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Kin Recognition, Mechanisms, and Inbreeding Avoidance in Cebus capucinus

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Kin Recognition, Mechanisms, and Inbreeding Avoidance in *Cebus capucinus*

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by

Irene Godoy

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ABSTRACT OF THE DISSERTATION

Kin Recognition, Mechanisms, and Inbreeding Avoidance
in *Cebus capucinus*

by

Irene Godoy
Doctor of Philosophy in Anthropology
University of California, Los Angeles, 2015
Professor Susan E. Perry, Chair

Anthropology has a long history of examining the important roles of kinship in human societies, and an important tool in that process has been the use of the comparative method. White-faced capuchin monkeys (*Cebus capucinus*) are an ideal model organism for comparison to human studies, because they share important similarities such as the presence of full siblings and multiple generations of kin within groups. Primate societies are highly structured – factors such as kinship, age, and dominance rank play crucial roles in determining how and at what frequencies individuals interact. This variation in turn has an impact on the strength of social bonds that develop between different individuals. Research on the mechanisms underlying inbreeding avoidance in capuchins can contribute substantially to our broader understanding of kin recognition and how its limits result in a wide diversity of social structures even within species. In this thesis, I draw upon behavioral, genetic, and hormonal data to study mechanisms of kin recognition, particularly in the context of inbreeding avoidance, in a wild population of capuchins living in or near the Lomas Barbudal Biological Reserve in Costa Rica. First, I show that capuchin infants have multiple potential cues available that can be used to detect close kinship and relatedness to group members: these being spatial proximity, age proximity, and male alpha status. Second, I show that inbreeding avoidance in capuchins is strongest between social partners related at the levels of father-daughter. Third, I provide evidence that early spatial proximity to group members is one of the mechanisms involved in inbreeding avoidance in capuchins.

The dissertation of Irene Godoy is approved.

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University of California, Los Angeles

2015

DEDICATION PAGE

To Pablo, Mezcla, Barbell, Ruckus, Dixie,
Diablita, Dante, Cassie, Yasuni,
all the other forest movers, shakers,
players, brayers, and drama scene makers.
To the gregarious capuchins of Lomas Barbudal;
they instilled in me this love of fieldwork for once and for all.

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CHAPTER ONE: CUES TO KINSHIP AND RELATEDNESS

INTRODUCTION

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). 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 in numerous primate species, particularly among maternal kin (Kapsalis, 2004; Silk, 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 (Chapais & 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 discriminate their own kin and preferentially associate with them, then early social familiarity is not likely to facilitate 1) father-offspring 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), rhesus macaques (Altmann et al., 1996; 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), long-tailed macaques (de Ruiter, 1994), 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; Charpentier et al., 2008; 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, paternally related 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; Schülke et al., 2013), and mandrills (Charpentier et al., 2005; 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 Lomas Barbudal 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 discrimination 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 close relatedness to males be predicted by male alpha status, age proximity, or spatial proximity? Can close relatedness to females be predicted by age proximity or spatial proximity? 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 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. This 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). 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 who survived their first year of life; we limited analyses to a subset of 130 (n=65 females) for which we also had genetic paternity data.

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. 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. Males first observed as adults were more difficult to assign age to, especially when the males were of full adult size, 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.

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., 2011b), 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 rank 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 instruction. 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 2007) (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, 2007) 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., 2011b) 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).

Likelihood-based paternity assignments were generated using the computational program CERVUS 3.0.7 [Marshall et al., 1998]. 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 (Csillery 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 1-1: Pedigree completeness for genotyped dyads in the dataset.

No. of known grandparents	Infants	Social partners
0	8 (6.2 %)	75 (28.4 %)
1	12 (9.2 %)	35 (13.3 %)
2	29 (22.3 %)	63 (23.9 %)
3	15 (11.5 %)	20 (7.6 %)
4	66 (50.8 %)	71 (26.9 %)

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. We restricted our behavioral dataset to pairs where both members of the dyad were genotyped (n=67 dyads dropped) and pairs with at least 30 group scans (n=71 dyads dropped), leaving us with 3 053 dyads. 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.

Statistics and Data Analysis

Statistical analyses were run in R v.3.2.2 (R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/) using the glmer or lmer function from the lme4 package (Bates et al., 2014). 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, 1992) - in turn impacting the probability of certain kin types and relatedness within groups - we include both as control predictors for all of our GLMMs.

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.

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 21.1% of genotyped dyads (n=688) 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 $0.5 > r \geq 0.25$ (38.2% of all dyads) (**Figure 1**), of which half siblings comprised 63.7% (paternal: 53.9%). Infants had from one to six partners related at the level of $r \geq 0.5$ (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=0.159, n=3 254 dyads) and infants were related to their fellow group members at an average estimated coefficient of relatedness of 0.227 (**Figure 3**).

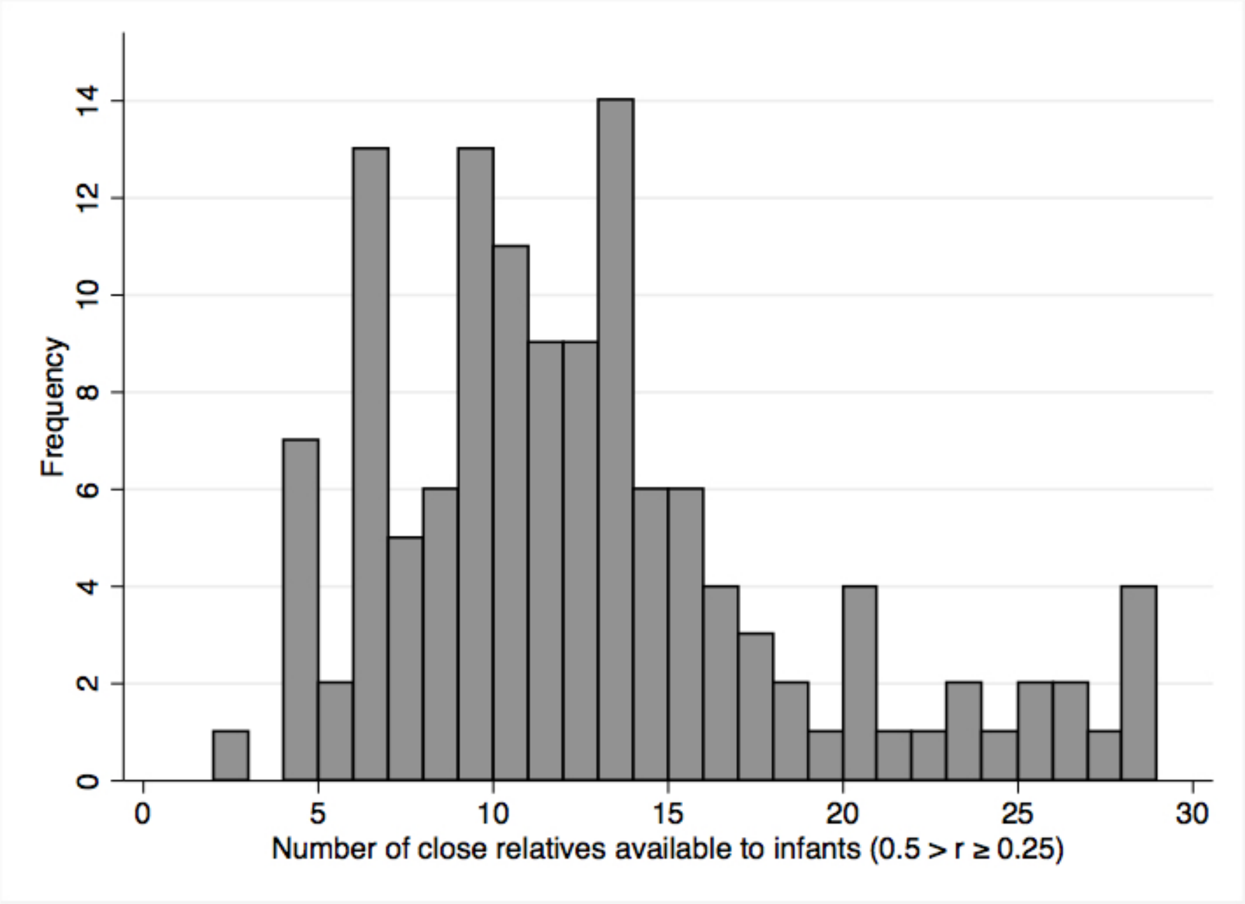

Figure 1-1: Distribution of the number of close relatives (0.5 > r ≥ 0.25) available to infants.

