 0.0001$, $N = 119$).

Group composition, average dyadic relatedness, and kin availability

Infants had available three to 40 potential social partners, including one to 10 adult males and three to 12 adult females. During the first year of life of 130 genotyped infants, 95.4% had a father present, 36.2% had at least one full sibling (range: 0-4), 46.9% had at least one maternal half sibling (range: 0-5), and 87.7% had one or more paternal half sibling (range: 0-19) available. Paternal half siblings represented 21.2% of genotyped dyads (n=689) in our dataset. Maternal siblings accounted for 6.1% of dyads (n=198), over a third of which were full siblings (n=75).

Infants had many partners that were related to them at the level of 0.5 > r ≥ 0.25 (38.3% of all dyads) (**Figure 1**), of which half siblings comprised 63.7% (paternal half siblings: 54%). Infants had from one to six partners related at the level of r ≥ 0.5 (10.8% of all dyads) (**Figure 2**), of which full siblings made up 21.4%, parents 72.6%, and the remaining 6% (n=21 dyads) were comprised of dyads involving 12 infants that were the product of inbreeding.

The average relatedness between genotyped infants and available social partners (including non-kin) was high (mean=0.221, std=0.158, n=3 255 dyads) and infants were related to their fellow group members at an average estimated coefficient of relatedness of 0.23 (std=0.07, n=130 infants) (**Figure 3**).

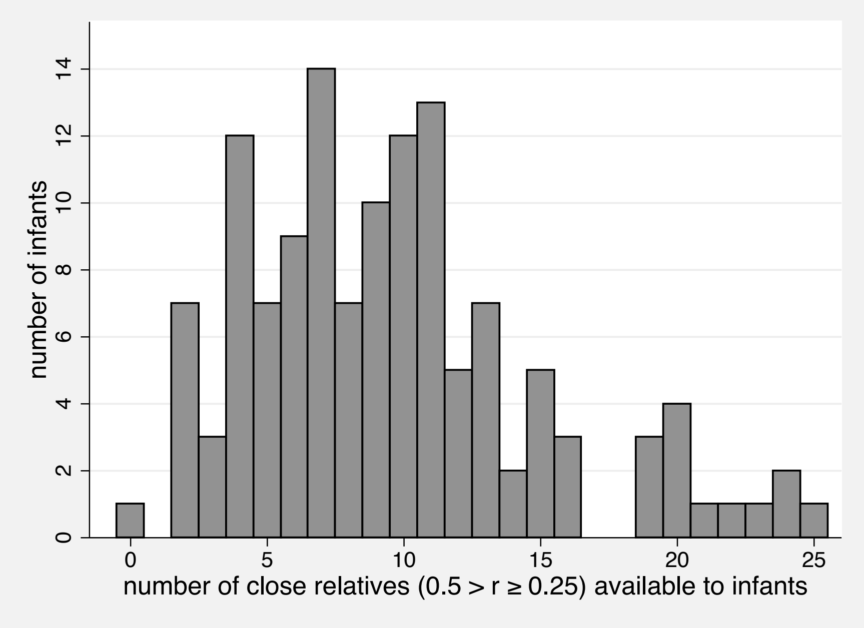

Figure 1: Distribution of the number of close relatives (0.5 > r ≥ 0.25) available to infants. The histogram shows the number of infants with zero to 25 social partners in their group related to them at the half-sibling level. These included but were not limited to half siblings, grandparents, full aunts and uncles, and full nieces and nephews.

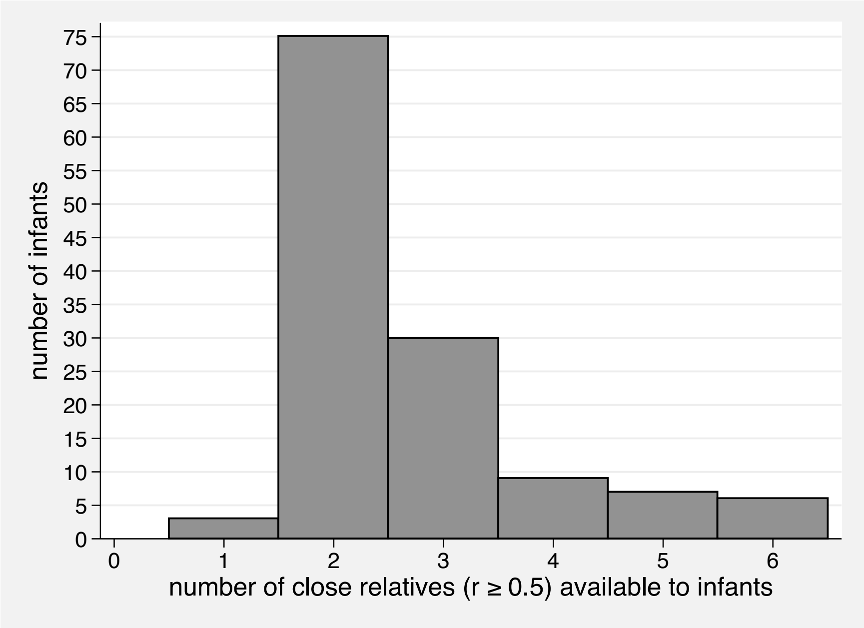

Figure 2: Distribution of the number of close relatives ($r \geq 0.5$) available to infants. The histogram shows the number of infants with one to six social partners in their group related to them at the full-sibling level. These social partners were primarily the parents and full siblings of infants.

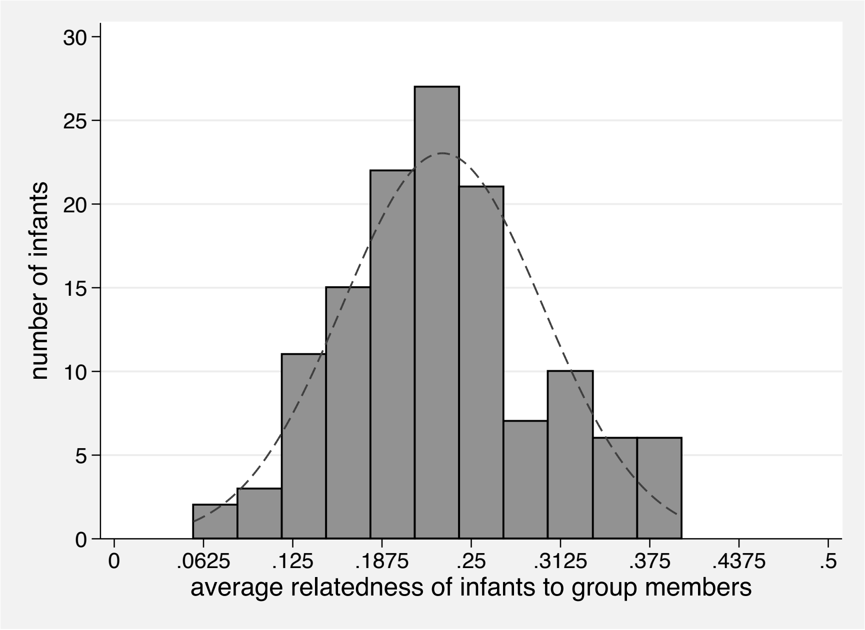

Figure 3: Distribution of the average of the estimated coefficient of relatedness between infants and other members of their groups. The dashed line indicates the normal density curve for the values. Incomplete pedigrees mean that the actual values may be higher.

