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

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36

37Abstract

38

39The ability to recognize kin has important impacts on fitness because it can allow for kin-
40biased affiliative behaviors and for avoidance of mating with close kin. While the presence
41and effects of kin biases have been widely studied, less is known about the process by
42which animals recognize close kin. Here we investigate potential cues that white-faced
43capuchin monkeys (*Cebus capucinus*) may use to detect half-siblings and closer kin. We
44focus on the first year of life in a sample of 130 infant (n=65 infant females) wild capuchins
45from the Lomas Barbudal population in Costa Rica. We show that (1) infant relatedness to
46juvenile and adult males at the level of half-sibling and higher can be predicted by male
47alpha status, spatial proximity, and age proximity, and that (2) infant relatedness to juvenile
48and adult females at the level of half-sibling or higher can be predicted by spatial proximity
49(but not age proximity). Furthermore, (1) the identities of infants' fathers can also be
50predicted by male alpha status and the spatial proximity between infants and adult males,
51and (2) age proximity (but not spatial proximity) is predictive of paternal sibship. These
52results suggest that infant capuchins have access to multiple cues to close relatedness and
53paternal kinship, though whether infants use these cues later in life remains to be explored
54in future research.

55

56Keywords: kin recognition, age proximity, early social familiarity, male dominance,

57capuchins

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

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

72 Kin recognition has been documented in a wide array of animal taxa, including, to name
73 only a few: Artic charr (*Salvelinus alpinus*) (Winberg & Olsén, 1992; Olsén & Winberg, 1996),
74 spadefoot toads (*Scaphiopus bombifrons*) (Pfennig et al., 1993), Golden hamsters (*Mesocricetus*
75 *auratus*) (Mateo & Johnston, 2000), and Belding's ground squirrels (*Spermophilus beldingi*) and
76 Arctic ground squirrels (*Spermophilus parryii*) (Holmes & Sherman, 1982). While there is also
77 ample evidence of kin discrimination or kin bias in numerous primate species, particularly
78 among maternal kin (Kapsalis, 2004; Silk, 2002, 2009), less is known about the mechanisms by
79 which organisms come to treat closely related individuals differently from more distantly related
80 kin and non-kin. Mammalian infants rely on milk produced by their mothers for nutrition, and as
81 a result, primates form early bonds with their mothers, which can continue throughout their lives

82depending on dispersal patterns. While well-maintained mother-offspring bonds likely explain
83patterns of maternal kin-biases in female philopatric species (Chapais, 2001; Chapais & Bélisle,
842004; Rendall, 2004), the mechanisms by which paternal kin recognition is possible remain less
85understood (Widdig, 2007).

86 Whereas primate studies commonly cite early social familiarity as the probable
87mechanism for kin discrimination in primates (Rendall, 2004; Berman, 2004), few studies
88quantify the usefulness of such a mechanism for accurately identifying different types of kin, as
89compared with other possible cues to relatedness such as age proximity for paternal sibship and
90adult male rank for paternity. Such quantification is critical, however, because the effectiveness
91of mechanisms determine the degree to which kin discrimination can occur in different species.
92For example, if early social familiarity because of maintained mother-offspring bonds is the
93mechanism for kin discrimination, then one can expect mother-offspring and maternal siblings to
94show patterns of kin recognition across their lifespan. However, if the fathers of infants do not
95preferentially associate with their own offspring, then early social familiarity is not likely to
96facilitate 1) offspring-father recognition unless in one-male units, or 2) paternal sibling
97recognition unless paternal siblings are concentrated into groups of similarly-aged peers.

98 This research project seeks to assess social cues infants might use to recognize their close
99kin in primates living in groups containing multiple adult females and males. First, male
100dominance rank could cue infants to the identity of their father, if alpha males sire most infants.
101Numerous studies have shown that higher ranking males typically sire more offspring than lower
102ranking males in multi-male, multi-female primate groups (savannah baboons (Alberts et al.,
1032003, 2006; Altmann et al., 1996), macaques (de Ruiter, 1994; Widdig et al., 2004; Rodriguez-
104Llanes et al., 2009), chimpanzees (Constable et al., 2001; Boesch et al., 2006; Wroblewski et al.,

1052009), bonobos (Gerloff et al., 1999), mountain gorillas (Bradley et al., 2005), mandrills
106(Charpentier et al., 2005; Setchell et al., 2005), red howler monkeys (Pope, 1990), white-faced
107capuchins (Jack & Fedigan, 2006; Muniz et al., 2006, 2010), red-fronted lemurs (Kappeler &
108Port, 2008), and sifakas (Kappeler & Schäffler, 2008)). If male dominance rank and group
109membership can remain relatively stable for longer than the typical gestation length for their
110species, then male dominance rank can serve as a cue to paternity for infants.

111 Second, individuals that spend more time near an infant may be more likely to be its kin.
112For example, if males have some degree of paternity certainty based on their mating history with
113females, then they may bias the amount of time that they spend with infants toward those that are
114more likely to be theirs. Thus, spatial proximity may also be a cue that infants use to detect
115which adult males are their fathers. Evidence for father-offspring kin recognition has been
116documented in savannah baboons (Buchan et al., 2003; Onyango et al., 2012), chacma baboons
117(Huchard et al., 2010, 2013), rhesus macaques (Langos et al., 2013), chimpanzees (Lehmann et
118al., 2006), and capuchin monkeys (Muniz et al., 2006, 2010). Additionally, paternal recognition
119and affiliative bias of fathers toward their own offspring may also lead paternal siblings to spend
120more time near each other because of mutual attraction to the same adult male. Thus, spatial
121proximity may also cue infants to paternal sibship with natal group members.

122 Third, if alpha males sire most offspring during short breeding tenures, individuals closer
123in age to an infant will be more likely to be its paternal siblings, compared to older individuals.
124Peer group membership can serve as a cue to paternal sibship in species in which one or a few
125males monopolize reproduction during short breeding tenures, since this concentrates paternal
126siblings into similarly aged cohorts (Altman, 1979; Widdig, 2007, 2013). Studies on baboons
127(Alberts, 1999; Silk et al., 2006; Smith et al., 2003), rhesus macaques (Widdig et al., 2001, 2002,

1282006; Schülke et al., 2013), and mandrills (Charpentier et al., 2007) suggest that some primates
129recognize paternal siblings. Membership in an age-cohort and – more generally – age proximity,
130have been hypothesized as a means for achieving paternal sibling recognition.

131 In addition to social mechanisms, phenotype matching, a process by which “an individual
132learns its own phenotype or those of its familiar kin by association” (Holmes & Sherman, 1983)
133may also play a role in kin recognition. Phenotype matching via various means has been
134postulated to play a role in primates (acoustic: Phefferle et al., 2015, Levréro, 2015; personality:
135Widdig, 2001; visual: Bower et al., 2012, Kazem & Widdig, 2013), but it is not a focus of our
136study because of limitations in our ability to estimate precise coefficients of relatedness between
137individuals in our study population. We do, however, discuss its potential role.

138**Study species**

139 White-faced capuchins are an interesting species in which to study the mechanisms of
140and limits to kin recognition, because individuals tend to have available to them many kin of
141varied relatedness, age, and familiarity. This is because alpha males sire a disproportionately
142large number of offspring (Jack & Fedigan, 2006; Muniz et al., 2006, 2010), generating a high
143frequency of paternal siblings within groups. For example, in the Lomas Barbudal population
144some 55% of capuchin dyads in the same cohort (less than two years apart in age) were paternal
145siblings (Perry et al., 2008) compared to 5% in Ngogo chimpanzees, 13% in Cayo rhesus
146monkeys, and 37% of Amboseli baboons (Langergraber et al., 2007). In addition, the Lomas
147Barbudal population is characterized by long male tenures, as several alpha males have been
148documented to hold their rank for more than six years and the longest alpha tenure has been
149estimated (through genetic paternity data) to be 17 years. With inter-birth intervals of
150approximately two years, long tenures theoretically also produce many co-resident full sibling

151dyads (Strier, 2004). The combination of high male reproductive skew and long alpha tenures in
152capuchins creates a social system in which individuals have more co-resident close kin than is
153found in most other primate species. Previous studies have detected father-daughter inbreeding
154avoidance (Muniz et al., 2006, 2010), but females fail to favor paternal half siblings for
155affiliative interactions in the same way that they favor maternal siblings (Perry et al., 2008).