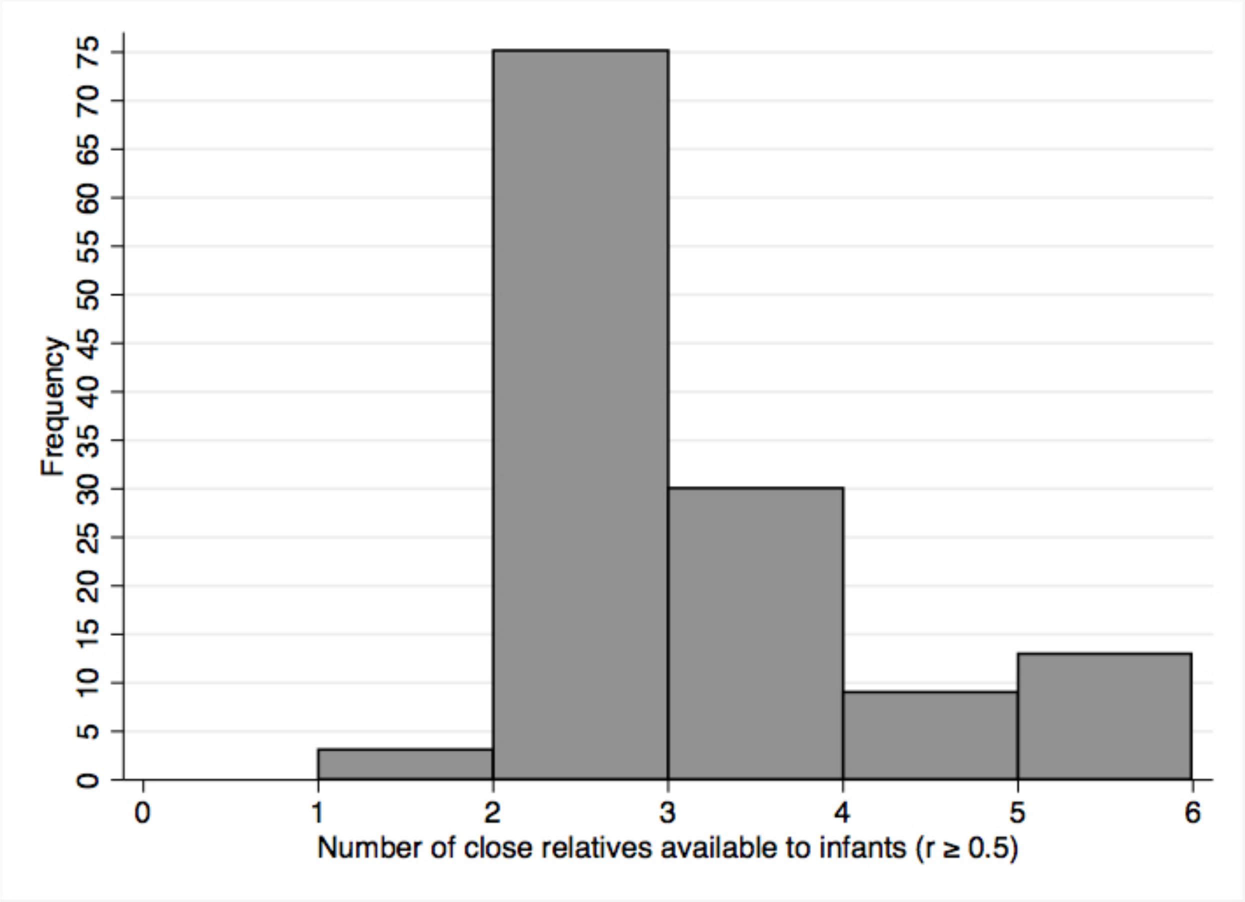

Figure 1-2: Distribution of the number of close relatives (r ≥ 0.5) available to infants.

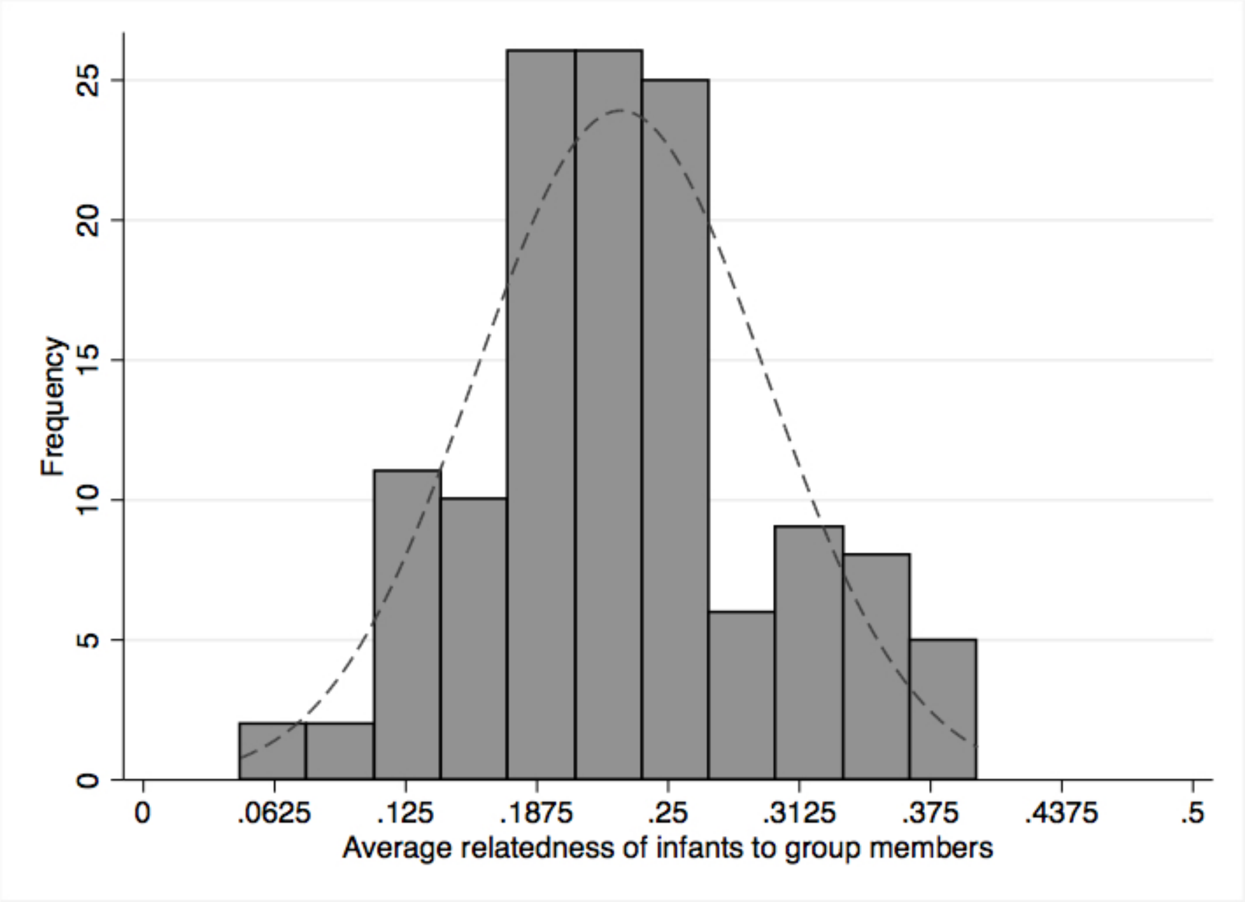

Figure 1-3: Distribution of the average of the estimated coefficient of relatedness between infants and other members of their groups. The dashed line indicates the normal density curve for the values. Incomplete pedigrees mean that the actual values may be higher.

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=1 417 dyads, n=130 infants, n=136 males). 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. The full model was significantly different from the null model (χ^2_3=38.942, 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 2**). 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 1-2: 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	14.245	0.0002	***
Spatial proximity	0.937	0.143	1	18.791	< 0.0001	***
Age proximity	-1.157	0.329	1	8.187	0.0042	**
Control variables						
# of adult males	-0.268	0.192	1	1.803	0.1794	ns
# of adult females	0.903	0.212	1	11.369	0.0007	***
Infant is male	-0.138	0.218	1	0.377	0.5392	ns

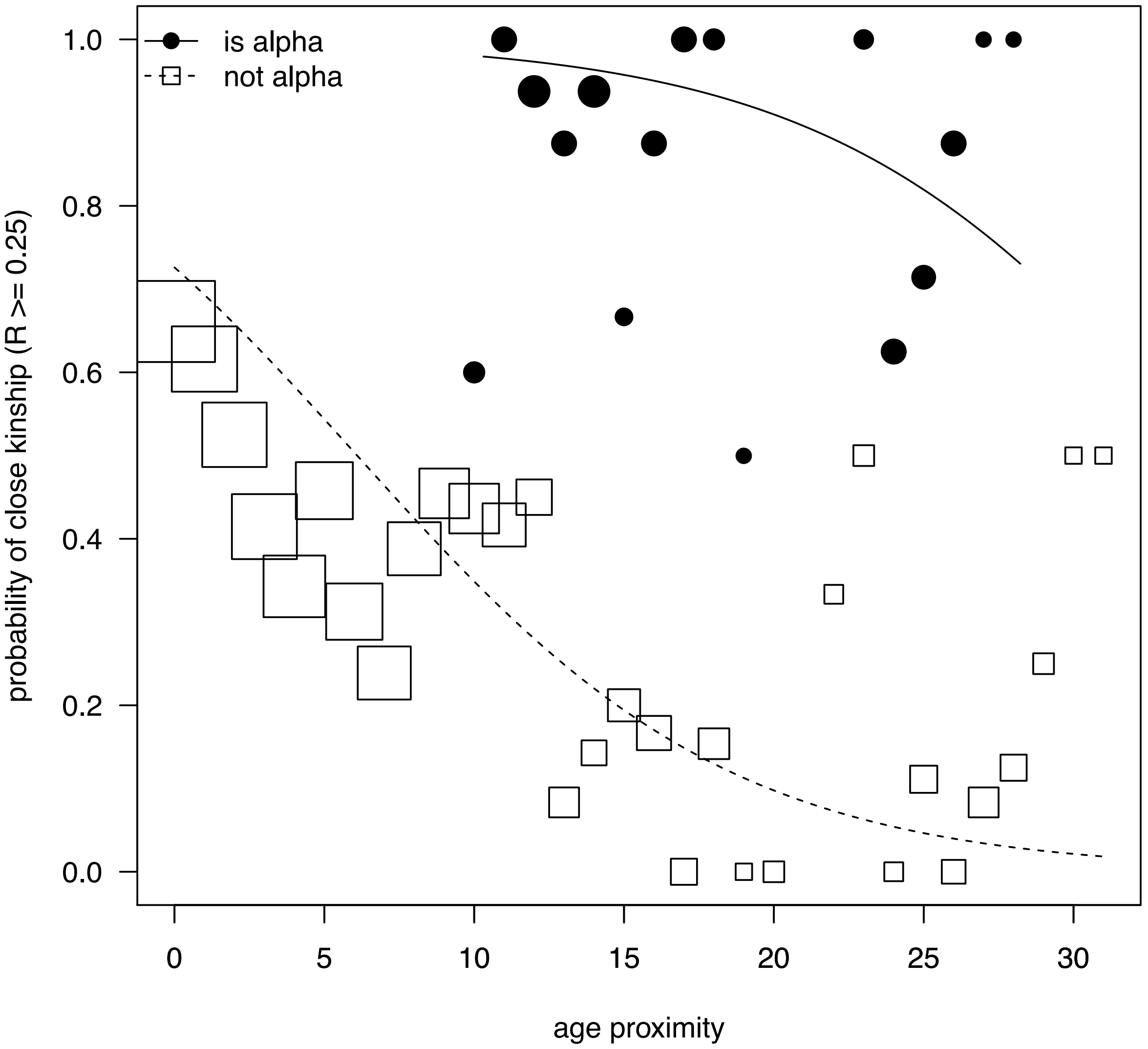

Figure 1-4: Probability of close relatedness (r ≥ 0.25) to males, contingent on age proximity. Bubbles represent the proportion of partners at that age proximity that were related to the infant at the level of paternal sibling or higher. The size of each bubble indicates sample size. The lines showing the predicted values control for spatial proximity, maternal sibship, number of adult males, number of adult females, and infant sex.