Cues to close relatedness to males

We tested the significance of spatial proximity, age proximity, and male alpha status as cues to close relatedness with males (n=1 418 dyads, n=130 infants, n=137 males, n=9 groups). Male social partners of all ages were included in this analysis. Our response variable was whether or not an infant-male dyad was related at the half-sibling level or higher ($r \geq 0.25$) (yes/no). We controlled for infant sex, the number of adult males, and the number of adult females in the group. We included the identities of the infants, males, and groups of residence as random factors. We did not differentiate between maternal and paternal kin. The full model was significantly different from the null model (χ^2_3=39.125, P<0.0001).

Whether or not a male was the alpha of a group was a significant predictor of close relatedness to focal infants, as were spatial proximity and age proximity (**Table 4**). Alpha males were more likely to be a close relative (typically their father or grandfather), as were males closer in age to an infant (**Figure 4**) and males with which infants spent more time (**Figure 5**). Similar results were found when limiting our analysis to data collected during the first four months of each infant's life (**Appendices**, **Table S6**).

Table 4: GLMM results for probability of close relatedness ($r \geq 0.25$) to males.

Fixed Effect	Estimate	SE	Df	LRT	Pr(Chi)	
(Intercept)	0.157	0.549				
Test variables						
Male is alpha	4.865	1.016	1	14.248	0.0002	***
Spatial proximity	0.937	0.143	1	18.816	< 0.0001	***
Age proximity	-1.157	0.329	1	8.185	0.0042	**
Control variables						
# of adult males	-0.268	0.192	1	1.816	0.1778	ns
# of adult females	0.903	0.212	1	11.384	0.0007	***
Infant is male	-0.138	0.218	1	0.380	0.5374	ns

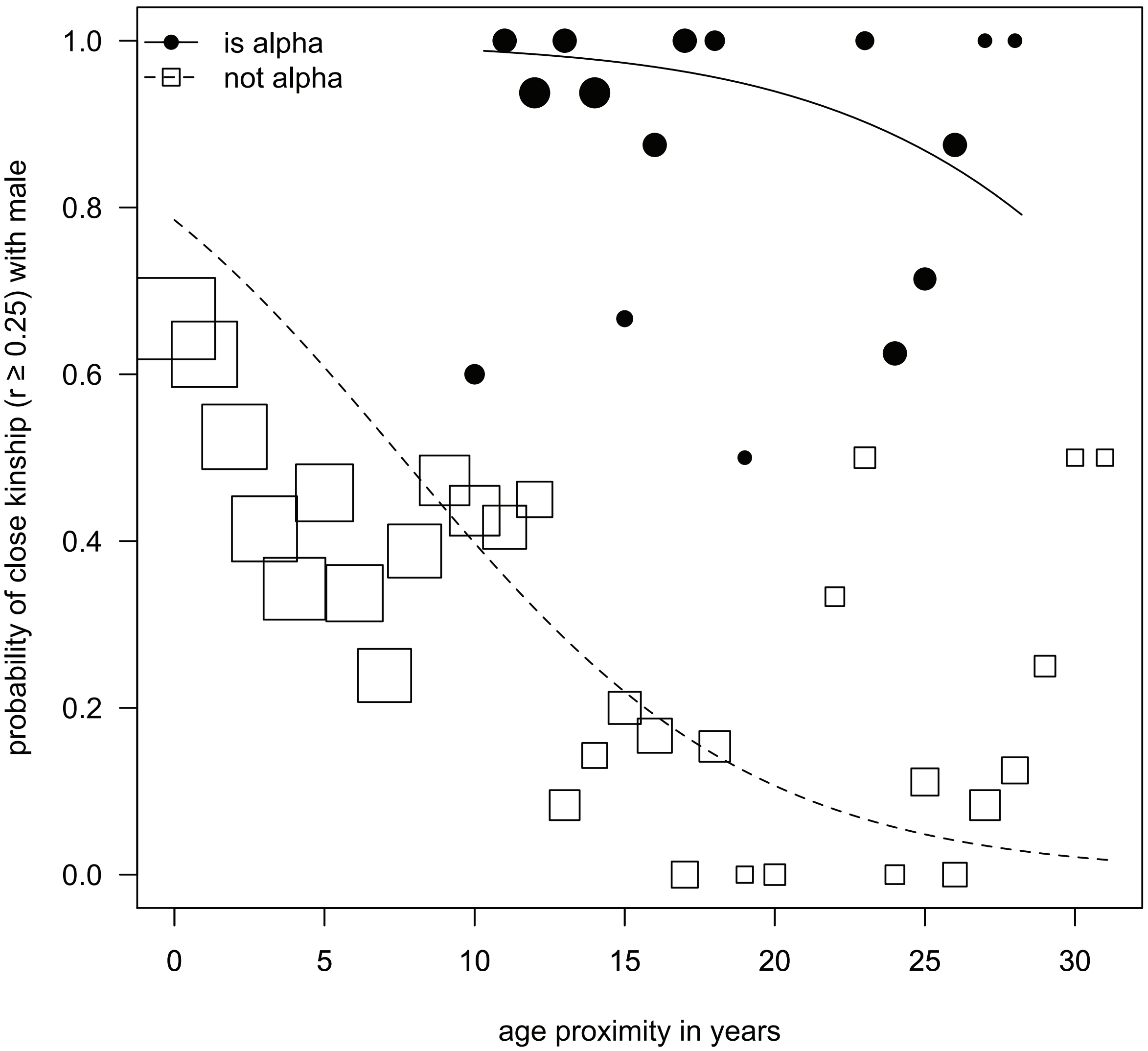

Figure 4: Probability of close relatedness (r ≥ 0.25) to males, contingent on age proximity. Bubbles represent the proportion of partners at that age proximity that were related to the infant at the level of paternal sibling or higher. The size of each bubble indicates sample size. The lines showing the predicted values control for spatial proximity, number of adult males, number of adult females, and infant sex.