156 In this study, we attempt to determine the usefulness of early social familiarity, age
157proximity, and male alpha status as cues for kin recognition in the Lomas Barbudal population of
158white-faced capuchin monkeys. We first reassess the evidence for high male reproductive skew
159and inbreeding avoidance in capuchins, since the breeding system in *Cebus capucinus* is integral
160to our understanding of typical kin availability in capuchin groups. We then test for cues to
161kinship and close relatedness that are potentially available to infants. Specifically, we ask four
162questions. Can infants potentially infer close relatedness to males (both juvenile and adult) by
163using male alpha status, age proximity, or spatial proximity as cues? Can infants potentially infer
164close relatedness to females (both juvenile and adult) by using age proximity or spatial proximity
165as cues? Can the identity of an infant's father be predicted by male alpha status or spatial
166proximity of infants to adult males? Can paternal sibship be inferred through age proximity or
167spatial proximity?

168METHODS

169Study Site and Subjects

170 Subjects in this study are members of nine habituated groups of wild, white-faced
171capuchin monkeys (*Cebus capucinus*) in the Lomas Barbudal Biological Reserve (10°29–32'N,
17285°21–24'W) and adjacent public and private lands in the Guanacaste province of Costa Rica
173(hereafter referred to as 'Lomas'). *C. capucinus* is a New World monkey that lives in multi-male,

174multi-female groups and females are typically the philopatric sex (Perry, 2012). Groups at Lomas
175range in size from 5 to 40 individuals (Perry et al., 2012). The Lomas population has been
176observed since 1990, with continuous monitoring since January 2002 as part of an infant
177development project (see Perry, 2012 and Perry et al., 2012 for more detailed information).
178Behavioral data were collected using focal-animal, scan, and *ad libitum* sampling methods
179(Altmann, 1974). Scan and *ad libitum* data were collected on all members of the eleven study
180groups at Lomas. Focal-animal sampling was done on select individuals depending on which
181particular projects were ongoing. Data included in this study are from an eleven-year period from
182January 2002 to December 2012, when one to three groups were typically monitored each day
183for 25-26 days per month. We analyze data from capuchins' first year of life, the period when
184they are particularly vulnerable to infanticide and when their closest social partners tend to be
185their mothers (Perry, 2012, Perry et al., 2012). We obtained behavioral data on 140 infants (born
186to 60 mothers) who survived their first year of life; we limited analyses to a subset of 130 infants
187(n=65 females) for which we also had genetic paternity data. This research was performed in
188compliance with the laws of Costa Rica. The UCLA Institutional Animal Care and Use
189Committee (IACUC), known as the Chancellor's Animal Research Committee (ARC), approved
190the protocol (ARC # 2005-084).

191**Proximity**

192 Proximity information was extracted from group scan data taken from infants born into
193regularly followed study groups. During a group scan, observers noted the activity of a monkey
194and the identity of any other monkey within ten capuchin body lengths of that focal individual. A
195body length was defined as that of an adult male, from nose to tail base (~40 cm). Monkeys were
196scanned at the moment in which they were first seen, and observers rotated through the group

197trying to scan as many monkeys as possible. Group scans included in this study were collected
198from over six dozen different researchers. Before collecting data, observers were required to
199routinely exhibit 100% accuracy in identifying monkeys, and to match at 97% with the
200behavioral coding of more experienced researchers. To assess inter-observer reliability, assistants
201were tested monthly for continued mastery of the code and syntax system used for data
202collection and if errors were detected the relevant data were either fixed or discarded. All data
203collected contained tags, which denote which observer collected the data (typist), and which
204other observers (spotters) were out with them in the field. Field assistants regularly rotated
205through field partners including senior staff (i.e. SEP, IG, and field site managers), and field
206assistants were trained to double-check each other's identification of monkeys. Focal-animal
207sampling in each study group was done according to a rotation plan to facilitate equal sampling
208of focal individuals, but group scans were taken opportunistically, and thus were not distributed
209evenly across the hours of the day, season, or age for each individual. Ten minutes or more
210separate group scans for any individual monkey. This source generated a total of 49 976 group
211scans for 130 infants (n=65 females) from nine social groups, with an average of 384 group
212scans per infant (range: 53 - 1 082).

213 We calculated the percentage of group scans in which group members were within ten
214body lengths (~4 meters) of the focal infants during their first year of life. This provides a
215general proxy for the amount of time members of a dyad spent around each other over a given
216time period. We use these percentage scores as our measure of spatial proximity.

217 During the first few months of a capuchin's life, it is predominantly in physical contact
218with its mother with a shift toward both reliance on allo-parents and infant spatial independence
219somewhere between 4-6 months of age (Perry, 2012). Therefore, throughout the first few months,

220an infant's proximity to group members is a function of 1) its mother's interest in other group
 221members and 2) the interest of other group members in either the infant or the mother. For this
 222reason, we also analyze the proximity data from the first four months of an infant's life
 223separately, since later periods will additionally be a function of the infant's own willingness to be
 224in proximity of other monkeys.

225Age approximation and classification

226 All infants in this study were either seen on the day of their birth (33.6%) or given birth
 227date estimates based on the size, coloration, and activity level of the infant. The majority of
 228births in this study (77.9%) were known to be accurate to within 14 days. For individuals not
 229seen as neonates but first observed as juveniles, age was approximated using physical and
 230behavioral characteristics (MacKinnon, 2002; Fragaszy et al., 2004) and assumed to be accurate
 231by plus or minus two years (Table 2). Males first observed as adults were more difficult to assign
 232age to, especially when the males were of full adult size (~10 years of age or older), but best
 233estimates were used based on the years of experience of field researchers at Lomas. The ages of
 234full-sized adult immigrant males from unknown natal groups and older females born prior to
 235group habituation were assumed to be accurate to a margin of plus or minus five years. Males
 236were classified as adults once they reached six years of age. All adult males were considered
 237potential sires of the infants in their groups.

238Table 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%)

239

240 **Male alpha status determination for paternity analyses**

241 Alpha males are typically easy to identify by the use of particular vocalizations and the
242 direction of dyadic submissive behaviors (Perry, 1998). The rank relations between subordinate
243 males, however, are much more difficult to determine and cannot always be detected (Perry,
244 1998; Schoof & Jack, 2014).

245 Consistent with the range of known gestation lengths in *Cebus capucinus* (Carnegie et al.,
246 2011), we generated conception windows beginning 145 and ending 166 days prior to the known
247 or estimated date of birth for an infant. We used these windows to exclude infants (n=11 out of
248 130) conceived during periods for which we could not be certain of the alpha status of their
249 fathers.

250 **Genetic Sample Collection and Analysis**

251 Faecal samples analyzed in this study were collected between 2004 and 2012.
252 Approximately 5 g of faecal samples were collected and then stored according to one of three
253 storage methods described in Nsubuga et al. (2004). Briefly, samples were placed into either (1)
254 50 ml conical tubes containing 20 g of silica gel beads, (2) tubes containing 10 ml of an
255 RNAlater preservation solution from Ambion, or (3) 50 ml conical tubes containing 30 ml of
256 97% ethanol. Samples placed in ethanol were stored for at least 24 hours before the solid matter
257 was transferred onto 50 ml conical tubes containing 20 g of silica beads (Roeder et al., 2004).

258 IG extracted DNA from the fecal samples of 161 individuals using the QIAmp DNA
259 Stool Mini Kit from Qiagen, with modifications of the manufacturer's protocol. Approximately
260 100 mg of faecal matter per sample was used following Morin et al. (2001). RNAlater samples
261 were extracted as described in Nsubuga et al. (2004), starting from 2 mL of the sample mixture.
262 DNA was eluted with AE buffer to a final volume of 200 μ L. DNA was extracted from one tissue

263sample from an infant that fell victim to infanticide. For this sample, IG used the DNeasy Blood
264&Tissue Kit from Qiagen and followed the manufacturer's instructions. 134 of the individuals
265sampled were born into one of the 11 study groups, 12 samples came from adult and subadult
266males that migrated into the study population, and 14 were unhabituated monkeys from non-
267study groups for which we opportunistically collected samples.

268 DNA was amplified at 18 tetranucleotide loci (Muniz & Vigilant 2008) (See **Appendices**,
269**Table S1**). Genetic information for 172 capuchins from the Lomas Barbudal population was
270available from previously published work (Muniz et al., 2006) and we reanalyzed DNAs from
271nine individuals from that study to ensure consistency in allele calling. The PCR protocol (Muniz
272& Vigilant, 2008) was adapted to allow for two-step multiplex PCR (Arandjelovic et al., 2009).
273Briefly, we added 5 uL of our DNA extract to a 15 uL master mix containing 16 of our 18
274primer pairs. Two primer pairs (Ceb115, Ceb130) did not amplify well under the new multiplex
275protocol and were analyzed according to the original protocol. After the first round of multiplex
276PCR, 5 uL of a 1:100 dilution of each tube was added to 16 new tubes, each containing 15 uL of
277a new master mix with one of the 16 primer pairs. All DNA samples were run in triplicate. IG
278analyzed the PCR products with an ABI PRISM3100 automated sequencer and Genemapper
279software. PCR protocols for first and second round amplifications, plus detailed primer pair
280information is available in the Appendices (**Tables S1, S2, and S3**). As per Arandjelovic et al.
281(2009), genotypes were assigned as heterozygous when each allele was seen at least two times
282from independent PCRs, and genotypes were assigned as homozygous after a minimum of 3
283independent PCRs.