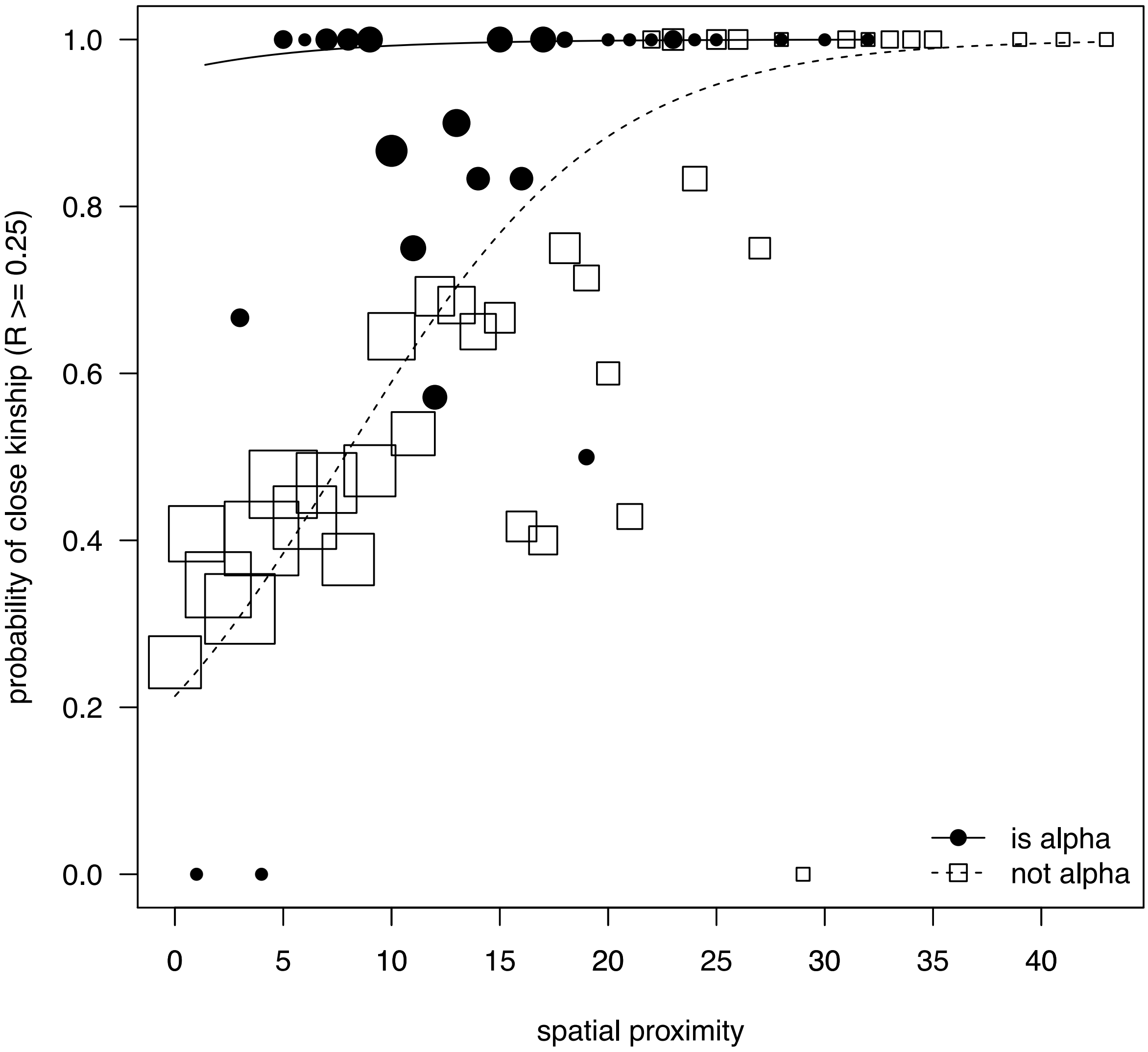

Figure 1-5: Probability of close relatedness (r ≥ 0.25) to males, contingent on spatial proximity. Bubbles represent the proportion of partners at that spatial proximity score that were related to the infant at the level of paternal sibling or higher. The size of each bubble indicates sample size. The 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). 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. The full model was significantly different from the null model (χ^2_2=25.115, P<0.0001).

Spatial proximity but not age proximity was a significant predictor of close relatedness to females (**Table 3**). 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 1-3: 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	.

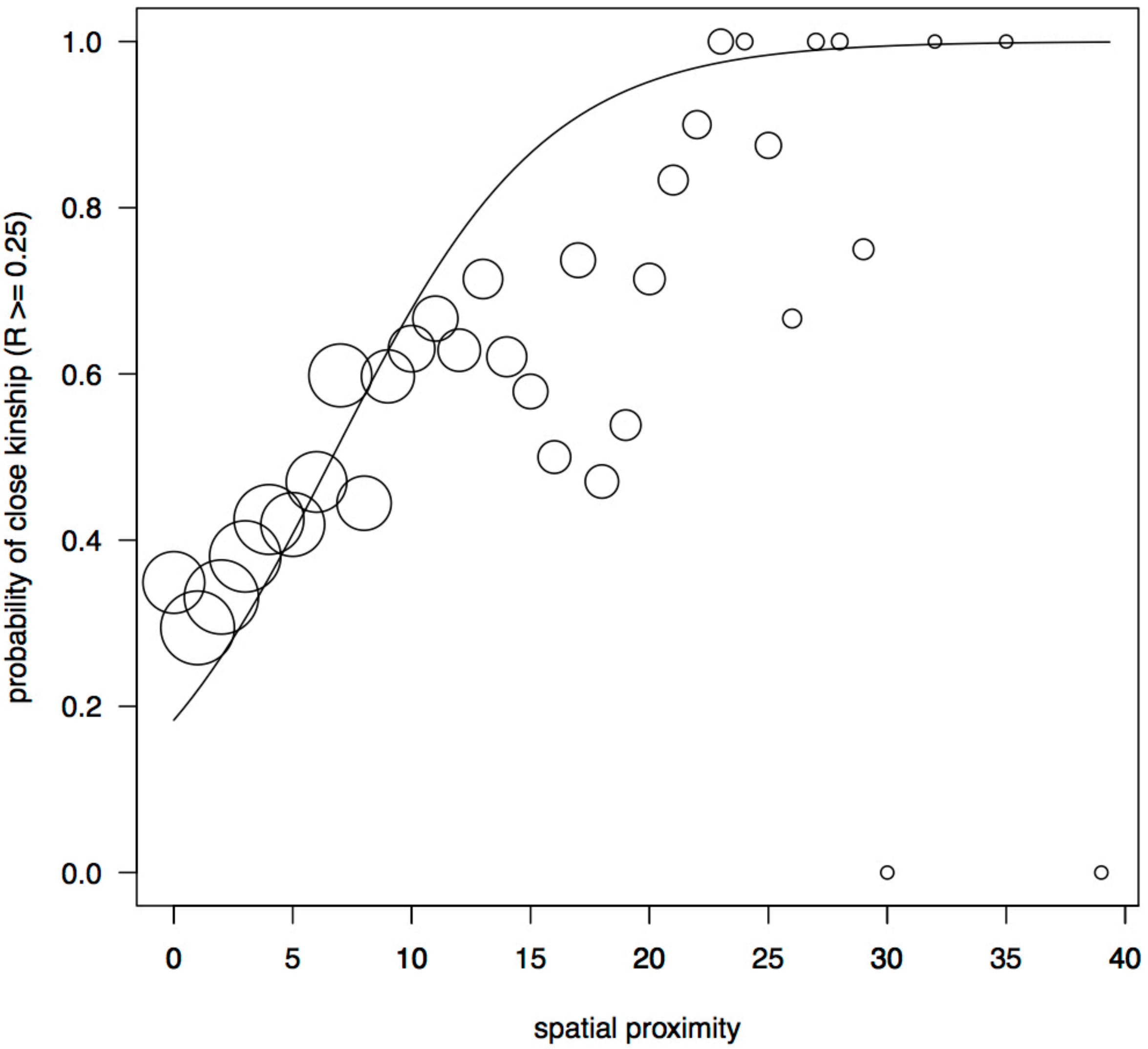

Figure 1-6: Probability of close relatedness (r ≥ 0.25) to females. Bubbles represent the proportion of partners at that spatial proximity score that were related to the infant at the level of paternal sibling or higher. The size of each bubble indicates sample size. The line showing the predicted values 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 a male was an infant's father. Our data set comprised 622 infant-male dyads formed with 57 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. 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 4**). 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 1-4: 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