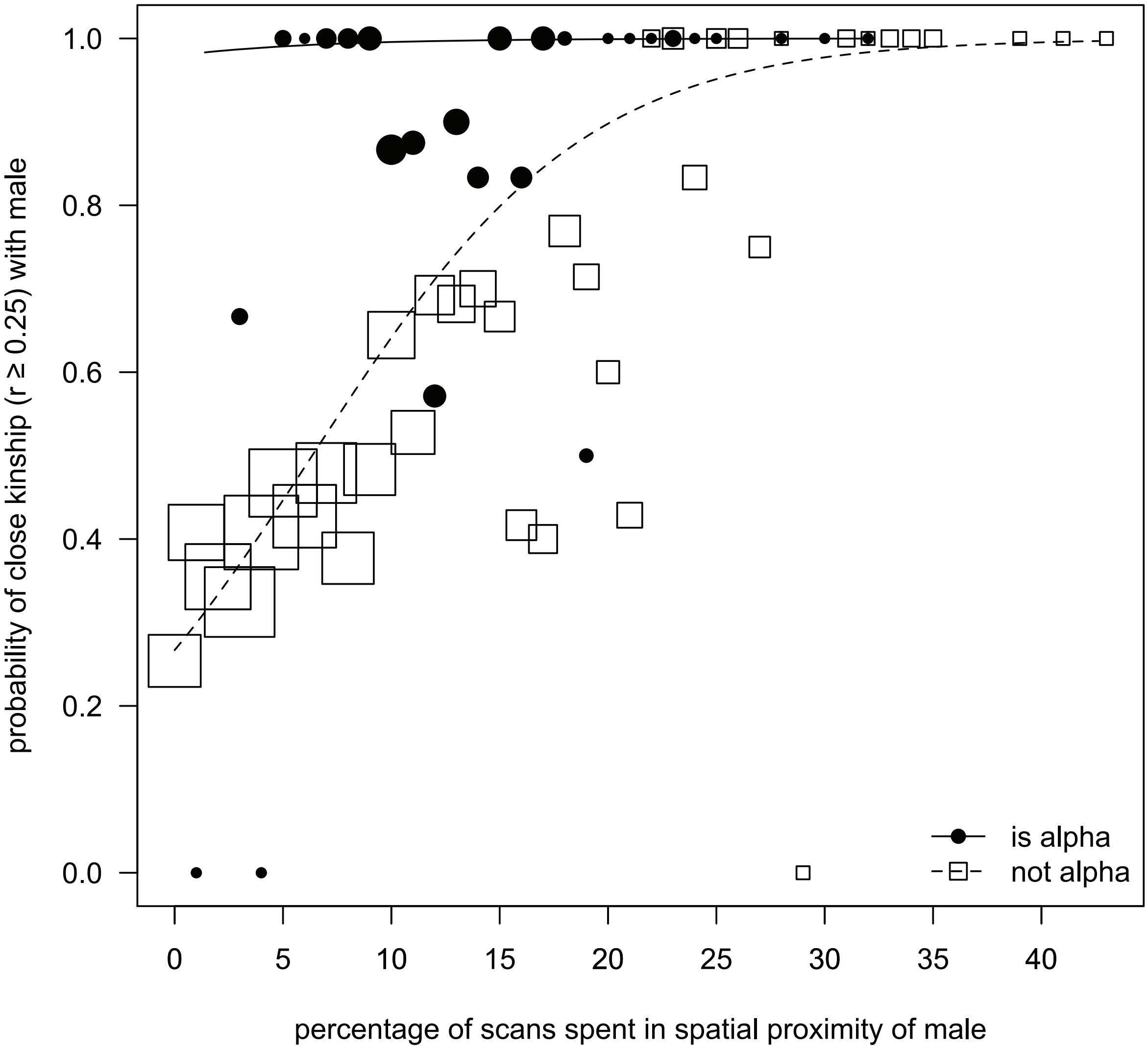

Figure 5: Probability of close relatedness (r ≥ 0.25) to males, contingent on spatial proximity. Bubbles represent the proportion of partners at that spatial proximity score that were related to the infant at the level of paternal sibling or higher. The size of each bubble indicates sample size. The lines showing the predicted values control for age proximity, number of adult males, number of adult females, and infant sex.

Cues to close relatedness to females ($r \geq 0.25$)

We tested the significance of spatial proximity and age proximity as cues to close relatedness with females (n=1 586 dyads, n=130 infants, n=127 females, n=9 groups). Females of all ages were included in this analysis. Our response variable was whether or not an infant-female dyad was related at the half-sibling level or higher ($r \geq 0.25$) (yes/no). We controlled for infant sex, the number of adult males, and the number of adult females in the group. We included the identities of the infants, females, and groups of residence as random factors. We did not differentiate between maternal and paternal kin. The full model was significantly different from the null model ($\chi^2_2=25.115$, $P<0.0001$).

Spatial proximity but not age proximity was a significant predictor of close relatedness to females (**Table 5**). Infants were more likely to be closely related to females with which they spent more time (**Figure 6**). Similar results were found when limiting our analysis to data collected during the first four months of each infant's life (**Appendices**, **Table S7**).

Table 5: GLMM results for probability of close relatedness ($r \geq 0.25$) to females.

Fixed Effect	Estimate	SE	Df	LRT	Pr(Chi)	
(Intercept)	-0.379	0.371				
Test variables						
Spatial proximity	1.288	0.175	1	23.344	< 0.0001	***
Age proximity	-0.645	0.456	1	1.690	0.1936	ns
Control variables						
# of adult males	-0.247	0.215	1	1.165	0.2805	ns
# of adult females	0.510	0.209	1	5.322	0.0211	*
Infant is male	0.587	0.258	1	3.618	0.0572	.