284 In order to guard against sample mix up or animal misidentification, all migrant males
285and individuals born into one of our study groups but with unknown mothers were genotyped

286twice using DNA extracted from two independent faecal samples. All infants of known maternity
287had their genotypes compared for mismatches to their mother's in order to guard against possible
288sample mix up. We used identity analysis to check for the same genotype appearing under
289different names, and compared genotypes between the Muniz dataset and the new one.

290 By including three standard deviations outside the estimated gestation length of wild
291capuchins (157.83 ± 8.13 days, Carnegie et al., 2011) we obtained a conception window of 49
292days between 183 and 133 days prior to the estimated birth date of each infant. We had census
293information for the conception window for 122 out of 134 (91%) genotyped individuals born into
294one of the 11 study groups. For these infants we included all group males older than 6 years of
295age around the time of an infant's conception as potential sires. Nine of the newly genotyped
296capuchins were born prior to the habituation of their natal group (NM group), but we assigned as
297candidate parents all adult males (i.e. 6 years or older) present in their group at the time of
298habituation, and all known habituated migrant males which were seen in the group during partial
299censuses after intergroup encounters and searches for other groups. The three other infants
300without census data were born into SP group, which was only sporadically monitored between
3012004 and 2008. For those infants we widened their conception windows to 94 (n=2) and 182
302days (n=1). The number of candidate fathers varied from 1 to 11 (median: 3, mean: 4.2, SD: 2.5).
303Males under six years of age would only be considered potential sires if we had good
304demographic records and, in using CERVUS we could not identify a sire with high statistical
305confidence. Such a case, however, did not arise (See **Appendices, Table S5**). In our previous
306genetic parentage analysis of infants that were conceived after habituation of their social groups,
307we have without exception been able to identify sires within the social group of the mother
308(Muniz et al. 2006, 2010), and the youngest age at which a male sired young was 7.72 years

309(Perry, 2012). In one case in the Muniz dataset (2006, 2010), two males were each genetically
310compatible as the father of a particular offspring, but one of these males was the full-sibling of
311the offspring and paternity was assigned to the older male.

312 Likelihood-based paternity assignments were generated using the computational program
313CERVUS 3.0.7 (Kalinowski et al., 2007). Simulation settings in CERVUS were set to 10 000
314offspring, 98% of loci typed, 1% of loci mistyped, 98% of candidate parents sampled, seven
315candidate fathers, and the minimum of 16 loci typed.

316 Although CERVUS showed no evidence for null alleles, previous analyses had detected
317one at locus Ceb115, which was carried by at least 12 members of FF group (Muniz et al., 2006,
3182010) and originated from the alpha male of FF group (FZ). One of those carriers (HE, a son of
319FZ) became alpha male of FL group and passed the null allele to one offspring there. Our current
320analysis has identified an additional 7 carriers of the null allele at Ceb115 (1 in FF group, 3 in FL
321group, and 4 in RF group), all of whom are descended (offspring or grandoffspring) from the
322former alpha male of FF group (FZ).

323Pedigrees and coefficients of relatedness

324 It is notoriously difficult to use microsatellite genotyping data to determine the kinship
325category or reliably estimate the pairwise coefficient of relatedness for two individuals in the
326absence of pedigree information (Csilléry et al., 2006; Van Horn et al., 2008; Langergraber et al.,
3272007). We therefore used pedigrees established through maternity and paternity analyses to
328calculate pairwise coefficients of relatedness using Ed Hagen's DESCENT software
329(<http://itb.biologie.hu-berlin.de/~hagen/Descent/>). After we provided the identity of each
330capuchin, as well as the identity of each capuchin's known mother and genetically assigned
331father, the DESCENT program generated estimated coefficients of relatedness for all possible

332dyads formed with each individual. Lack of complete pedigrees means that the estimated
333coefficients of relatedness generated by the software can be lower than their actual measure.

334 16 of 166 (9.6%) adult females in our study population (including females not in data
335analyses presented here) had mothers that were unknown to us because the females were born
336prior to group habituation and we had no genetic samples from their mothers. We lacked
337complete pedigree information for more adult males (68 of 246, 27.6%), because they were
338immigrants from unknown social groups. These migrant males, however, were assumed to be
339unrelated to monkeys in our study group unless they were later determined to be the fathers of
340infants. Since males of *Cebus capucinus* often emigrate with natal kin (Perry, 2012, Perry et al.,
3412008, 2012; Wikberg et al., 2014), it is likely some non-natal males that were assigned as non-
342kin of infants are actually the paternal uncles (or more distant kin) of infants. Of the 39 males
343known to have sired infants at Lomas Barbudal, 56.4% (n=22) had unknown parents.

344 For 50.8% of infants in this study and 26.9% of their available genotyped social partners,
345we could reconstruct full pedigrees two generations back (i.e. we identified the 4 grandparents)
346(**Table 1**). As a result of limited pedigrees for many of our dyads, we ran analyses considering
347close relatives defined as having a coefficient of $r=0.25$ or higher, because we could be more
348confident about relatedness at this level and not at more distantly related levels. For example,
349kinship categories at ≥ 0.25 for which we are confident include parents, full siblings, half
350siblings, full nephews/nieces, and grandparents of infants, while categories that may be under-
351sampled due to incomplete multi-generational pedigrees are full aunts/uncles and double full first
352cousins. However, there were no known double full first cousins in our dataset.

353

354 **Table 2: Pedigree completeness for genotyped dyads in the dataset.** The table shows data for
 355 130 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 %)

356

357 Dyads in the datasets

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

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

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

375groups. Our behavioral dataset thus totaled 3 054 dyads formed between 130 infants and 265
 376social partners (Table 3).

377 In our models that include male alpha status as a test predictor, we dropped an additional
 37850 dyads that were formed between infants (n=20) and alpha males (n=18) during unstable years
 379when there were rank reversals in the alpha male position. Including these dyads in analyses did
 380not change whether or not any of our predictor variables were significant or not, nor the direction
 381of their effects.

382

383**Table 3: Study subjects and study group information.** This table shows the number of study
 384infants per group, their female and male social partners, as well as the range of group sizes per
 385study group. Female and male social partners can appear in more than one study group as a result
 386of migrations or group fissions. Only genotyped social partners are included in this table and in
 387our 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

388^a Fission product of AA

389^b Fission product of RR

390^c Fission product of FF

391^d Fission product of MK

392

393Statistics and Data Analysis

394 Statistical analyses were run in R v.3.2.2 (R Core Team, 2015) using the `glmer` or `lmer`
 395function from the `lme4` package (Bates et al., 2015). We ran Generalized Linear Mixed Models
 396(GLMM, Baayen, 2008) with binomial error structure and logit link function to assess the

397significance of our predictor variables for detecting close kin during infancy.

398 For all models, we included random intercepts for infant identities, partner identities, and
399primary group of residence as well as random slopes where possible. We confirmed model
400stability by excluding all levels of all random effects one by one and comparing the estimates
401with estimates derived from the model based on the full data set. We assessed collinearity –
402excessive correlation among our explanatory variables – by calculating Variance Inflation
403Factors (Field, 2005) using the function “vif” of the “car” package (Fox and Weisberg, 2011).
404The highest Variance Inflation Factor in any model was 2.04 suggesting no collinearity problems.
405In order to establish the significance of the test predictors, we conducted a full versus null model
406comparison (Forstmeier & Schielzeth, 2011) using a likelihood ratio test (Dobson & Barnett,
4072008). The null model comprised all terms in the full model except the test predictors. P-values
408for individual predictors were also obtained using likelihood ratio tests via the “drop1” function
409in R. We z-transformed all quantitative fixed effects to a mean of 0 and standard deviation of 1.

410 Since the number of adult females and the number of adult males can limit the ability of
411dominant males to monopolize reproduction (Cowlshaw & Dunbar, 1991) - in turn impacting
412the probability of certain kin types and relatedness within groups - we include both as control
413predictors for all of our GLMMs.

414 Our models were all stable, meaning that no one infant, social partner, or group of
415residence drove the results that are shown in these analyses.

416RESULTS

417*Reproductive Skew*

418 We genotyped 162 monkeys at 18 loci and combined these data with published data for a
419total of 334 genotyped individuals. For all 129 newly genotyped individuals with known

420mothers, CERVUS assigned a single well-supported father (**Appendices, Table S5**). For 4 out of
4215 individuals in NM group for which we did not know the identity of their mother, CERVUS also
422assigned only one well-supported father, while one older female had no assigned father. The
423youngest assigned father in dataset was 6.25 years old at the time of his infant's conception.
424There was one case of extra-group paternity. We included the male as a candidate father because
425the mother of the infant had previously been seen spending a night in that male's social group,
426after having been separated from her own group during an intergroup encounter. The sire in this
427case was a familiar male (i.e. he emigrated out from the female's natal group) and was alpha of a
428neighboring group. Thus, there is little evidence that females seek mates outside of their social
429group.