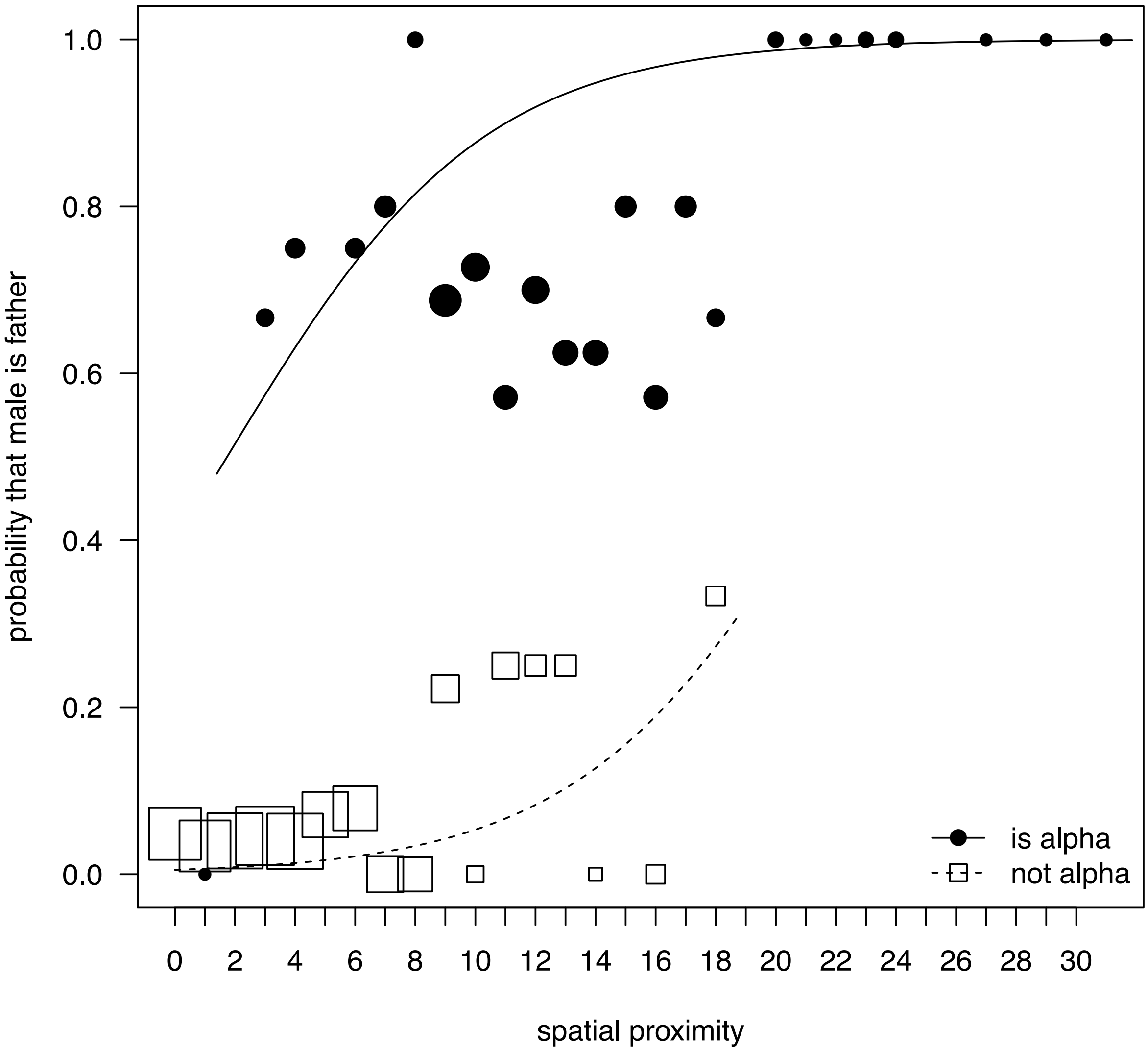

Figure 1-7: Probability that an adult male is an infant's father, contingent on spatial proximity and male alpha status. Bubbles represent the proportion of males at that spatial proximity score that were also an infant's father. The size of each bubble indicates sample size. The lines showing the predicted 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 5**).

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 1-5: 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). 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 full model was significantly different from the null model (χ^2_4=20.368, 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 6**). 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 1-6: GLMM results for probability of infant's partner being a paternal sibling.

Fixed Effect	Estimate	SE	Df	LRT	Pr(Chi)	
(Intercept)	-9.608	0.898				
Test variables						
Spatial proximity	0.380	0.261	1	2.327	0.1271	ns
Age proximity	-15.817	3.098	1	12.817	0.0003	***
Control variables						
Is maternal sibling	1.020	0.454	1	2.972	0.0847	.
# of adult males	-0.098	0.717	1	0.019	0.8894	ns
# of adult females	1.809	0.991	1	2.914	0.0878	.
Infant is male	-0.272	0.803	1	0.115	0.7347	ns
Partner is male	0.798	0.562	1	2.020	0.1552	ns

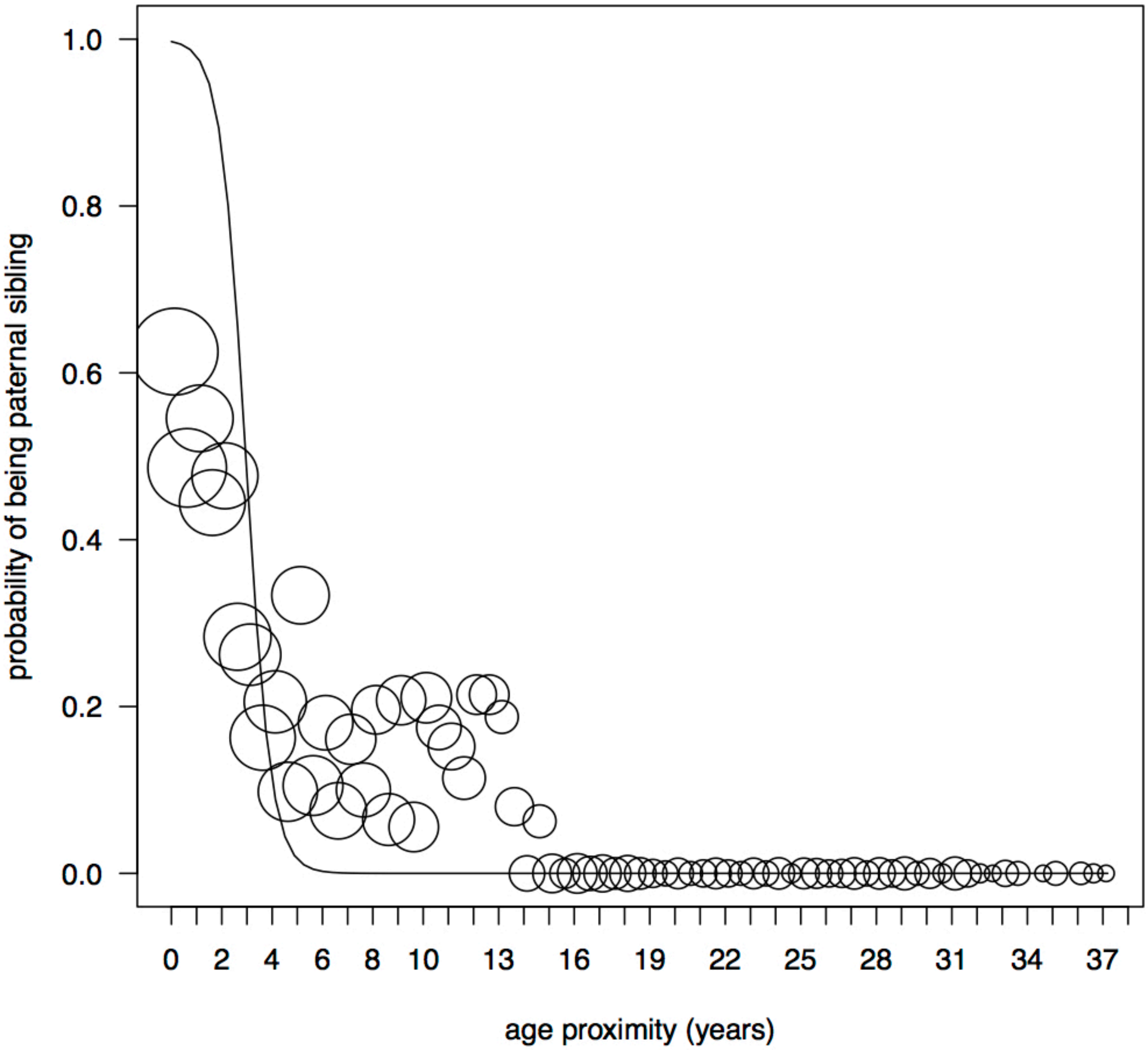

Figure 1-8: Probability of infant's partner being a paternal sibling, contingent on age proximity. Bubbles represent the proportion of partners at six-month increments in age differences that were also paternal siblings. The size of each bubble indicates sample size. The line showing the predicted values 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.

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.

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 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.

Multiple reliable cues may facilitate the ability of capuchins to identify their fathers and grandfathers, but the ability to identifying 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 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.

Our results show the availability of multiple cues to kinship and close relatedness for infant capuchins. 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 relatedness.

Close maternal perinatal association (i.e. primary caretaking and breast-feeding) between mothers and their dependent offspring provide 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.

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.

CHAPTER TWO: INBREEDING AVOIDANCE

INTRODUCTION

Ever since Charles Darwin's time, attention has been drawn to the deleterious effects associated with inbreeding (Darwin, 1868, 1976). Studies across different taxa have illustrated a range of potential costs that can arise when close kin produce offspring (Charlesworth & Charlesworth, 1987; Crnokrak & Roff, 1999; Keller & Waller, 2002), and studies of wild mammal populations show higher costs than those found in captive populations (Crnokrak & Roff, 1999). For these reasons, inbreeding in the wild has typically been considered maladaptive (Pusey & Wolf, 1996), particularly for mammalian females who bear a higher cost than males if offspring are not viable. Indeed, in primates, inbreeding avoidance is the most commonly cited form of female mate choice (Manson, 2007), indicating that there has been strong selection for it. In a review of the breeding records in captive primate colonies Ralls and Ballou (1982) found higher infant mortality (before 6 months of age) in 15 out of the 16 colonies investigated.

Despite the common view that inbreeding is necessarily deleterious, models based on evolutionary theory also predict that there is an optimal degree of similarity between parents that helps keep co-adapted genes in a population together ('optimal outbreeding', Bateson, 1983), and that some degree of inbreeding should be allowed or tolerated when the inclusive fitness benefits of mating with kin or the costs of finding alternative mates outweigh any potential costs to infant fitness (Jamieson et al., 2009; Kokko & Ots, 2006; Lehmann & Perrin, 2003; Lehtonen & Kokko, 2015; Puurtinen, 2011; Smith, 1979; Waser et al., 1986). However, investigation of the prevalence and impact of inbreeding in wild mammal population is challenging. Recent research has questioned whether much of the research on inbreeding depression in wild populations has sufficiently dealt with issues arising from, for instance, using non-pedigree based estimates of relatedness (Pemberton, 2004, 2008; Szulkin et al., 2013). A further hindrance in estimating the impact of inbreeding in the wild is the large proportion of offspring that die before genetic samples can be collected. For example, in savannah baboons, 35% of pregnancies end in either miscarriage or early infant death (Beehner et al., 2006a,b). If inbred offspring are less viable than outbred offspring, early fetal loss and infant mortality can mask many of the costs to inbreeding, and inflate the apparent frequency of inbreeding avoidance. Thus, accurately documenting the avoidance of and effects of inbreeding, if they are present in a population, can be challenging.