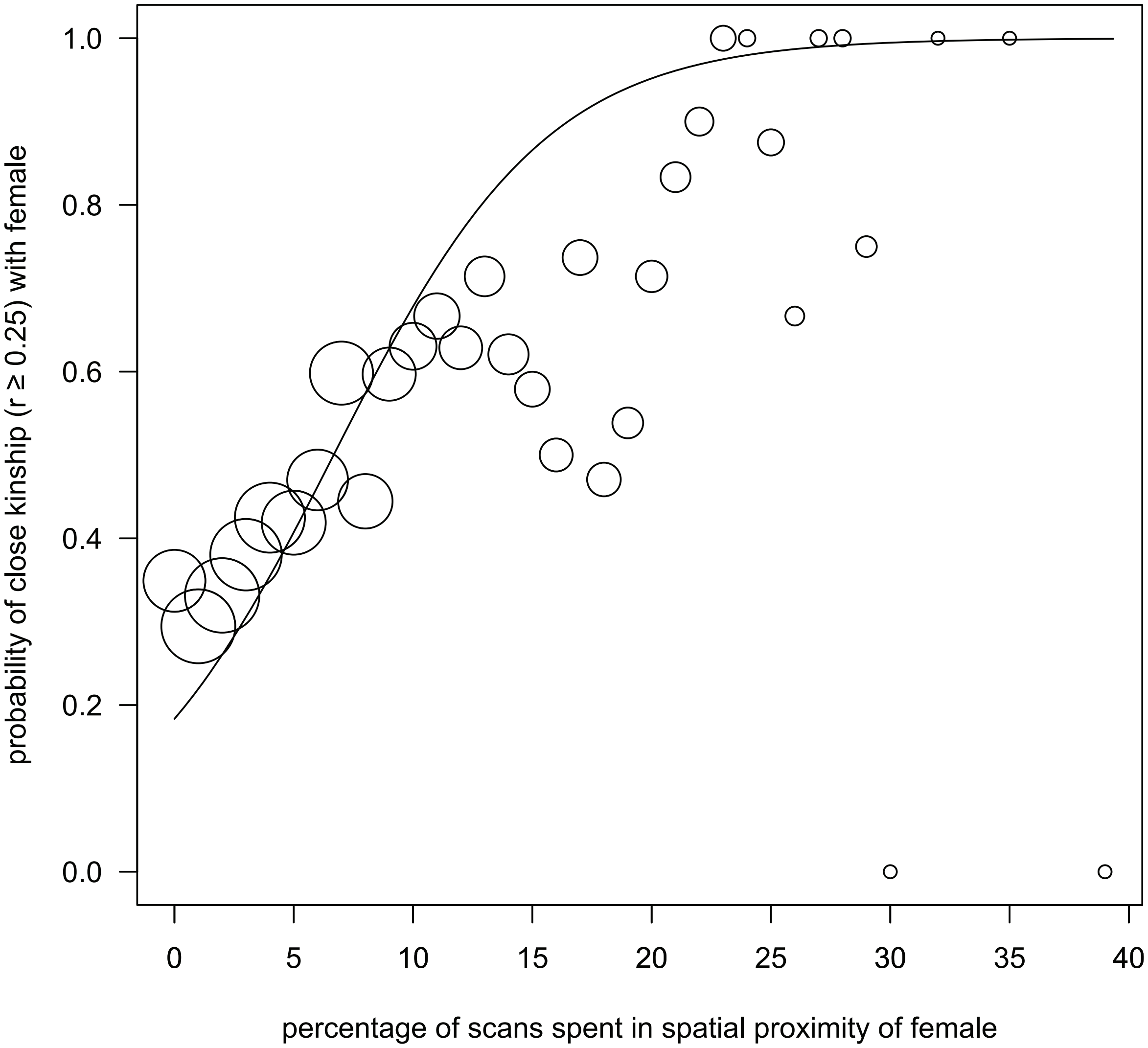

Figure 6: Probability of close relatedness (r ≥ 0.25) to females. Bubbles represent the proportion of partners at that spatial proximity score that were related to the infant at the level of paternal sibling or higher. The size of each bubble indicates sample size. The line showing the predicted values controls for age proximity, number of adult males, number of adult females, and infant sex.

Cues to paternity

We assessed the significance of male alpha status and spatial proximity during infancy as cues for whether an adult male was an infant's father. Our data set comprised 622 infant-male dyads formed with 57 adult males in 9 groups. The response was whether or not the male was the father of the infant. We included spatial proximity and whether or not a male was the alpha of the group as test predictors. We also included male age as a control variable, since older males might be less able to compete for reproduction in a group. We also controlled for the sex of the infant. The identities of the infants, adult males, and groups of residence were included as random factors. Our full model was significantly different from the null model comprised of only control variables (χ^2_2=19.404, P<0.0001).

Male alpha status and spatial proximity were significant predictors of the likelihood that an adult male was the father of an infant (**Table 6**). Alpha males were more likely to be the father of an infant, as were adult males with which infants spent more time (**Figure 7**). Similar results were found when limiting our analysis to data collected during the first four months of each infant's life (**Appendices**, **Table S8**).

Table 6: GLMM results for probability that an adult male is the father of an infant.

Fixed Effect	Estimate	SE	Df	LRT	Pr(Chi)	
(Intercept)	-2.953	0.544				
Test variables						
Male is alpha	4.721	1.270	1	12.371	0.0004	***
Spatial proximity	1.210	0.513	1	6.640	0.0099	**
Control variables						
Male age	0.772	0.582	1	1.313	0.2519	ns
# of adult males	0.285	0.501	1	0	0.9240	ns
# of adult females	0.281	0.440	1	0	0.4046	ns
Infant is male	-0.621	0.749	1	0	0.3999	ns