430 For 119 newly genotyped infants we knew the alpha male during the time of their
431conception and found that they sired the majority (83.2%, n=99) of infants. However, while
432alpha males sired 94.1% (n=96 of 102) of infants born to females that were not their daughters or
433granddaughters, they only sired 17.6% (n=3 of 17) of infants born to females that were their
434descendants, and this difference was significant (Fisher's Exact test: $P < 0.0001$, $N = 119$).

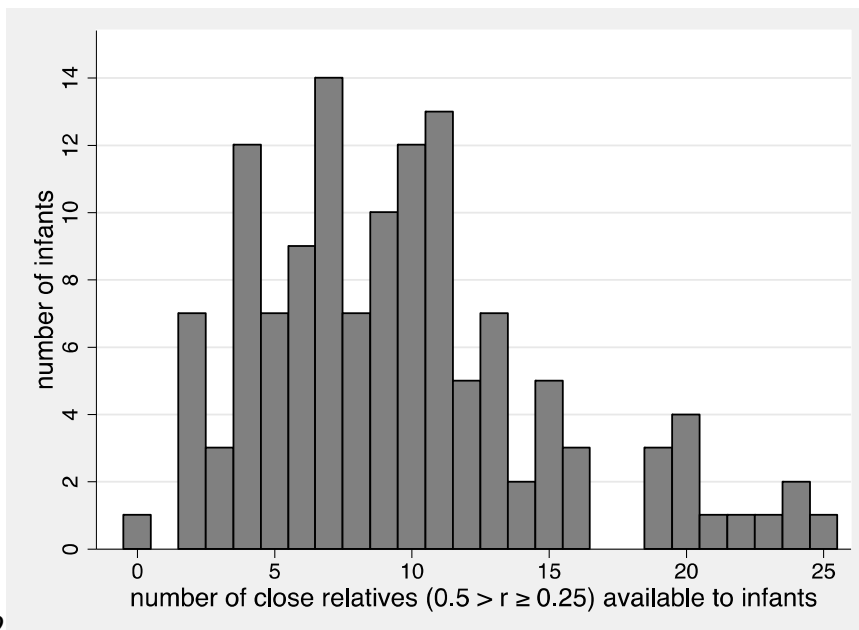
435 ***Group composition, average dyadic relatedness, and kin availability***

436 Infants had available three to 40 potential social partners, including one to 10 adult males
437and three to 12 adult females. During the first year of life of 130 genotyped infants, 95.4% had a
438father present, 36.2% had at least one full sibling (range: 0-4), 46.9% had at least one maternal
439half sibling (range: 0-5), and 87.7% had one or more paternal half sibling (range: 0-19) available.
440Paternal half siblings represented 21.2% of genotyped dyads (n=689) in our dataset. Maternal
441siblings accounted for 6.1% of dyads (n=198), over a third of which were full siblings (n=75).
442Infants had many partners that were related to them at the level of $0.5 > r \geq 0.25$ (38.3% of all

443dyads) (**Figure 1**), of which half siblings comprised 63.7% (paternal half siblings: 54%). Infants
 444had from one to six partners related at the level of $r \geq 0.5$ (10.8% of all dyads) (**Figure 2**), of
 445which full siblings made up 21.4%, parents 72.6%, and the remaining 6% ($n=21$ dyads) were
 446comprised of dyads involving 12 infants that were the product of inbreeding.

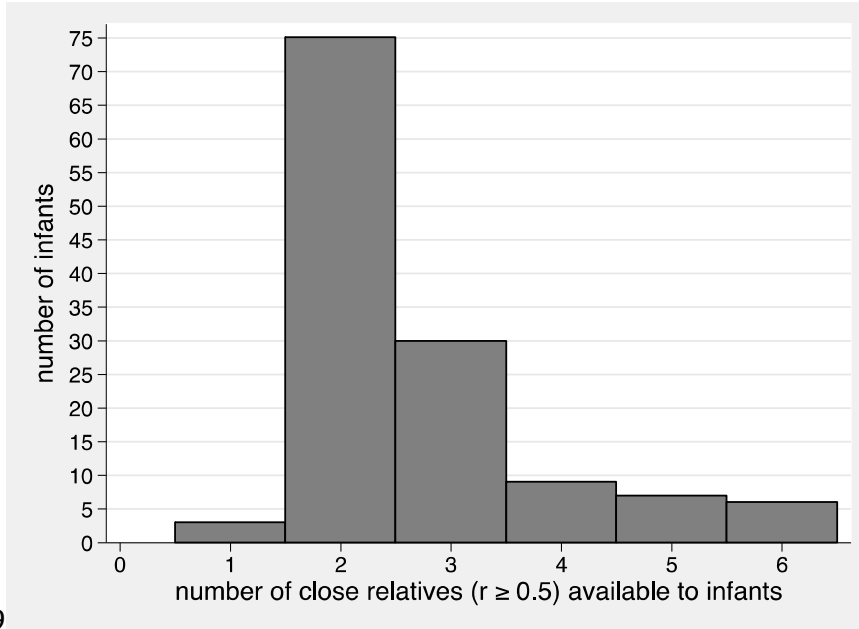
447 The average relatedness between genotyped infants and available social partners
 448(including non-kin) was high (mean=0.221, std=0.158, $n=3\ 255$ dyads) and infants were related
 449to their fellow group members at an average estimated coefficient of relatedness of 0.23
 450(std=0.07, $n=130$ infants) (**Figure 3**).

451



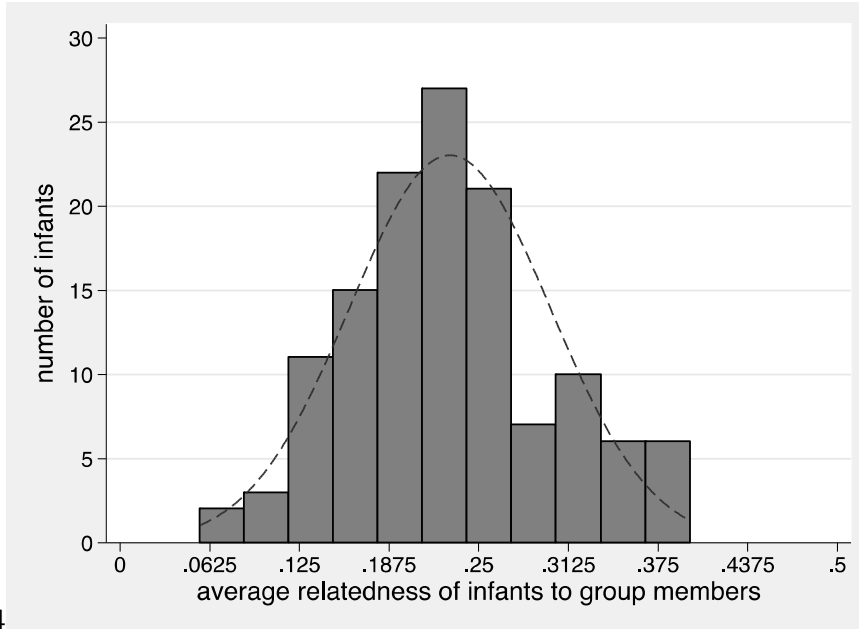
452
 453**Figure 1: Distribution of the number of close relatives ($0.5 > r \geq 0.25$) available to infants.**
 454The histogram shows the number of infants with zero to 25 social partners in their group related
 455to them at the half-sibling level. These included but were not limited to half siblings,
 456grandparents, full aunts and uncles, and full nieces and nephews.

457
 458



459

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



464

465 **Figure 3: Distribution of the average of the estimated coefficient of relatedness between**

466 **infants and other members of their groups.** The dashed line indicates the normal density curve

467 for the values. Incomplete pedigrees mean that the actual values may be higher.