White-faced capuchin monkeys (*Cebus capucinus*) are an excellent species in which to study inbreeding avoidance for several reasons. In capuchins, socially dominant alpha males achieve a virtual monopoly on reproduction, at least during the early stages of their tenures (Jack & Fedigan, 2006; Muniz et al., 2006, 2010). These males also often retain their top rank for tenures exceeding five years, which corresponds to the age at which their daughters reach reproductive age. Importantly, long male alpha tenures facilitate co-residency of paternal half siblings and full siblings of varied ages, as natal males are less likely to migrate out of their group if there is stability in the alpha position and if their fathers are still present (Perry et al., unpublished). Although male migration from natal groups decreases the likelihood of inbreeding by siblings, adult and sub-adult males often do co-reside with their sexually mature sisters, and males have been known to become alphas of their own natal groups.

While sexually mature opposite-sex individuals can reside together in capuchin groups, inbreeding avoidance has been documented between females and alpha males (Muniz et al., 2006, 2010; Godoy et al., unpublished). Adult female relatedness to alpha males (i.e. whether they are a daughter or granddaughter) is the largest factor negatively affecting the probability that an alpha male is the sire of an infant (Muniz et al., 2010). Whether inbreeding avoidance extends to other kinship categories such as paternal siblings, however, is still unknown as is whether or not there are fitness costs to inbreeding in the population.

The availability of 25 years of demographic data, maternal pedigrees, and genetic paternity information at Lomas allows for us to 1) measure the extent of inbreeding potential in the population, 2) measure the prevalence of inbreeding in the population, 3) rule out non-behavioral explanations for inbreeding avoidance, and 4) measure potential costs to inbreeding at different levels of relatedness.

METHODS

Field site and study species

The subjects of this study are wild white-faced capuchin monkeys (*Cebus capucinus*) from the Lomas Barbudal Biological Reserve and adjacent public and private lands in Guanacaste, Costa Rica. This population has been studied since 1990 with continuous monitoring since 2002 (See Perry, 2012, Perry et al., 2012 for more details on the history of the project). Behavioral data were available from 11 habituated groups (**Table 1**), for 9 of which we also have genetic information on paternity for infants born into those groups. The AA group was habituated in 1990, the RR group in 1996, and the FF group in 2002. The NM group was sporadically monitored beginning December 2002 when two natal males from the AA group and one natal male from the RR group migrated there. The NM group was not fully habituated until 2008 after a natal male from the FF group migrated there.

The AA group produced two fission products. Specifically, the FL group split from the AA group in 2003 and the CE group from the AA group in 2012. TheRR group produced three fission products. The SP group split off in 1999, the MK group in 2004, and the DI group in 2012. The SP group was only sporadically monitored before 2008, during intergroup encounters and while searching for other groups. The MK group further split into the CU group in 2007. The FF group produced one fission product, the RF group, which split from the FF group in 2007.

Table 2-1: Study groups.

Group	Genotyped natal members	Genotyped plus conception data
AA	78	66
RR	66	47
FF	53	28
SP	23	18
FL	16	16
MK	12	9
CU	7	7
RF	8	7
NM	13	5
CE	0	0
DI	0	0

Group composition

Group composition was determined using long-term census data from the Lomas Barbudal Capuchin Monkey Project. Prior to July 2006 census data were determined by extracting information from data files for each observation day with a group. Starting July 2006, observers made records all members seen present in a group during an observation day, along with any wounds, suspected pregnancies, and births.

Infant conception windows

Using the known gestation lengths of wild capuchins (158 ± 8 days, Carnegie et al., 2011), we generated conservative conception windows for each birth. These windows were three standard deviations (i.e. 24 days) before and after each estimated conception date. Thus, these 49-day windows covered the period 182 to 134 days prior to the known or estimated birth dates for infants. We used these windows to determine which males were present during an infant's conception, and thus which males were available as potential mates for each infant's mother. All males six years of age or older were considered potential sires of infants, since the youngest sire in the Lomas population was 6.25 years old at the time of his infant's conception (Godoy, unpublished data).

Male dominance rank

Male dominance rank was determined by using the direction of avoids and cowers in dyadic interactions (Perry, 1998a,b). The male alpha position in a group is typically easy to determine because alpha males are more central, show more display behaviors, are more often piloerect, and are more vocal relative to subordinates (Perry, 1998a,b, Campos et al., 2007).

Estimating degrees of relatedness using pedigrees

Paternity information was available from previous work (See Muniz et al., 2006, Godoy et al., unpublished). Briefly, we have genotyped 334 capuchins from the Lomas Barbudal population using 18 microsatellites (Muniz & Vigilant, 2008) and DNA obtained primarily through non-invasively collected faecal samples and occasional sampling of tissue samples harvested from dead capuchins.

Although microsatellite markers can be reliably used to determine parent-offspring relationships, they are insufficient for identifying other types of kin relationships, such as half-siblings, because of the higher variance in the number of alleles shared per locus (Csilléry et al., 2006). We therefore used pedigree information to calculate estimated coefficients of relatedness for our dyads using Ed Hagen's DESCENT software (http://itb.biologie.hu-berlin.de/~hagen/Descent/). Since incomplete pedigrees (particularly for older natal females born before habituation of their natal groups) limit our ability to generate accurate coefficients of relatedness, we binned each dyad into one of four relatedness categories and treated them as categorical variables. Category 0 included all unrelated dyads, Category 1 included dyads with inferred coefficients of relatedness greater than 0 but lower than 0.25, Category 2 included those greater than or equal to 0.25 but lower than 0.5, and Category 3 included those equal to or greater than 0.5 (higher estimated scores than 0.5 could be generated because of inbreeding). Dyads with estimated coefficients of relatedness equal to zero, but where both members of the dyad were born in the same natal group, were also conservatively binned into the Category 1 group ($0.25 > r > 0$). Immigrant males of unknown origin were considered unrelated to natal females, unless genetic paternity assignment showed otherwise.

Generalized linear mixed models

Statistical analyses were run in R v.3.2.0 (R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/) using the glmer function from the lme4 package (Bates et al., 2014). To assess the significance of our predictor variables, we ran Generalized Linear Mixed Models (GLMM, Baayen, 2008) 1) with binomial error structure and logit link function on all our models involving a binomial response ('yes'/'no'). We included 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 checked for the presence of strong collinearity between our predictor variables by calculating Variance Inflation Factors (Field, 2005), which measure the degrees to which variance of the estimated regression coefficients are inflated compared to when the predictor variables are not colinear. The highest VIF in any model was 1.478 suggesting no 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 comprised all terms in the full model except the test predictors. P-values for individual predictors were also obtained using likelihood ratio tests.

RESULTS

Potential for inbreeding in the population

Most conceptions occurred at times when a related male could have impregnated the mother. Out of 363 conceptions for which we had group composition data, 261 (71.9%) were cases where the mother co-resided with adult male kin. Females were resident with at least one paternal half brother in 30% of cases and with their father in 17.1% (**Table 2**). Thus, a large proportion of the females in our study population had the potential to breed with close adult male kin (i.e. related males over the age of 6 years), particularly fathers and paternal brothers.

Table 2-2: Female potential for inbreeding. The table shows the number of conceptions for which females had at least one adult male available that fit into a particular relatedness or kinship category.

Relatedness Category	At least one	Percentage
0: $r = 0$	319	87.9 %
1: $0 < r < 0.25$	182	50.1 %
2: $0.25 \leq r < 0.5$	152	41.9 %
3: $r \geq 0.5$	117	32.2 %
Kinship Category	**At least one**	**Percentage**
Non-kin	319	87.9 %
Grandfather	6	1.7 %
Paternal half brother	109	30.0 %
Maternal half brother	8	8.0 %
Full brother	14	8.0 %
Son	22	12.4 %
Father	62	17.1 %

For 90 females (with age accuracies within 2 years, 92.2% known to within one year) we had information on their group composition during their fifth year of life, which is when most females conceive for the first time (the youngest female age at first birth in this population is estimated at 5.35 years, Godoy, unpublished). 44.4% of those females (n=40) were still resident with their fathers at age five, and 32.2% (n=29) resided with at least one adult paternal half brother. Only 4.4% (n=4) lived with an adult maternal half brother and another 5.6% (n=5) with an adult full brother. Even at age 10, 20.4% (n=11 of 54) of females still co-resided with their father. During the early part of their breeding careers (ages 5-15), females continued to live with adult male kin, particularly males related to them at the half sibling level (**Figure 1**).

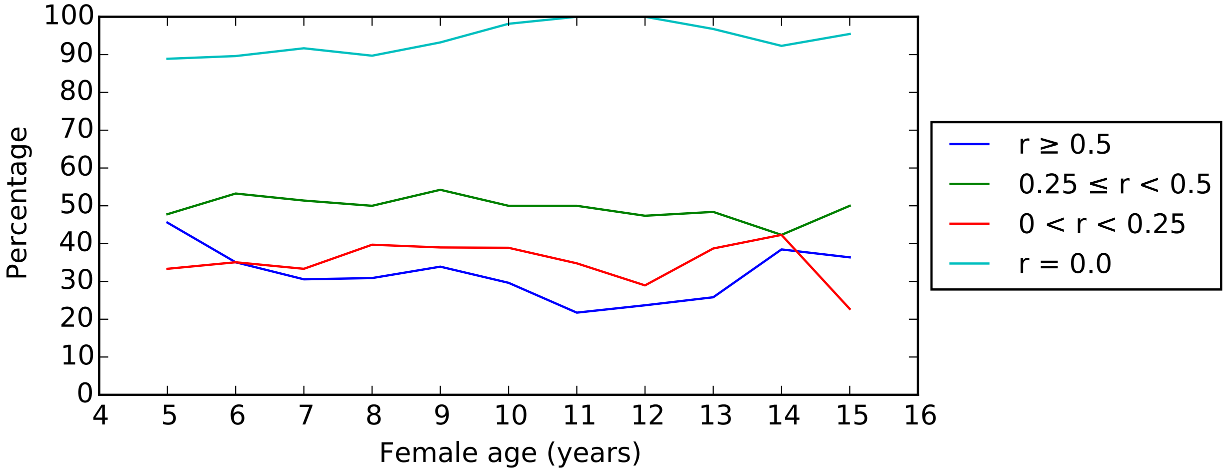

Figure 2-1: Percentage of females at each age, with at least one adult male in the relatedness category. Sample sizes for each bin are as follows: age 5, 90; age 6, 77; age 7, 72; age 8, 68; age 9, 59; age 10, 54; age 11, 46; age 12, 38; age 13, 31; age 14, 26; age 15, 22.