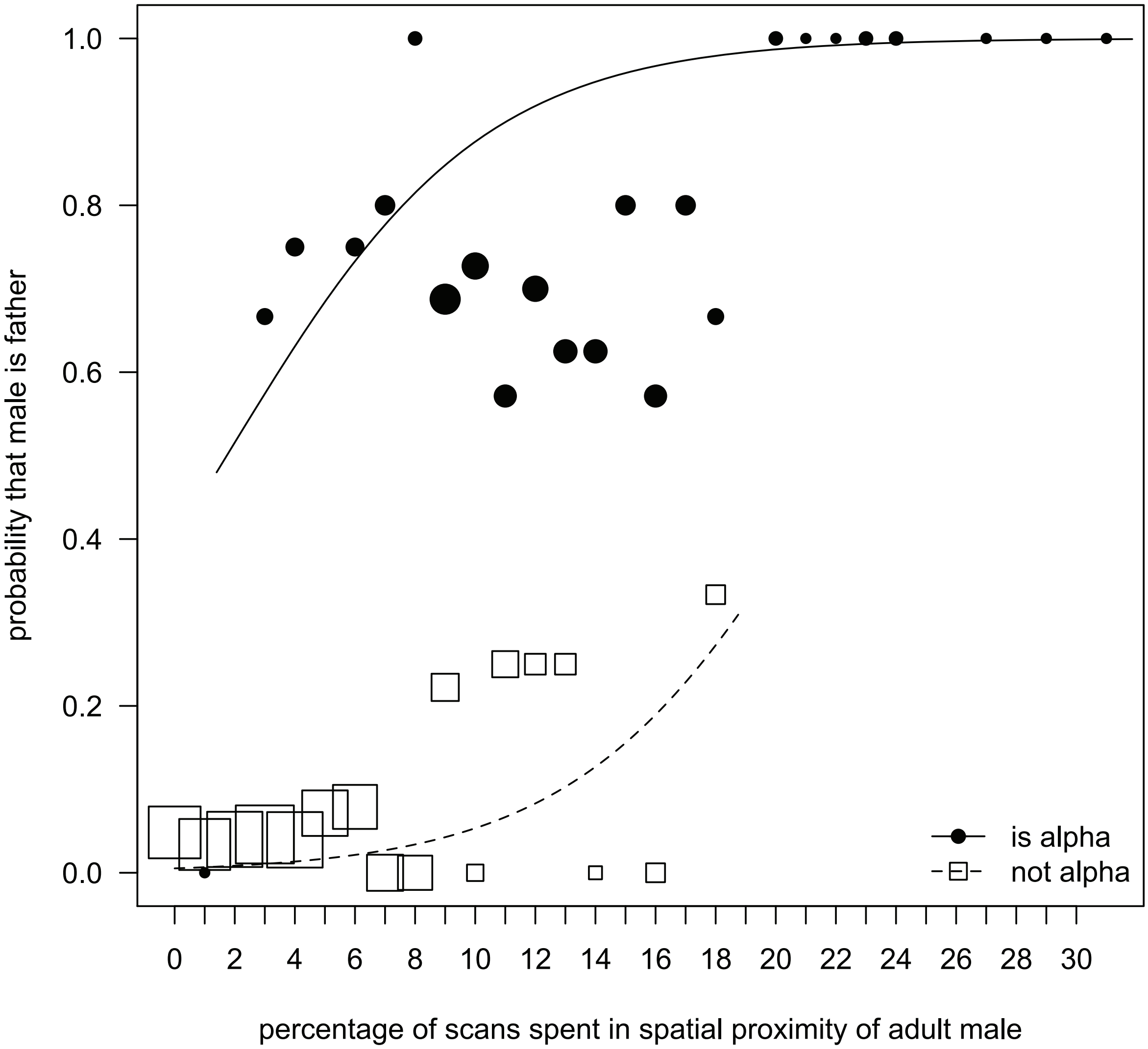

Figure 7: Probability that an adult male is an infant's father, contingent on spatial proximity and male alpha status. Bubbles represent the proportion of males at that spatial proximity score that were also an infant's father. The size of each bubble indicates sample size. The lines showing the predicted values control for male age, number of adult males, number of adult females, and sex of the infant.

Of the 110 infants that lived with stable alpha males for the duration of their first year of life, the majority (83.6%, n=92) spent the most time with the alpha male, and for most infants (80.9%, n=89) their closest adult male associate was either their father (n=73) or grandfather (n=16) (**Table 7**).

In 22 cases where an infant lived with both a father and grandfather, the father was alpha in four cases, the grandfather in 16, and neither in two. When the grandfathers were alpha, infants spent more time around their grandfathers than they did around their fathers (15 of 16). Similarly, when the alpha was their father, infants spent more time around him than around their grandfather (3 of 4).

Table 7: Closest adult male associate of infants

Kin type	**Male is alpha**		**Total**
	Yes	No	
Father	69	5	74
Grandfather	14	2	16
Other kin	5	7	12
Non-kin (r=0)	4	5	9
Total	92	18	110

Cues to paternal sibship

We tested the significance of age proximity and spatial proximity as cues to paternal sibship, using a dataset of dyads formed with all group members other than mothers and alpha males (n=2 893 dyads). Male and female social partners of all ages were included in this analysis. The response was whether or not the other member of the dyad was a paternal sibling (yes/no). We controlled for the possible effects of maternal sibship, infant sex, the number of adult males in the group, the number of adult females in the group, and any possible interaction effect of partner sex on age proximity, spatial proximity, maternal sibship, and infant sex. The identities of the infants, social partners, and groups of residence were included as random factors. The full model was significantly different from the null model (χ^2_4=20.298, P=0.0004). All interaction terms (formed with partner sex) were non-significant and were dropped from the final model.

Age proximity, but not spatial proximity, was a significant predictor of paternal sibship (**Table 8**). Social partners closer in age to infants were more likely to be their paternal siblings (**Figure 8**). Similar results were found when limiting our analysis to data collected during the first four months of each infant's life (**Appendices**, **Table S9**).

Table 8: GLMM results for probability of infant's partner being a paternal sibling.

Fixed Effect	Estimate	SE	Df	LRT	Pr(Chi)	
(Intercept)	-9.600	0.898				
Test variables						
Spatial proximity	0.395	0.259	1	2.514	0.1129	ns
Age proximity	-15.776	3.080	1	12.864	0.0003	***
Control variables						
Is maternal sibling	1.010	0.453	1	2.939	0.0865	.
# of adult males	-0.115	0.717	1	0.022	0.8832	ns
# of adult females	1.815	0.989	1	2.942	0.0863	.
Infant is male	-0.275	0.804	1	0.126	0.7225	ns
Partner is male	0.816	0.562	1	2.098	0.1475	ns