468 **Cues to close relatedness to males**

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

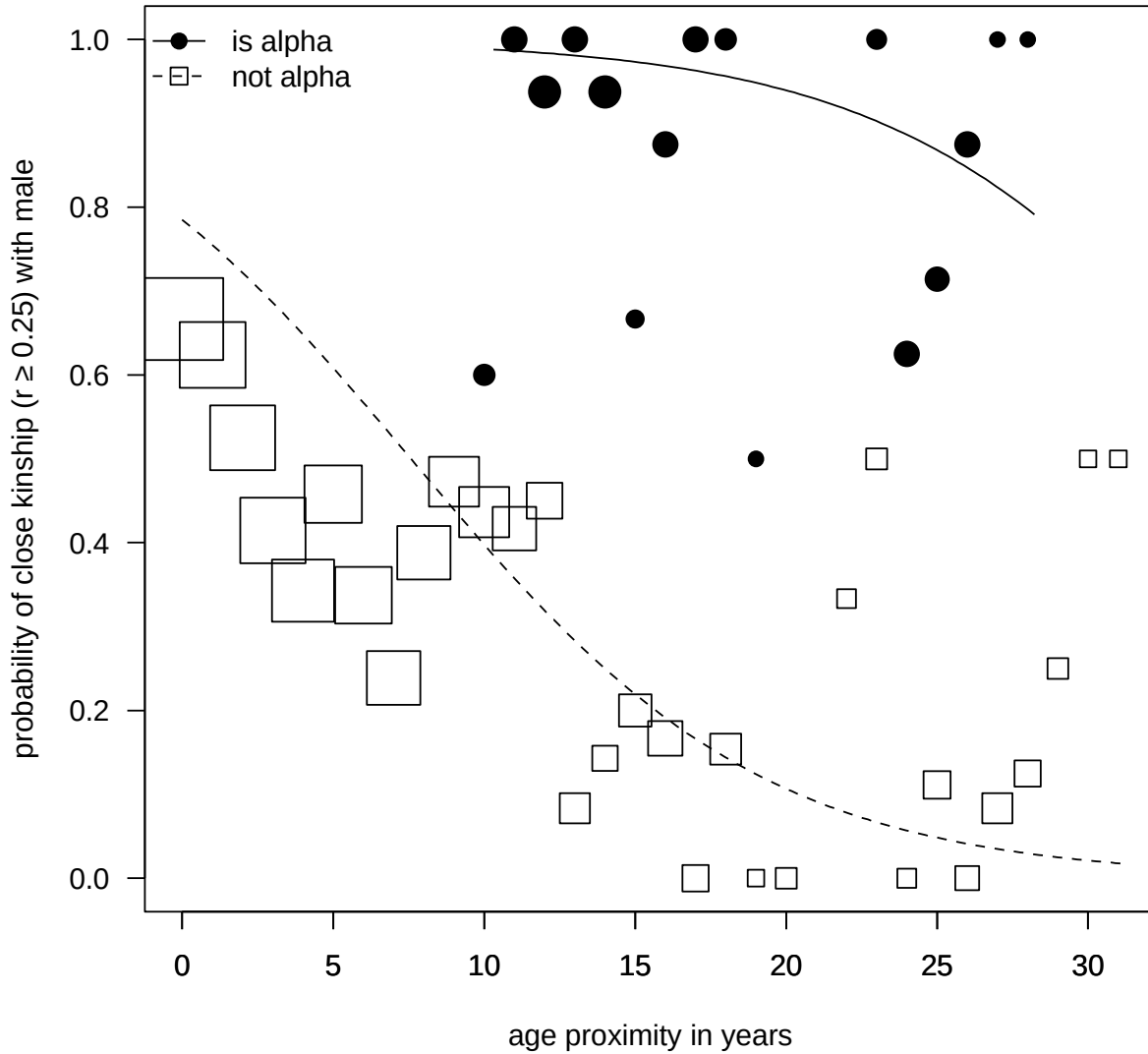
477 Whether or not a male was the alpha of a group was a significant predictor of close
 478 relatedness to focal infants, as were spatial proximity and age proximity (**Table 4**). Alpha males
 479 were more likely to be a close relative (typically their father or grandfather), as were males
 480 closer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

483

484 **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

485

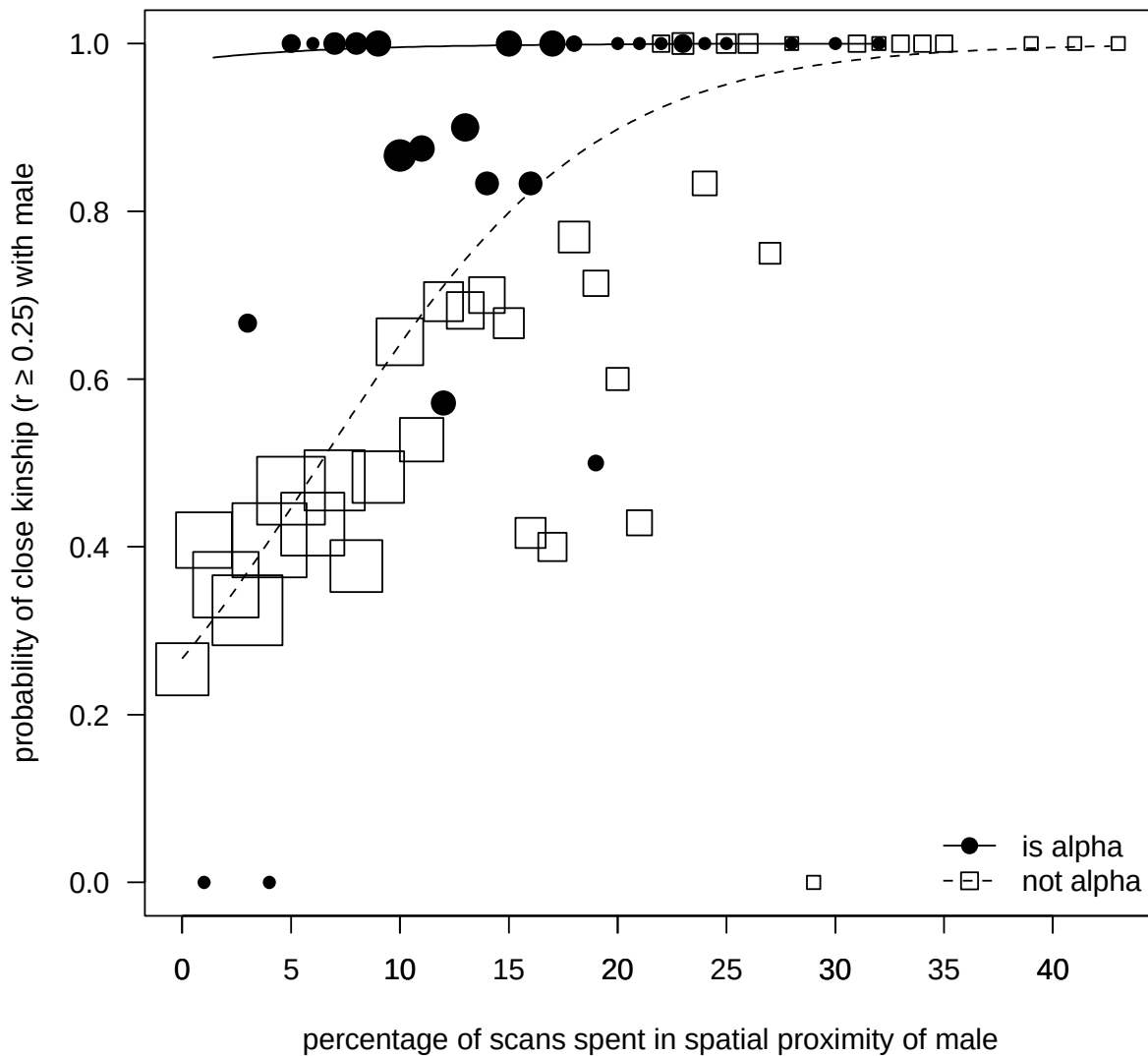


487

488 **Figure 4: Probability of close relatedness ($r \geq 0.25$) to males, contingent on age proximity.**

489 Bubbles represent the proportion of partners at that age proximity that were related to the infant
 490 at the level of paternal sibling or higher. The size of each bubble indicates sample size. The lines
 491 showing the predicted values control for spatial proximity, number of adult males, number of
 492 adult females, and infant sex.

493



494

495 **Figure 5: Probability of close relatedness ($r \geq 0.25$) to males, contingent on spatial**

496 **proximity.** Bubbles represent the proportion of partners at that spatial proximity score that were
 497 related to the infant at the level of paternal sibling or higher. The size of each bubble indicates
 498 sample size. The lines showing the predicted values control for age proximity, number of adult
 499 males, number of adult females, and infant sex.