Factors affecting whether an alpha male is the father of an infant

The response variable was whether or not an alpha male was the father of an infant (‘yes’/’no’). The identities of the mother and alpha male were included as random effects. We included random slopes where possible. The predictor variables were whether or not the mothers of infants were related to the alpha male at the level of a) $0 < r < 0.25$, b) $0.25 \leq r < 0.5$, or c) $r \geq 0.5$. The number of adult males and number of adult females in a group were included as control variables in our model because previous research had shown the possible influence of each variable on alpha paternity (Muniz et al., 2010). However, due to a limited dataset in the Muniz et al. study, both variables could not be included in the same model. The dataset was comprised of 193 infant conceptions involving 69 females and 23 alpha males from 9 groups. The full model was significantly different from the null model, which consisted of only control variables and random effects ($\chi^2_3=46.747$, $P<0.0001$).

Alpha males sired 141 (73.1%) out of the 193 genotyped infants that were born during stable periods. Furthermore, alpha males sired 90.1% (109 of 121) of offspring born to unrelated females and only 44.4% (32 of 72) of offspring born to related females, with the percentage of infants sired varying by the estimated coefficient of relatedness **(Table 3)**. However, relative to the $r = 0$ relatedness category, alpha males sired significantly fewer offspring only with females in the $r \geq 0.5$ and $0.25 \leq r < 0.5$ categories **(Table 4).** Alpha males were no less likely to sire offspring with females in the $0 < r < 0.25$ category than they were to sire infants with unrelated females. In 38.7% (n=12 of 31) of the cases of inbreeding, there were no non-kin males available for the female to choose from.

Table 2-3: Percentage of offspring sired by alpha males, categorized by the coefficient of relatedness between infants' mothers and alpha males.

Relatedness category	Percentage	N
0: $r = 0$	90.1	121
1: $0 < r < 0.25$	78.9	19
2: $0.25 \leq r < 0.5$	65.0	20
3: $r \geq 0.5$	12.1	33

Table 2-4: Final GLMM results on probability of alpha males siring infants.

Fixed effects	Estimate	SE	Df	LRT	Pr(Chi)	
(Intercept)	6.411	1.692				
Predictor variables						
1: $0 < r < 0.25$	-1.014	1.110	1	0.798	0.3717	ns
2: $0.25 \leq r < 0.5$	-2.837	1.097	1	9.101	0.0026	**
3: $r \geq 0.5$	-5.422	1.289	1	45.195	< 0.0001	***
Control variables						
# of adult males	-0.381	0.161	1	4.595	0.0321	*
# of adult females	-0.168	0.170	1	0.971	0.3244	ns

Factors affecting which subordinate males are the fathers of infants

We analyzed data for only those conceptions during stable alpha periods where a subordinate male was the sire of the infant (n=52 infants) and we excluded the alpha males from the analysis. The response variable was whether or not a subordinate male was the father of an infant ('yes'/'no'). The identities of the mother, subordinate male, and infant were included as random effects. We included random slopes where possible. The predictor variables were whether or not the mothers of infants were related to the subordinate male at the level of a) $0 < r < 0.25$, b) $0.25 \leq r < 0.5$, or c) $r \geq 0.5$. The number of adult males and number of adult females in a group were included as control variables. Random slopes were included where possible. The dataset was comprised of 313 dyads formed between 30 females and 59 subordinate adult males.

The full model was significantly different from the null model, which consisted of only control variables and random effects (χ^2_3=10.557, P<0.0144).

There was no inbreeding between females and subordinate males related at the level of r ≥ 0.5 r ≥ 0.5 (**Table 5**), though there were 20 such dyads (n=14 unique) in our dataset (sons: n=8, fathers: n=2, full brothers: n=10). Relative to the r = 0 relatedness category, subordinate males sired significantly fewer offspring only with females in the r ≥ 0.5 and 0.25 ≤ r < 0.5 categories, after controlling for the number of adult males and adult females in the group (**Table 6**). Subordinate males were not significantly less likely to sire offspring with females in the 0 < r < 0.25 category than they were to sire infants with unrelated females, but there was a trend in that direction.

Table 2-5: Percentage of offspring sired by subordinate males, categorized by the coefficient of relatedness between infants' mothers and subordinate males.

Relatedness category	Percentage	N
0: r = 0	65.4	34
1: 0 < r < 0.25	17.3	9
2: 0.25 ≤ r < 0.5	15.4	8
3: r ≥ 0.5	0.0	0

Table 2-6: Final GLMM results on probability of subordinate males siring infants.

Fixed effects	Estimate	SE	Df	LRT	Pr(Chi)	
(Intercept)	-1.429	0.972				
Predictor variables						
1: 0 < r < 0.25	-0.982	0.607	1	2.713	0.0995	.
2: 0.25 ≤ r < 0.5	-1.579	0.572	1	7.688	0.0056	**
3: r ≥ 0.5	-17.087	[a]	1	5.742	0.0166	*
Control variables						
# of adult males	-0.275	0.133	1	3.824	0.0505	.
# of adult females	-0.077	0.114	1	0.449	0.5026	ns

[a] Standard error not shown because it is meaningless as a result of complete separation.

Inbreeding in the population

Looking at all genotyped individuals (regardless of alpha status or group stability) for whom we knew their father and mother (n=248 infants), 21.4 % (n=53) were the product of some degree of inbreeding (**Table 7**). For 51 out of 53 of the inbred offspring, we had information on the group composition around the time of their conception. In 45.1% (n=23) of the cases, the mothers did not have any non-kin males available in their group. For the remaining 28 cases, 20 of the infants were sired by the alpha of the group (71.4%) and the remaining 8 were sired by males that were either more distantly related to the mother (n=7) or as equally related to the mother (n=1) as was the alpha male.

Table 2-7: Paternity of genotyped infants, categorized by males' kinship and relatedness to infants' mothers.

Relatedness Category	Offspring	Percentage
0: $r = 0$	195	78.6
1: $0 < r < 0.25$	25	10.1
2: $0.25 \leq r < 0.5$	23	9.3
3: $r \geq 0.5$	5	2.0
Kinship Category	**Offspring**	**Percentage**
Non-kin	195	78.6
Other kin	25	10.1
Full uncle	1	0.4
Full nephew	0	0.0
Grandfather	0	0.0
Paternal half brother	22	8.9
Maternal half brother	0	0.0
Full brother	0	0.0
Son	1	0.4
Father	4	1.6

Out of 22 known instances of inbreeding between paternal half siblings, 63.6% (n=14) were cases where the brother was also the alpha male of the group at some point during the infant conception window. Similarly, all five parent-offspring inbreeding events involved a male who was confirmed to be or likely to have been the alpha during the infant conception window.

There was one case of mother-son inbreeding. It involved a male (BA) that migrated into and became the alpha of a fission product (SP group) of his natal group (RR group). SP group had fissioned from RR group more than five years previous to BA's migration, but it still included BA's mother (KK) as well as one unfamiliar adult maternal half sister (FA, born after the RR-SP fission) and one familiar paternal half sister (LR, born before the fission). BA remained alpha of SP group for three years and may have also produced offspring with his maternal sister, but both of FA's infants died (one after BA was deposed) without any genetic samples collected. During his alpha tenure of SP group, BA produced three offspring with his paternal half sister (LR), and four additional offspring with four more distantly related females. BA sired all the genotyped infants that were born during his alpha tenure.

The four cases of father-daughter inbreeding involved two dyads (CM-FZ and GL-NM), which both produced offspring twice. The females were born prior to habituation of their natal groups and we have no information as to group composition or male alpha status during their early life.

We have documented only one instance of extra-group paternity in the Lomas population. The case involved a female that resided in a group with two paternal half brothers, one of which was alpha, and an unrelated male that we estimate (based on siring information) had been resident in her natal group all her life. Even in this case of extra-group paternity, the father of her infant was a familiar paternal half brother that was the alpha male in a nearby group. Thus, it appears that extra-group paternity is extremely rare at Lomas and does not constitute an alternative female reproductive strategy for preventing inbreeding.

Non-behavioral explanations for inbreeding avoidance patterns

Female-alpha relatedness and female age at first birth

Our data set included a small subset of females (n=37) whose age at first birth was known to be accurate to within 3 months, and who lived in a group containing a stable alpha from age 4.5 (presumably before commencing cycling) through to their first infant's conception (**Table**). We ran a GLMM to assess whether the relatedness level between females and the alpha males of their groups impacted the age at which females had their first-born offspring. Our dataset included data on 13 alpha males from seven social groups. Our response variable was each female's age at first birth. Our test variables were the levels of relatedness between the infants' mothers and the alpha males; $0 < r < 0.25$, $0.25 \leq r < 0.5$, and $r \geq 0.5$. The identities of the alphas, females, and groups of residence were included as random effects. The full model was not significantly different from the null model (χ^2_3=2.657, P=0.4477). Similar results were found when comparing only kin versus non-kin (χ^2_1=0.299, P=0.5843).

Table 2-8: Female age at first birth, categorized by female relatedness to alpha.