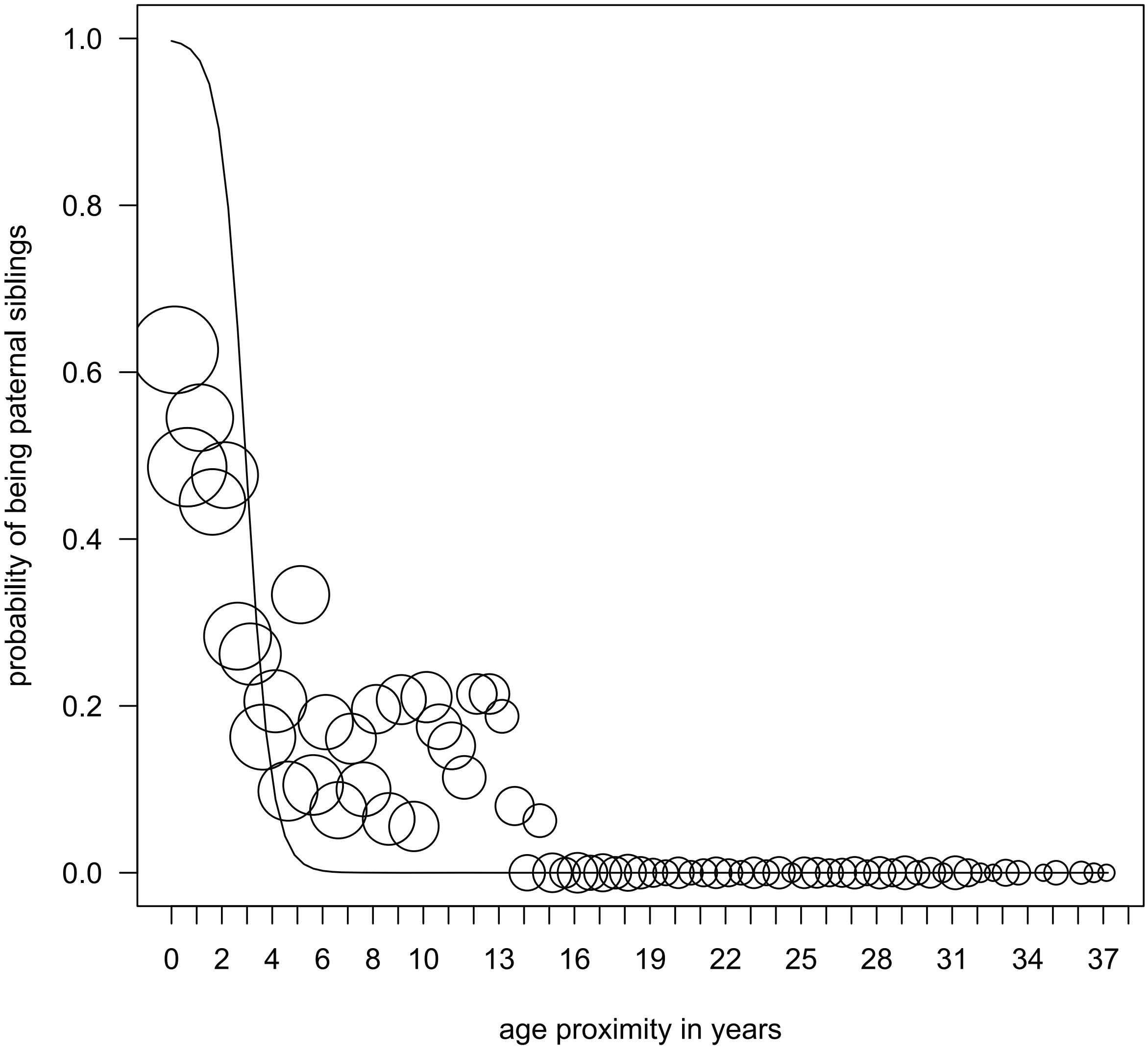

Figure 8: Probability of infant's partner being a paternal sibling, contingent on age proximity. Bubbles represent the proportion of partners at six-month increments in age differences that were also paternal siblings. The size of each bubble indicates sample size. The line showing the predicted values controls for spatial proximity, maternal sibship, number of adult males, number of adult females, partner sex, and infant sex.

DISCUSSION

Our data show that wild capuchin infants have information available to them – male alpha status, age proximity, and spatial proximity - that can serve as cues to close relatedness ($r \geq 0.25$) and even paternal kinship (i.e. paternity and paternal sibship). Further research is needed to establish whether or not infants actually use these potential cues later in life.

Male alpha status was a significant predictor of close relatedness ($r \geq 0.25$) to males and also of who the fathers of infants were. Infants that survived their first year of life were likely to have their fathers still present in their group (95.3%), and their fathers were usually alpha males (78%). Male alpha status is also more generally highly informative as to close relatedness, because alpha males tend to be the father or grandfather of surviving infants. In general, whether male rank is a useful cue to relatedness in a species is dependent on the degree of male reproductive skew, as well as the stability of male dominance rank and group membership. As a consequence of both the high degree of male reproductive skew seen at Lomas and the stability in male alpha rank, alpha status is an excellent marker of the paternal descent of infants in this population. In another primate with extreme male reproductive skew toward alpha males, Verreaux's sifakas (*Propithecus verreauxi*), dominant non-natal males residing in groups containing other non-natal adult males sire approximately 91% of offspring (Kappeler & Schäffler, 2008). Alpha male status should thus also be an informative marker for close relatedness, and more specifically paternity in these sifakas. Indeed, there is some evidence for later father-daughter discrimination in the species in the form of inbreeding avoidance (Kappeler & Schäffler, 2008).

Age proximity was a significant predictor of paternal sibship regardless of infant sex or partner sex. That is, males and females closer in age to an infant were more likely to have the same father as the infant. Age proximity was also a significant predictor of close relatedness to males, but not to females. This likely reflects the fact that male migration from their natal groups reduces the availability of older non-alpha adult male kin in groups. Natal male kin are therefore more concentrating into younger juvenile and sub-adult categories, while female kin remain distributed across a wider range of ages. Age proximity, and particularly peer group membership, is an important regulator of social interactions in capuchins (Schoof & Jack, 2014) and various other animals: gazelles (Walther, 1972), impalas (Murray, 1981), savannah baboons (Pereira, 1988; Alberts, 1999; Silk et al., 2006, 2010), rhesus macaques (Janus, 1992; Widdig et al., 2001, 2002), chimpanzees (Mitani, 2009), humpback whales (Ramp et al., 2010), and giraffes: (Bercovitch & Berry, 2013). In species featuring high male reproductive skew during brief tenures, such as rhesus macaques, strong associations with peers can allow for different treatment of paternal half siblings as compared to more distant kin (Altmann, 1979; Widdig, 2007, 2013).

Spatial proximity was a significant predictor of paternity. Adult males with which infants spent more time were more likely to be their fathers. Spatial proximity was also more generally a significant predictor of close relatedness to males and to females. Males and females with which infants spent more time were more likely to be related to them at the level of half sibling or higher ($r \geq 0.25$). Spatial proximity, however, was not a significant predictor of paternal sibship.

Male alpha status and spatial proximity to adult males were both significant predictors of who the fathers of infants were. Male alpha status and spatial proximity were also predictive of close relatedness to males ($r \geq 0.25$), with the closest adult male associates of infants typically being a father (66.7%) or grandfather (14.7%). Thus, capuchin infants have available to them multiple reliable cues that can be used to discriminate their direct male ancestors. Multiple cues may even explain why inbreeding between alpha males and their daughters and granddaughters is rare in this population - a result replicated in this paper. In other words, inbreeding avoidance among daughter-father pairs may be attributed to female sexual aversion to males with which they spent more time during their infancy (akin to the Westermarck effect (Westermarck, 1891)), female sexual aversion to males that were alpha during their infancy, or a combination of the two. In mountain gorillas (*Gorilla beringei beringei*), male-immature associations are primarily driven by male dominance rank and not paternity (Rosenbaum et al., 2015). However, since dominant males typically sire the majority of infants, even in multi-male groups (Bradley et al., 2005; Vigilant et al., 2015), early spatial proximity to males may still be informative as to paternity alongside male alpha status. In other words, differential treatment of adult males according to their former dominance status, and/or the time spent in proximity to them may facilitate recognition of fathers. Interestingly, paternity patterns in gorillas, similar to those seen in capuchins, are also indicative of father-daughter inbreeding avoidance (Vigilant et al., 2015).