500

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

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

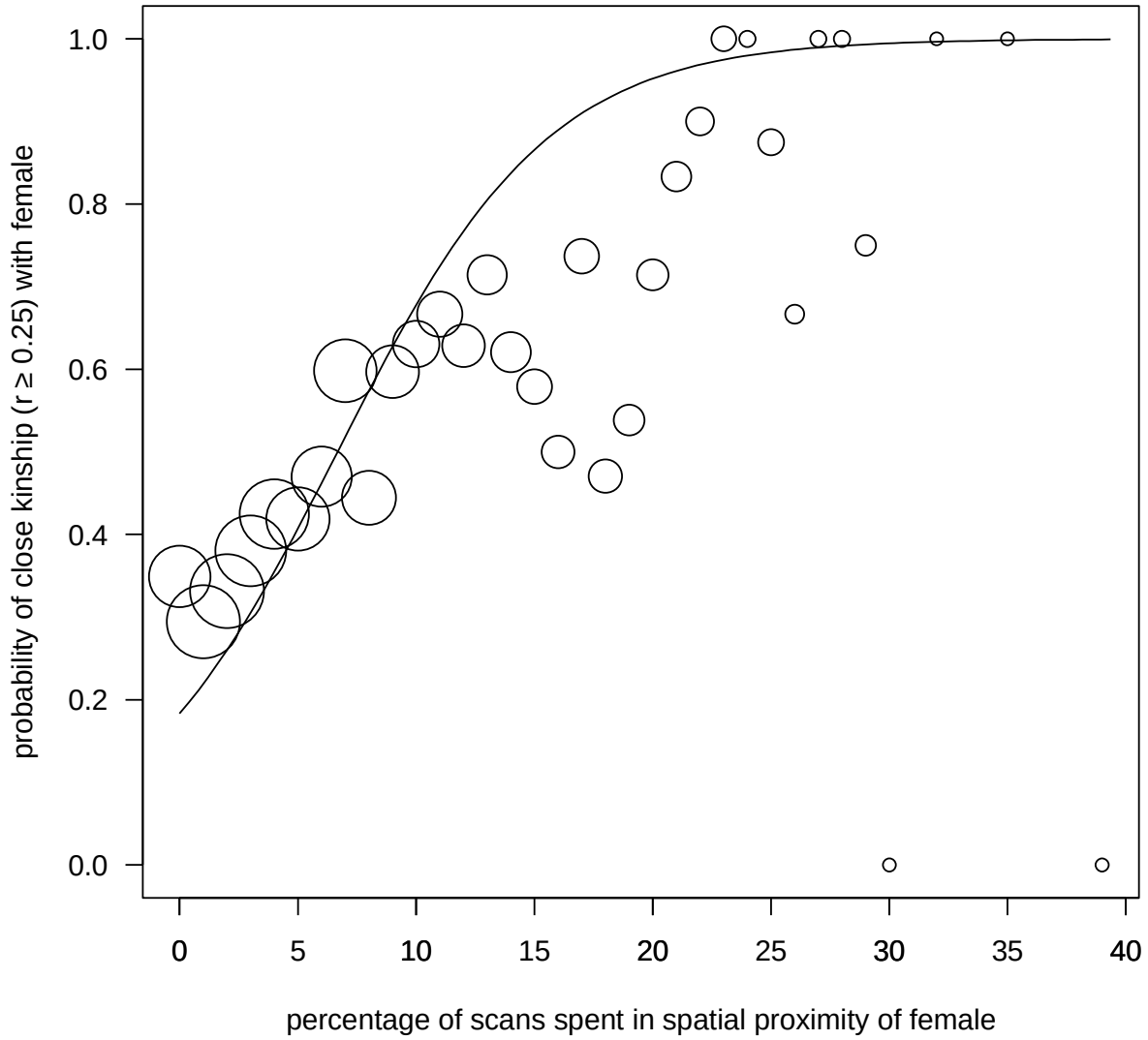
510 Spatial proximity but not age proximity was a significant predictor of close relatedness to
 511 females (**Table 5**). Infants were more likely to be closely related to females with which they
 512 spent more time (**Figure 6**). Similar results were found when limiting our analysis to data
 513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

514

515 **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	.

516



518

519 **Figure 6: Probability of close relatedness ($r \geq 0.25$) to females.** Bubbles represent the

520 proportion of partners at that spatial proximity score that were related to the infant at the level of

521 paternal sibling or higher. The size of each bubble indicates sample size. The line showing the

522 predicted values controls for age proximity, number of adult males, number of adult females, and

523 infant sex.

524

525 **Cues to paternity**

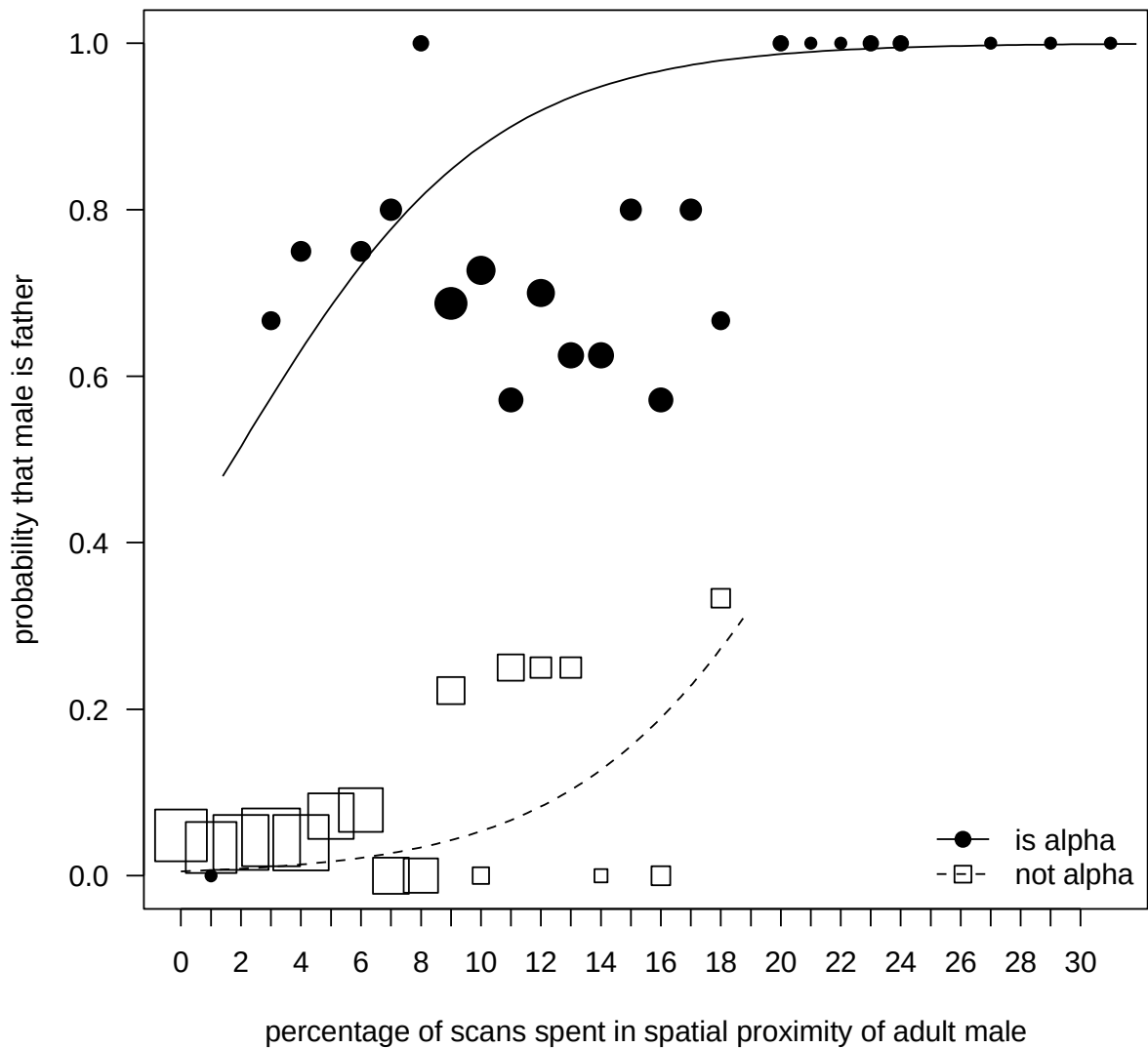
526 We assessed the significance of male alpha status and spatial proximity during infancy as
 527 cues for whether an adult male was an infant’s father. Our data set comprised 622 infant-male
 528 dyads formed with 57 adult males in 9 groups. The response was whether or not the male was the
 529 father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

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

540
 541 **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

542
 543



544

545 **Figure 7: Probability that an adult male is an infant's father, contingent on spatial**

546 **proximity and male alpha status.** Bubbles represent the proportion of males at that spatial

547 proximity score that were also an infant's father. The size of each bubble indicates sample size.

548 The lines showing the predicted values control for male age, number of adult males, number of

549 adult females, and sex of the infant.

550 Of the 110 infants that lived with stable alpha males for the duration of their first year of
 551life, the majority (83.6%, n=92) spent the most time with the alpha male, and for most infants
 552(80.9%, n=89) their closest adult male associate was either their father (n=73) or grandfather
 553(n=16) (**Table 7**).