Relatedness Category	Avg. age	Std. Dev.	SE	N	[95% Conf. Interval]
0: $r = 0$	6.079	0.369	0.091	13	[5.882 6.277]
1: $0 < r < 0.25$	5.946	0.523	0.147	6	[5.569 6.324]
2: $0.25 \leq r < 0.5$	6.255	0.375	0.127	6	[5.929 6.580]
3: $r \geq 0.5$	6.208	0.488	0.152	12	[5.874 6.541]

Female-alpha relatedness and inter-birth intervals

We analyzed a subset of inter-birth intervals (n=91), for which the following criteria were met; 1) the first infant survived its first year of life, 2) the alpha male, during the conception window of the subsequent infant, was the same male that was alpha during the first infant's conception window, and 3) the IBI estimate was accurate to within 3 months (**Table 9**). We dropped one IBI outlier, which was more than 5 standard deviations higher than the population mean (mean: 749 days, st.dev: 145, Perry et al., 2012).

We ran a GLMM to test the significance of relatedness between females and alpha males on the inter-birth intervals for females. Our dataset comprised 52 mothers and 14 alpha males from nine social groups. Our test variables were the levels of relatedness between the infants' mothers and the alpha males; $0 < r < 0.25$, $0.25 \leq r < 0.5$, and $r \geq 0.5$. We included the identities of females, alphas, and groups of residence as random effects. The full model was not significantly different from the null model (χ^2_3=4.339, P=0.2271). Similar results were found when comparing kin versus non-kin (χ^2_1=0.0985, P=0.7536).

Table 2-9: Inter-birth intervals (days), categorized by female relatedness to alpha.

Relatedness category	Avg. IBI	Std. Dev.	SE	N	[95% Conf. Interval]	
0: $r = 0$	753.0	132.6	18.6	51	[715.7	790.2]
1: $0 < r < 0.25$	804.7	118.9	37.6	10	[719.7	889.7]
2: $0.25 \leq r < 0.5$	871.0	139.5	38.7	13	[786.7	955.3]
3: $r \geq 0.5$	743.2	126.6	31.6	16	[675.7	810.6]

Female-alpha relatedness and probability of infant death

There was a sample of 246 births (regardless of whether they were genotyped) where the male alpha position remained stable from the estimated conception window of the infant through to either 1) the end of the infant's first year of life or 2) the infant's death (**Table**). We ran a GLMM to test the significant of relatedness between infants' mothers to the alpha male on the probability of an infant dying during early infancy. Our dataset was comprised of 89 mothers and 24 alpha males from 11 social groups. Our response variable was whether an infant died before reaching the age of one (yes/no). Our test variables were the levels of relatedness between the infants' mothers and the alpha males; $0 < r < 0.25$, $0.25 \leq r < 0.5$, and $r \geq 0.5$. The identities of mothers, alphas, and groups of residence were included as random effects. The full model was not significantly different from the null model (χ^2_3=1.860, P=0.6020). Similar results were found when comparing kin versus non-kin (χ^2_1=0.591, P=0.4419).

Table 2-10: First year infant mortality rates, categorized by mother's relatedness to alpha.

Relatedness category	Deaths	N	Mortality
0: $r = 0$	33	151	21.9 %
1: $0 < r < 0.25$	10	31	32.3 %
2: $0.25 \leq r < 0.5$	8	28	28.6 %
3: $r \geq 0.5$	6	36	16.7 %

Potential costs to inbreeding

Juvenile mortality

We had a sample of 186 infants born before 2011 that survived their first year of life and for which we knew their father and mother. Discarding infants that died during their first year of life allowed us to avoid any sampling issues for non-genotyped infants and avoid inclusion of infant deaths due to infanticide after change at the alpha male position. We looked for increased mortality rates between inbred offspring relative to outbred offspring, by measuring survival into the fourth year of life (before male migration from groups was likely to bias our mortality data) (**Table 11**).

We ran a GLMM on the probability of surviving the juvenile period. The dataset was comprised of 69 mothers and 37 fathers from nine social groups. Our response variable was whether or not an infant reached the age of four. The identities of the fathers, mothers, and groups of residence were added in as random effects. Since our sample size was rather small for $r \geq 0.5$ (n=4), our test variables were relatedness at $0 < r < 0.25$ and $r \geq 0.25$. In the model the relatedness level refers to the relatedness level between the parents of each infant. The full model was not significantly different from the null model (χ^2_2=2.668, P=0.2635). Similar results were found when running the same model but comparing kin versus non-kin (χ^2_1=0.724, P=0.3949).

Table 2-11: Juvenile mortality, categorized by relatedness of parents.

Relatedness category	Deaths	N	Mortality
0: $r = 0$	17	136	12.5 %
1: $0 < r < 0.25$	3	24	12.5 %
2: $0.25 \le r < 0.5$	6	22	27.3 %
3: $r \ge 0.5$	1	4	25.0 %

Female age at first birth

We had a sample of 58 females for which we could estimate their age at first birth to an accuracy of within 90 days (**Table 12**). We looked for older ages at first birth for females that were the product of inbreeding. The identity of the natal group was added in as a random effect. Since our sample sizes were small, our test variable was relatedness at any level between the parents on inbred offspring. The full model was significantly different from the null model (χ^2_1=7.046, P=0.0079). Inbred females gave birth significantly later than did non-inbred females (**Table 13**) (**Figure 2**).

Table 2-12: Female age at first birth, categorized by level of relatedness between the female's parents.

Relatedness Category	Avg. age	Std. Dev.	SE	N	[95% Conf. Interval]
0: $r = 0$	6.246	0.473	0.070	46	[6.106 6.387]
1: $0 < r < 0.25$	6.854	1.014	0.383	7	[5.915 7.792]
2: $0.25 \le r < 0.5$	6.634	0.471	0.236	4	[5.884 7.384]
3: $r \ge 0.5$	6.253	-	-	1	-

Table 2-13: Female age at first birth, categorized by whether or not her parents were related.

Fixed effect	Estimate	SE	Df	LRT	Pr(Chi)
(Intercept)	6.246	0.080			
Female is inbred	0.484	0.177	1	7.046	0.0079 **

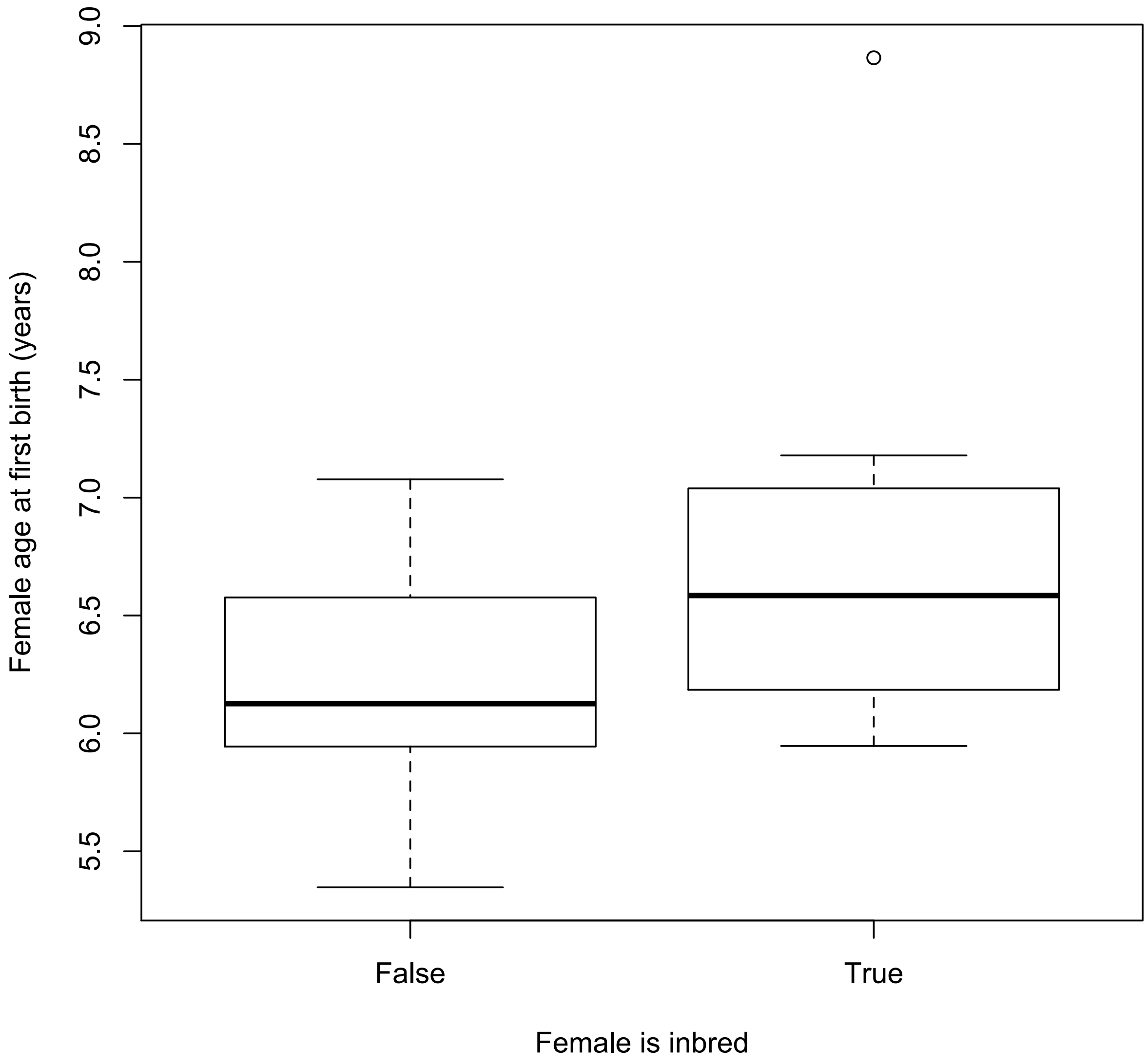

Figure 2-2: Female age at first birth, categorized by relatedness between her parents.

Only one of the inbred females in our dataset gave birth to an infant that survived past its first year of life (IBI: ~803 days). Thus, we could not do any analysis on the effects of inbreeding on inter-birth intervals.