Multiple reliable cues may facilitate the ability of capuchins to identify their fathers and grandfathers, but the ability to identify paternal siblings appears more difficult. Generally, cohort membership in primates is a good indicator of paternal sibship when high reproductive monopolization occurs during short alpha male tenures (Altmann 1979; Widdig 2007, 2013). Given the long tenures that alpha males can achieve in capuchins, however, the age difference between paternal siblings can be large enough that cohort membership is not as reliable an indicator of relatedness for two main reasons. First, the strength of male reproductive skew decreases with length of tenure because the daughters and granddaughters of current alpha males breed with subordinate males. Second, prior to the sexual maturation of an alpha male's daughters, six years pass during which the alpha male is the sire of almost all offspring in his group. Therefore, group members outside of an age cohort are also very likely to be paternal siblings during intermediately long (more than one year and less than six years) alpha tenures. Even if individuals lack the ability to recognize paternal siblings, biased behavior toward similarly aged peers could result in strong patterns of preferential association with paternal siblings if paternal siblings are concentrated in peer groups. In our sample of infants, however, group members outside of the peer group (i.e. more than one year apart in age) constituted a larger proportion of paternal siblings (60.6%, 462 of 763). The considerable number of older paternal siblings thus makes age cohort membership alone an insufficient cue for discriminating paternal siblings because older individuals are also likely to have the same father.

Infants in our dataset were related to their fellow group members at an average estimated coefficient of relatedness of 0.23, just below the level of half sibling. With such a large number of group members related to infants at the level of $0.5 > r \geq 0.25$ (37.9% of all dyads in our dataset), the ability to discriminate paternal half siblings from other kin may not be so important in capuchins because of the abundance of equally related or more highly related group members. With such high levels of within-group relatedness, one may even expect lower nepotism among close maternal kin because preferential support toward close maternal kin comes at the expense of other closely related group members (Wilson et al., 1992; Queller, 1994; West et al., 2001; Langergraber, 2012). Indeed, in a population where individuals have few kin available, it is not relevant to consider kin competition, as the benefits of cooperating with kin are much higher than the costs of competing with kin if there are very few kin to outcompete. However, in a population with abundant kin dyads, it is the variance in kinship in the population that will matter. For example, in a population like this one where most individuals have both close (parent, full sibling) and less close (half-sibling) kin present, one would expect a preference for the closest, easily identifiable maternal kin, which is what is observed. For instance, adult female affiliation in capuchins is strongest amongst mother-daughter and maternal sister pairs (Perry et al., 2008).

Our results show the availability of multiple cues to kinship and close relatedness for infant capuchins. Future work will examine whether cues such as age proximity, former alpha male status, and early social familiarity, influence how capuchins at older ages interact with each other in the context of mate choice, agonistic interactions, and affiliative behaviors. While high male reproductive skew and male rank stability can explain why male alpha status and age proximity are informative cues to infants, our data do not indicate why spatial proximity to group members is informative. The proximity of infants to other group members during their first few months of life reflects the partner preferences of their mothers and primary allo-parents, and the interest and tolerance that other group members show them. Thus, further research on mechanisms of kin recognition in older individuals is necessary in order to understand why spatial proximity is a useful, though limited, cue to infants with regard to kinship and close relatedness.

Close maternal perinatal association (i.e. primary caretaking and breast-feeding) between mothers and their dependent offspring provides a highly informative cue of relatedness to older siblings for detecting younger maternal siblings (Lieberman et al., 2007). This cue would also be valuable to grandmothers for identifying the infants of their own daughters and to aunts identifying the offspring of their maternal sisters. Because of generational overlaps and generally slow life histories, the enduring mother-offspring bond can also allow for other categories of maternal kin to become familiar with each other (Chapais, 2001; Berman, 2004; Rendall, 2004). For example, even in the absence of any attraction among maternal sisters, these sisters can become particularly familiar with each other because mutual attraction to the same mother dictates that the sisters will inevitably spend more time around each other. Infants would also spend more time around their grandmothers if their mothers still preferentially affiliated with their own mothers even as adults. Thus, maternal perinatal association and enduring mother-offspring bonds may explain why spatial proximity is an informative cue that infants can use to assess their relatedness to other group members. More research is necessary to understand why spatial proximity is informative regarding paternity, even when accounting for male alpha status. Mother-mediated proximity to the fathers of infants and continued attraction of infants to the same male (i.e. father) can theoretically increase familiarity between paternal siblings (Widdig, 2007), though we have yet to find evidence that paternal siblings discriminate each other from more distantly related kin.

Two mechanisms are generally thought to explain kin discrimination in animals: social familiarity (Walters, 1987; Halpin, 1991) and phenotype matching (Holmes & Sherman, 1983; Lacy & Sherman, 1983), or some combination of the two where phenotype matching is dependent on prior exposure to kin. Currently, we are unable to assess phenotype matching because of the limited availability of multi-generational pedigrees that would create precise coefficients of relatedness. We hope in the near future to be able to assess the possible role of phenotype matching more closely.

APPENDICES

Table S1: Microsatellite markers used in genotyping. The observed heterozygosity was estimated using all genotyped individuals in the Lomas population, including those analyzed by Muniz et al. (2006). Allelic dropout rates were determined by looking at those samples analyzed by IG; we limited data to heterozygous loci, calculated the proportion of times that the loci was falsely scored as homozygous, and divided those numbers over the total number of PCRs for the loci as per Arandjelovic et al. (2009).

Locus	Alleles	Multiplex PCR	Observed heterozygosity	Allelic dropout
Ceb01	4	Yes	0.5158	0.45
Ceb02	3	Yes	0.2110	0.78
Ceb03	7	Yes	0.6782	1.88
Ceb04	6	Yes	0.5361	0.98
Ceb07	4	Yes	0.5578	1.36
Ceb08	6	Yes	0.6138	2.66
Ceb09	9	Yes	0.6571	2.73
Ceb10	4	Yes	0.6447	1.62
Ceb11	8	Yes	0.8023	1.23
Ceb105	3	Yes	0.5431	3.13
Ceb115	5	No	0.6745	1.74
Ceb119	6	Yes	0.6686	5.91
Ceb120	6	Yes	0.6667	1.11
Ceb121	5	Yes	0.7061	1.62
Ceb127	4	Yes	0.5115	5.21
Ceb128	5	Yes	0.7069	0.39
Ceb130	8	No	0.6667	3.53
D7S794	3	Yes	0.5845	1.37

Table S2: PCR protocol for first round of amplifications. First round PCR was carried out for 16 primer pairs: Ceb01, Ceb02, Ceb03, Ceb04, Ceb07, Ceb08, Ceb09, Ceb10, Ceb11, Ceb105, Ceb119, Ceb120, Ceb121, Ceb127, Ceb128, and D7S794. Primer pairs Ceb115 and Ceb130 were not run in this first round of amplifications.

Temperature (°C)	Time (MM:SS)	Cycles
94	9:00	1
94	0:30	3
62	0:30	
72	0:30	
94	0:30	3
60	0:30	
72	0:30	
94	0:30	3
58	0:30	
72	0:30	
94	0:30	3
55	0:30	
72	0:30	
94	0:30	28
52	0:30	
72	0:30	
72	30:00	1

Table S3: PCR protocol for second round of amplifications. For primer pairs Ceb115 and Ceb130 this was the only round of amplifications.