554 In 22 cases where an infant lived with both a father and grandfather, the father was alpha
 555in four cases, the grandfather in 16, and neither in two. When the grandfathers were alpha,
 556infants spent more time around their grandfathers than they did around their fathers (15 of 16).
 557Similarly, when the alpha was their father, infants spent more time around him than around their
 558grandfather (3 of 4).

559**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

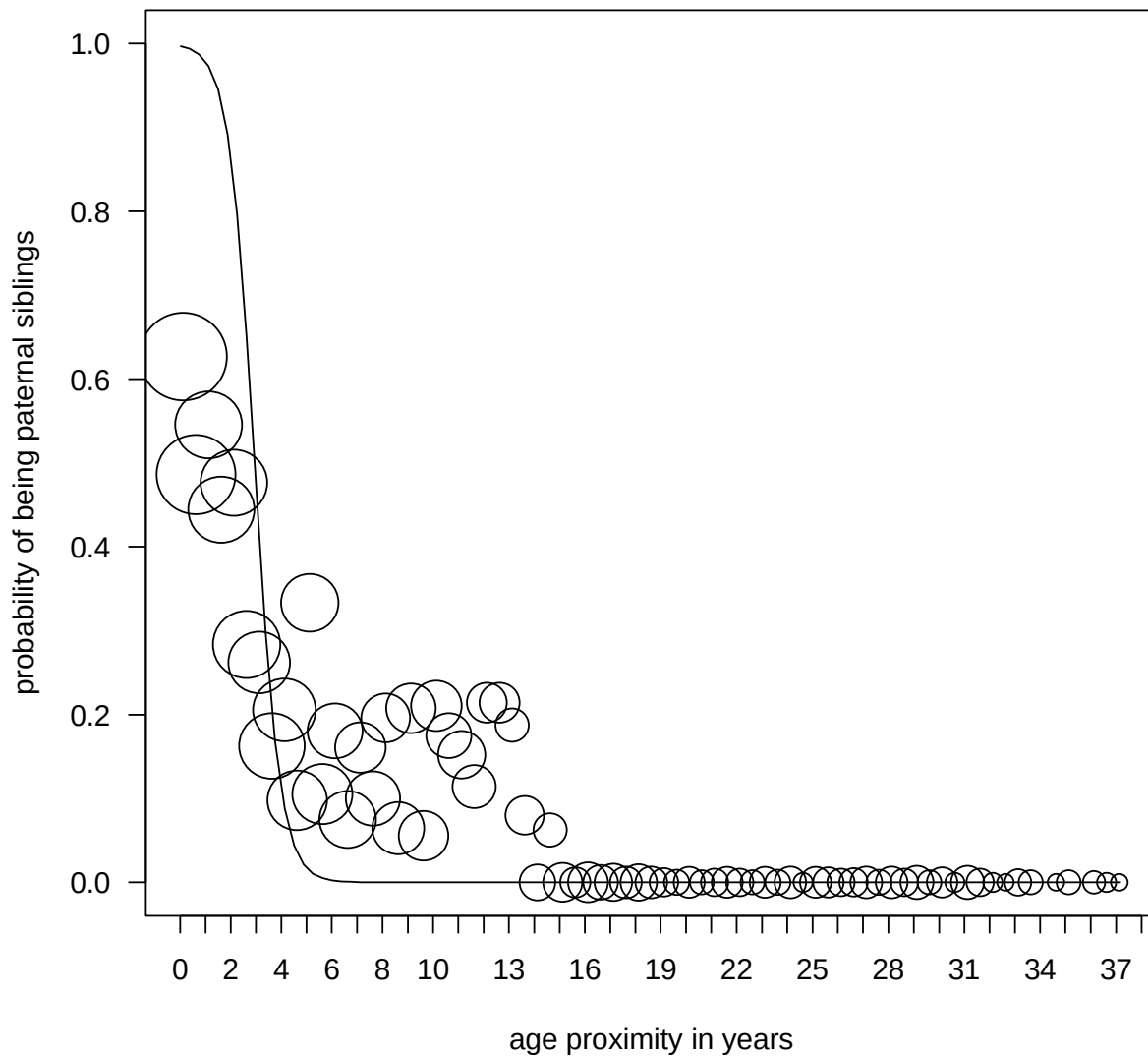
562 We tested the significance of age proximity and
 563spatial proximity as cues to paternal sibship, using a dataset of dyads formed with all group
 564members other than mothers and alpha males (n=2 893 dyads). Male and female social partners
 565of all ages were included in this analysis. The response was whether or not the other member of
 566the dyad was a paternal sibling (yes/no). We controlled for the possible effects of maternal
 567sibship, infant sex, the number of adult males in the group, the number of adult females in the
 568group, and any possible interaction effect of partner sex on age proximity, spatial proximity,
 569maternal sibship, and infant sex. The identities of the infants, social partners, and groups of
 570residence were included as random factors. The full model was significantly different from the
 571null model ($\chi^2_4=20.298$, $P=0.0004$). All interaction terms (formed with partner sex) were non-
 572significant and were dropped from the final model.

574 Age proximity, but not spatial proximity, was a significant predictor of paternal sibship
 575(**Table 8**). Social partners closer in age to infants were more likely to be their paternal siblings
 576(**Figure 8**). Similar results were found when limiting our analysis to data collected during the
 577first four months of each infant’s life (**Appendices, Table S9**).

578

579**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



580

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

586DISCUSSION

587 Our data show that wild capuchin infants have information available to them – male
588alpha status, age proximity, and spatial proximity - that can serve as cues to close relatedness ($r \geq$
5890.25) and even paternal kinship (i.e. paternity and paternal sibship). Further research is needed to
590establish whether or not infants actually use these potential cues later in life.

591 Male alpha status was a significant predictor of close relatedness ($r \geq 0.25$) to males and
592also of who the fathers of infants were. Infants that survived their first year of life were likely to
593have their fathers still present in their group (95.3%), and their fathers were usually alpha males
594(78%). Male alpha status is also more generally highly informative as to close relatedness,
595because alpha males tend to be the father or grandfather of surviving infants. In general, whether
596male rank is a useful cue to relatedness in a species is dependent on the degree of male
597reproductive skew, as well as the stability of male dominance rank and group membership. As a
598consequence of both the high degree of male reproductive skew seen at Lomas and the stability
599in male alpha rank, alpha status is an excellent marker of the paternal descent of infants in this
600population. In another primate with extreme male reproductive skew toward alpha males,
601Verreaux's sifakas (*Propithecus verreauxi*), dominant non-natal males residing in groups
602containing other non-natal adult males sire approximately 91% of offspring (Kappeler &
603Schäffler, 2008). Alpha male status should thus also be an informative marker for close
604relatedness, and more specifically paternity in these sifakas. Indeed, there is some evidence for
605later father-daughter discrimination in the species in the form of inbreeding avoidance (Kappeler
606& Schäffler, 2008).

607 Age proximity was a significant predictor of paternal sibship regardless of infant sex or
608partner sex. That is, males and females closer in age to an infant were more likely to have the

609same father as the infant. Age proximity was also a significant predictor of close relatedness to
610males, but not to females. This likely reflects the fact that male migration from their natal groups
611reduces the availability of older non-alpha adult male kin in groups. Natal male kin are therefore
612more concentrating into younger juvenile and sub-adult categories, while female kin remain
613distributed across a wider range of ages. Age proximity, and particularly peer group membership,
614is an important regulator of social interactions in capuchins (Schoof & Jack, 2014) and various
615other animals: gazelles (Walther, 1972), impalas (Murray, 1981), savannah baboons (Pereira,
6161988; Alberts, 1999; Silk et al., 2006, 2010), rhesus macaques (Janus, 1992; Widdig et al., 2001,
6172002), chimpanzees (Mitani, 2009), humpback whales (Ramp et al., 2010), and giraffes:
618(Bercovitch & Berry, 2013). In species featuring high male reproductive skew during brief
619tenures, such as rhesus macaques, strong associations with peers can allow for different treatment
620of paternal half siblings as compared to more distant kin (Altmann, 1979; Widdig, 2007, 2013).

621 Spatial proximity was a significant predictor of paternity. Adult males with which infants
622spent more time were more likely to be their fathers. Spatial proximity was also more generally a
623significant predictor of close relatedness to males and to females. Males and females with which
624infants spent more time were more likely to be related to them at the level of half sibling or
625higher ($r \geq 0.25$). Spatial proximity, however, was not a significant predictor of paternal sibship.