Temperature (°C)	Time (MM:SS)	Cycles
94	9:00	1
94	0:30	40
*	0:30	
72	0:30	
72	30:00	1

* Primer pair specific temperatures indicated in Table 4-3.

Table S4: Primer pair information.

Locus	**Primer**	**Sequence (5’-3’)**	**5’ label**	**Annealing temperature (°C)**	**MgCl2 (mM)**
Ceb_01	Forward	CCAGGCAAGCCAGCAATC	6-FAM	58	1.5
Ceb_01	Reverse	GAGCCAATTCCCCTAATAAATGTC			
Ceb_02	Forward	ACAGCGAGCAATATAACCT	HEX	55	1.5
Ceb_02	Reverse	TCCTTCCCTATGCAAATTC			
Ceb_03	Forward	TGGAACTGTGGGTATCAGTGT	6-FAM	58	1.5
Ceb_03	Reverse	TGTCATTGCTTTTAGGGGTTC			
Ceb_04	Forward	CTTGAACTCGGGAAATGG	HEX	57	2.0
Ceb_04	Reverse	TGTGAGGCTTGCTTTTAAC			
Ceb_07	Forward	ACCCAGGACAGGCAAAGG	6-FAM	55*	1.5
Ceb_07	Reverse	ATTATGGAGGGTCGGTGTG			
Ceb_08	Forward	GCCTGGGTAACAAGAGCA	HEX	58	1.5
Ceb_08	Reverse	TATTTGAAACGGTGGGTCAG			
Ceb_09	Forward	GGGCTTCTCAGCCTCCAC	HEX	60*	1.5
Ceb_09	Reverse	CAGGGTTCTCCAAAGAAAGAGA			
Ceb_10	Forward	TTGCTGATGCTTGCCTTC	6-FAM	61	1.5
Ceb_10	Reverse	TGGCAGATTGTGGACTTCTC			
Ceb_11	Forward	GCTTTCTGACTTGGGCTGAC	6-FAM	59	1.5
Ceb_11	Reverse	TGGTTTGGATGCCTCTGAC			
Ceb_105	Forward	GCACTCCCCTGTCTGTTCC	HEX	60	2.0
Ceb_105	Reverse	TAGGACTTGGGCTGGCTTC			
Ceb_115	Forward	CCTGGGCAACAGAGTGAG	HEX	58	1.5
Ceb_115	Reverse	TACACACAGTATTGGGAGACCA			
Ceb_119	Forward	TGGGCAACAGAGCAAGAC	HEX	62	2.0
Ceb_119	Reverse	ACTTGAGAGGTTGAAGCATGAG			
Ceb_120	Forward	TTTGGGACTTGGACTGGTTC	6-FAM	60*	1.5
Ceb_120	Reverse	CCGGGTGTATTAGGGTCCTC			
Ceb_121	Forward	CCATTTAGGGGAGGAGAAGG	HEX	59	1.5
Ceb_121	Reverse	TTGGTTGGTAGGCAGGTAGG			
Ceb_127	Forward	TGAGGCTTTGAGAGGGTATGTG	6-FAM	60	1.5
Ceb_127	Reverse	AGGCAGGCAGGCAGACAG			
Ceb_128	Forward	CAGCGAGGTTTCATCTCAAG	6-FAM	60	1.5
Ceb_128	Reverse	TATTGCCAGGTCCAAAAGTG			
Ceb_130	Forward	CAAAGTCCACTCACTTAACCAC	HEX	59*	1.5
Ceb_130	Reverse	AGAAGACCCTGCCTCAAG			
D7S794	Forward	GCCAATTCTCCTAACAAATCC	6-FAM	52	1.5
D7S794	Reverse	TATGCCCATGTGTTAGGGTT			

* 2 cycles at +2°C, 2 cycles at +1°C, then 36 cycles at specified annealing temperature.

Table S5: Cervus output. Write authors to receive this as an excel file, as it is too large to present in table form.

Table S6: GLMM results for probability of close relatedness ($r \geq 0.25$) to males. Model was run using spatial proximity scores from the first four months of each infant's life.

Fixed Effect	Estimate	SE	Df	LRT	Pr(Chi)	
(Intercept)	0.183	0.742				
Test variables						
Male is alpha	9.197	2.579	1	13.944	0.0002	***
Spatial proximity	0.969	0.178	1	13.522	0.0002	***
Age proximity	-2.170	0.544	1	10.404	0.0013	**
Control variables						
# of adult males	-0.060	0.213	1	0.071	0.7899	ns
# of adult females	0.859	0.231	1	6.760	0.0093	**
Infant is male	-0.309	0.271	1	1.078	0.2991	ns

Table S7: GLMM results for probability of close relatedness ($r \geq 0.25$) to females. Model was run using spatial proximity scores from the first four months of each infant's life.

Fixed Effect	Estimate	SE	Df	LRT	Pr(Chi)	
(Intercept)	-0.272	0.515				
Test variables						
Spatial proximity	1.261	0.185	1	16.811	< 0.0001	***
Age proximity	-1.148	0.491	1	3.507	0.0611	.
Control variables						
# of adult males	-0.331	0.221	1	1.919	0.1659	ns
# of adult females	0.373	0.231	1	2.446	0.1178	ns
Infant is male	0.543	0.256	1	4.182	0.0409	*

Table S8: GLMM results for probability that an adult male is the father of an infant. Model was run using spatial proximity scores from the first four months of each infant's life.

Fixed Effect	Estimate	SE	Df	LRT	Pr(Chi)	
(Intercept)	-3.428	0.469				
Test variables						
Male is alpha	4.846	1.067	1	12.013	0.0005	***
Spatial proximity	0.619	0.248	1	5.756	0.0164	*
Control variables						
Male age	0.545	0.287	1	3.309	0.0732	.
# of adult males	-0.149	0.310	1	0.201	0.6536	ns
# of adult females	0.280	0.311	1	0.792	0.3735	ns
Infant is male	-0.217	0.377	1	0.329	0.5665	ns

Table S9: GLMM results for probability of infant's partner being a paternal sibling. Model was run using spatial proximity scores from the first four months of each infant's life.

Fixed Effect	Estimate	SE	Df	LRT	Pr(Chi)	
(Intercept)	-13.159	1.545				
Predictor variables						
Spatial proximity	0.065	0.363	1	0.045	0.8325	ns
Age proximity	-24.833	5.267	1	11.876	0.0006	***
Control variables						
Is maternal sibling	1.164	0.680	1	1.884	0.1698	ns
# of adult males	0.635	0.973	1	0.466	0.4949	ns
# of adult females	4.559	1.385	1	10.335	0.0013	**
Infant is male	-0.468	1.179	1	0.185	0.6673	ns
Partner is male	1.332	1.059	1	1.643	0.1999	ns

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