626 Male alpha status and spatial proximity to adult males were both significant predictors of
627who the fathers of infants were. Male alpha status and spatial proximity were also predictive of
628close relatedness to males ($r \geq 0.25$), with the closest adult male associates of infants typically
629being a father (66.7%) or grandfather (14.7%). Thus, capuchin infants have available to them
630multiple reliable cues that can be used to discriminate their direct male ancestors. Multiple cues
631may even explain why inbreeding between alpha males and their daughters and granddaughters

632 is rare in this population - a result replicated in this paper. In other words, inbreeding avoidance
633 among daughter-father pairs may be attributed to female sexual aversion to males with which
634 they spent more time during their infancy (akin to the Westermarck effect (Westermarck, 1891)),
635 female sexual aversion to males that were alpha during their infancy, or a combination of the
636 two. In mountain gorillas (*Gorilla beringei beringei*), male-immature associations are primarily
637 driven by male dominance rank and not paternity (Rosenbaum et al., 2015). However, since
638 dominant males typically sire the majority of infants, even in multi-male groups (Bradley et al.,
639 2005; Vigilant et al., 2015), early spatial proximity to males may still be informative as to
640 paternity alongside male alpha status. In other words, differential treatment of adult males
641 according to their former dominance status, and/or the time spent in proximity to them may
642 facilitate recognition of fathers. Interestingly, paternity patterns in gorillas, similar to those seen
643 in capuchins, are also indicative of father-daughter inbreeding avoidance (Vigilant et al., 2015).

644 Multiple reliable cues may facilitate the ability of capuchins to identify their fathers and
645 grandfathers, but the ability to identify paternal siblings appears more difficult. Generally, cohort
646 membership in primates is a good indicator of paternal sibship when high reproductive
647 monopolization occurs during short alpha male tenures (Altmann 1979; Widdig 2007, 2013).
648 Given the long tenures that alpha males can achieve in capuchins, however, the age difference
649 between paternal siblings can be large enough that cohort membership is not as reliable an
650 indicator of relatedness for two main reasons. First, the strength of male reproductive skew
651 decreases with length of tenure because the daughters and granddaughters of current alpha males
652 breed with subordinate males. Second, prior to the sexual maturation of an alpha male's
653 daughters, six years pass during which the alpha male is the sire of almost all offspring in his
654 group. Therefore, group members outside of an age cohort are also very likely to be paternal

655siblings during intermediately long (more than one year and less than six years) alpha tenures.
656Even if individuals lack the ability to recognize paternal siblings, biased behavior toward
657similarly aged peers could result in strong patterns of preferential association with paternal
658siblings if paternal siblings are concentrated in peer groups. In our sample of infants, however,
659group members outside of the peer group (i.e. more than one year apart in age) constituted a
660larger proportion of paternal siblings (60.6%, 462 of 763). The considerable number of older
661paternal siblings thus makes age cohort membership alone an insufficient cue for discriminating
662paternal siblings because older individuals are also likely to have the same father.

663 Infants in our dataset were related to their fellow group members at an average estimated
664coefficient of relatedness of 0.23, just below the level of half sibling. With such a large number
665of group members related to infants at the level of $0.5 > r \geq 0.25$ (37.9% of all dyads in our
666dataset), the ability to discriminate paternal half siblings from other kin may not be so important
667in capuchins because of the abundance of equally related or more highly related group members.
668With such high levels of within-group relatedness, one may even expect lower nepotism among
669close maternal kin because preferential support toward close maternal kin comes at the expense
670of other closely related group members (Wilson et al., 1992; Queller, 1994; West et al., 2001;
671Langergraber, 2012). Indeed, in a population where individuals have few kin available, it is not
672relevant to consider kin competition, as the benefits of cooperating with kin are much higher than
673the costs of competing with kin if there are very few kin to outcompete. However, in a
674population with abundant kin dyads, it is the variance in kinship in the population that will
675matter. For example, in a population like this one where most individuals have both close
676(parent, full sibling) and less close (half-sibling) kin present, one would expect a preference for
677the closest, easily identifiable maternal kin, which is what is observed. For instance, adult female

678affiliation in capuchins is strongest amongst mother-daughter and maternal sister pairs (Perry et
679al., 2008).

680 Our results show the availability of multiple cues to kinship and close relatedness for
681infant capuchins. Future work will examine whether cues such as age proximity, former alpha
682male status, and early social familiarity, influence how capuchins at older ages interact with each
683other in the context of mate choice, agonistic interactions, and affiliative behaviors. While high
684male reproductive skew and male rank stability can explain why male alpha status and age
685proximity are informative cues to infants, our data do not indicate why spatial proximity to group
686members is informative. The proximity of infants to other group members during their first few
687months of life reflects the partner preferences of their mothers and primary allo-parents, and the
688interest and tolerance that other group members show them. Thus, further research on
689mechanisms of kin recognition in older individuals is necessary in order to understand why
690spatial proximity is a useful, though limited, cue to infants with regard to kinship and close
691relatedness.

692 Close maternal perinatal association (i.e. primary caretaking and breast-feeding) between
693mothers and their dependent offspring provides a highly informative cue of relatedness to older
694siblings for detecting younger maternal siblings (Lieberman et al., 2007). This cue would also be
695valuable to grandmothers for identifying the infants of their own daughters and to aunts
696identifying the offspring of their maternal sisters. Because of generational overlaps and generally
697slow life histories, the enduring mother-offspring bond can also allow for other categories of
698maternal kin to become familiar with each other (Chapais, 2001; Berman, 2004; Rendall, 2004).
699For example, even in the absence of any attraction among maternal sisters, these sisters can
700become particularly familiar with each other because mutual attraction to the same mother

701dictates that the sisters will inevitably spend more time around each other. Infants would also
702spend more time around their grandmothers if their mothers still preferentially affiliated with
703their own mothers even as adults. Thus, maternal perinatal association and enduring mother-
704offspring bonds may explain why spatial proximity is an informative cue that infants can use to
705assess their relatedness to other group members. More research is necessary to understand why
706spatial proximity is informative regarding paternity, even when accounting for male alpha status.
707Mother-mediated proximity to the fathers of infants and continued attraction of infants to the
708same male (i.e. father) can theoretically increase familiarity between paternal siblings (Widdig,
7092007), though we have yet to find evidence that paternal siblings discriminate each other from
710more distantly related kin.

711 Two mechanisms are generally thought to explain kin discrimination in animals: social
712familiarity (Walters, 1987; Halpin, 1991) and phenotype matching (Holmes & Sherman, 1983;
713Lacy & Sherman, 1983), or some combination of the two where phenotype matching is
714dependent on prior exposure to kin. Currently, we are unable to assess phenotype matching
715because of the limited availability of multi-generational pedigrees that would create precise
716coefficients of relatedness. We hope in the near future to be able to assess the possible role of
717phenotype matching more closely.

718 **APPENDICES**

719

720 **Table S1: Microsatellite markers used in genotyping.** The observed heterozygosity was
 721 estimated using all genotyped individuals in the Lomas population, including those analyzed by
 722 Muniz et al. (2006). Allelic dropout rates were determined by looking at those samples analyzed
 723 by IG; we limited data to heterozygous loci, calculated the proportion of times that the loci was
 724 falsely scored as homozygous, and divided those numbers over the total number of PCRs for the
 725 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

726

727

728Table S2: PCR protocol for first round of amplifications. First round PCR was carried out for 72916 primer pairs: Ceb01, Ceb02, Ceb03, Ceb04, Ceb07, Ceb08, Ceb09, Ceb10, Ceb11, Ceb105, 730Ceb119, Ceb120, Ceb121, Ceb127, Ceb128, and D7S794. Primer pairs Ceb115 and Ceb130 were 731not run in this first round of amplifications.

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

732

733

734Table S3: PCR protocol for second round of amplifications. For primer pairs Ceb115 and 735Ceb130 this was the only round of amplifications.

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

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

737**Table S4: Primer pair information.**

Locus	Primer	Sequence (5'-3')	5' label	Annealing temperature (°C)	MgCl ₂ (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	TGGAAGTGTGGGTATCAGTGT	6-FAM	58	1.5
Ceb_03	Reverse	TGTCATTGCTTTTTAGGGGTTT			
Ceb_04	Forward	CTTGAAGTCTGGGAAATGG	HEX	57	2.0
Ceb_04	Reverse	TGTGAGGCTTGTCTTTAAC			
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	GCACTCCCCTGTCTGTTC	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			

738* 2 cycles at +2°C, 2 cycles at +1°C, then 36 cycles at specified annealing temperature.

740 **Table 5: Write authors to receive this as an excel file, as it is too large to present in table**
 741 **form.**

742

743 **Table S6: GLMM results for probability of close relatedness ($r \geq 0.25$) to males.** Model was
 744 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

745

746

747 **Table S7: GLMM results for probability of close relatedness ($r \geq 0.25$) to females.** Model
 748 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	*

749**Table S8: GLMM results for probability that an adult male is the father of an infant.**

750Model 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

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756**Table S9: GLMM results for probability of infant’s partner being a paternal sibling.** Model

757was 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

758

759

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