DISCUSSION

Among the Lomas Barbudal capuchins, alpha males co-residing with close adult female kin (i.e. at the half sibling level and higher) sired far fewer offspring with them than would be expected in the absence of some form of behavioral inbreeding avoidance (see also Muniz et al., 2006, 2010). The same results were found when looking at subordinate males. Only 2% of genotyped infants were a product of inbreeding at the $r \geq 0.5$ level. Co-resident kin at the level of $0.25 \leq r < 0.5$ (i.e. half sibling level) also produced less offspring than expected by chance, but this effect was weaker than inbreeding avoidance at the $r \geq 0.5$ (i.e. father-daughter) level. In over a third of the cases of inbreeding, the females had no non-kin adult male groupmates available as potential mates. Age at first birth did not vary as a function of female relatedness to the alpha male, and extra-group paternity was extremely rare, suggesting that neither delaying reproduction nor mating outside the group were viable alternative female strategies. Less closely related dyads did not appear to avoid inbreeding: co-resident male-female pairs related at $0 < r < 0.25$ were no less likely to produce offspring than were unrelated pairs.

Apparent parent-offspring behavioral inbreeding avoidance could, alternatively, result from reduced viability of inbred offspring. Matings between close kin might occur at higher than apparent frequencies, but result in either early stage fetal loss or early infant death (i.e. before fecal samples can be collected for genotyping). If early infant death of non-genotyped infants explained the rarity of inbreeding between parents and offspring instead of inbreeding avoidance, then one would expect higher first year mortality rates among infants born to females residing in groups where the alpha is their father or son. Infant mortality rates in stable groups (i.e. where no alpha turnover took place), however, did not significantly vary according to the relatedness between mothers and alpha males. Additionally, both (1) female age at first birth and (2) the lengths of inter-birth intervals for females living with their alpha male relatives did not differ from those of females living with non-kin alphas. These results are consistent with those from a smaller sample analyzed in Muniz et al. (2006). These findings together provide further evidence against father-daughter inbreeding avoidance patterns being the result of fetal loss or early infant mortality, and instead are suggestive of mate choice.

That there would be mechanisms in place to prevent inbreeding between father-daughter pairs make sense in this particular population, given than over 44.4% of our females resided with their fathers at the age when they reached sexual maturity (i.e. in their fifth year of life). Furthermore, selection may be particularly strong for father-daughter inbreeding avoidance in capuchins because if no mechanism were in place, multiple-generations of inbreeding could occur given that in some cases adult females are also resident with their grandfathers. Indeed, another primate with high male reproductive skew toward one dominant and long dominance tenures is the mountain gorilla (*Gorilla beringei beringei*), and this species has also been documented to show father-daughter inbreeding avoidance in the wild (Vigilant et al., 2015).

Inbreeding at the level of paternal half siblings and more distantly related kin was more common in the Lomas population, 8.2% and 10.2% of genotyped infants respectively. Dyads related at $0.25 \leq r < 0.5$ appeared to also avoid inbreeding, but to a more limited degree than parent-offspring and full sibling dyads, while the dyads related at $0 < r < 0.25$ did not differ significantly from unrelated dyads. While this may reflect an inability to accurately detect more distant kin categories, it may also reflect a reduced cost to inbreeding at these lower coefficients of relatedness. For example, alpha males may also benefit from not inbreeding with their daughters because of the added benefit of having reproductively available females as incentives for male allies to remain in the group (Perry, 2012). If parent-offspring matings do produce less viable young, then father-daughter inbreeding avoidance may be a form of reproductive concession that does not negatively impact overall alpha male reproductive success. This would, however, be a larger reproductive trade-off for alpha males less closely related to the females in their group, since (1) any costs of inbreeding would theoretically be lower and (2) males would have less inclusive fitness benefits from the offspring born to more distantly related females. Our current data suggest that there is indeed a cost to inbreeding, as inbred females have a later age at first birth than do non-inbred females, but a larger sample size will be needed to see whether there is a threshold level of relatedness where inbreeding is less costly. Furthermore, more severe costs, such as higher juvenile mortality for inbred offspring, have thus far not been detected in the population. Delayed age at first birth in inbred females has also been documented in captive Barbary sheep (*Ammotragus lervia sahariensis*) (Cassinello & Alados, 1996). Interestingly, in semi-free ranging mandrills (*Mandrillus sphinx*) age at first conception is accelerated, not delayed, in inbred females (Charpentier et al., 2006). To our knowledge, our results are the first evidence of delayed female reproduction as a consequence of inbreeding in non-human primates.

If alpha males are related to the subordinate males in their groups, different outcomes to inbreeding avoidance should be expected. In concession models of reproductive skew (see Port & Kappelar, 2010 for a review on issues in the application of reproductive skew models to male primates, since they were originally created with eusocial insects or cooperatively breeding birds in mind), higher relatedness generally results in higher reproductive skew (Vehrencamp, 1983a,b; Reeve & Ratnieks, 1993; Keller & Reeve, 1994) whereas in tug-of-war models relatedness either has no effect on skew or results in lower skew (Cant, 1998; Johnstone & Cant, 1999; Reeve et al., 1998). While the different models make predictions as to what the effect of relatedness between group members will be on the level of skew in a group, the expected outcome depends on different assumptions about the values of the other parameters in the models such as dispersal costs, group productivity levels, the number of subordinates in a group, and fighting ability. Any true tests of the validity of different reproductive skew models for understanding primate mating systems require a testing of the assumption of models first (Magrath et al., 2000; Clutton-Brock, 1998; Port & Kappeler, 2010), which has yet to be done. Relatedness between males, however, should also be considered in light of male relatedness to breeding females. If the level of relatedness between an alpha male and a breeding female is the same as the level of relatedness between that same female and another male, then all other things being equal, the alpha male should prefer to procreate with her than to have her procreate with his male relative. This may also help explain why inbreeding between dyads other than parent-offspring dyads is more commonplace in capuchins. For example, natal males that take over the alpha position of their group after the death of their father (n=2 cases) have co-resided with at least one other paternal half brother and no maternal sisters. In these cases, the alpha male has been as equally related to group females as his subordinate brother was. So far, these two alpha males have not shown strong signs of inbreeding avoidance with their paternal sisters or more distant female kin (siring 16 of 17 genotyped infants), but several recent offspring in their groups have still to be genotyped. More thorough testing is needed to see how relatedness between group males and their relatedness to group females impact inbreeding avoidance and reproductive skew in this species, and whether males and females are equally responsible for behaviors that prevent inbreeding.

CHAPTER THREE: MECHANISMS

INTRODUCTION

Inbreeding depression, or reduced fitness in a population as a result of inbreeding, is believed to occur because of an accumulation of deleterious recessive alleles (Charlesworth & Charlesworth, 1987). In primates, inbreeding has been accompanied by fitness costs in both captive and wild populations (Ralls & Ballou, 1982; Charpentier et al., 2007). Generally among mammals, the fitness costs for inbreeding are higher for wild versus captive populations (Crnokrak & Roff, 1999). Perhaps for this reason, inbreeding avoidance is the most commonly cited form of female mate choice in primates (Manson, 2007), and has been documented both in terms of behavioral mating patterns (Japanese macaques: Enomoto, 1974; rhesus macaques: Missakian, 1973; Barbary macaques: Kuester et al., 1994; olive baboons: Packer, 1979; chimpanzees: Goodall, 1986; and rhesus macaques: Manson & Perry, 1993) and genetic paternity data (capuchins: Muniz et al., 2006, 2010, gorillas: Vigilant et al., 2015). While the occurrence of inbreeding avoidance across various primate species has been documented, the mechanisms of kin discrimination involved are not known.

Early social familiarity has been postulated to be the mechanism by which individuals recognize and avoid mating with close kin, because familiarity during infancy is thought to be correlated with close relatedness (Kuester et al., 1994). The use of this mechanism, akin to the Westermark effect in humans (Westermarck, 1891), may explain in particular why matings between mothers and sons, and between maternal siblings, are rare in primates (Goodall, 1986; Kuester et al., 1994; Pusey, 1980; Walters, 1987). Sons, obviously, experience familiarity with their mothers during infancy, and enduring mother-offspring bonds ensure that maternal siblings will have close relationships during the younger sibling’s infancy. If early social familiarity is the mechanism by which individuals develop sexual aversion toward each other, then certain predictions follow. First, individuals will show a general social preference for unfamiliar versus familiar breeding age opposite-sex individuals, at least during periods when females are more likely to conceive. Second, among familiar individuals, individuals will exhibit preferences for those opposite-sexed individuals with whom they spent less time during their infancy and adolescence. This project seeks to test these predictions in a wild primate species, while also accounting for other factors and constraints that can influence mate choice.

The role of female preferences for males

Male dominance rank is associated with higher male reproductive success in many primate species (Alberts et al., 2003, 2006, Altmann et al., 1996; Widdig et al., 2004; Rodriquez-Llanes et al., 2009, Constable et al., 2001; Boesch et al., 2006; Wroblewski et al., 2009, Gerloff et al., 1999, Bradley et al., 2005, Charpentier et al., 2005; Setchell et al., 2005, de Ruiter, 1994, Pope, 1990, Jack & Fedigan, 2006; Muniz et al., 2006, 2010, Kappeler & Port, 2008, Kappeler & Schäffler, 2008). The potential role that female mate choice plays in these behavioral and genetic patterns remains under explored, however, as comparative studies on male reproductive skew largely focus on male-male competition (Kutsukake & Nunn, 2006, 2009; Ostner et al., 2008). However, female mate choice is important to consider. For example, tufted capuchins (*Cebus apella*) exhibit persistent courtship solicitations of males in their groups in both wild (Janson, 1984, 1986; Fragaszy et al., 2004, Alfaro 2005) and free-ranging (Welker et al., 1990) populations, with alpha males being solicited at higher frequencies than subordinate males. For a fuller understanding of what factors impact reproductive skew, both male and female mate preferences must be considered, as well as competition within each sex, and sexual coercion.

Since female sexual preferences for genetically dissimilar males (Schwensow et al., 2008; Setchell et al., 2010: Setchell & Huchard, 2010) may be at odds with general preferences for more dominant males, or alternatively, with dominant males' ability to guard females (Kutsukake & Nunn, 2006, 2009; Ostner et al., 2008), it is useful to account for both in the same models when assessing female-male association patterns. Also, if dominant males are preferred mates, as is possible given the degree of male reproductive skew seen in many species, female access to these males will also likely be impacted by their own dominance rank if females must compete for access to those males (O'Brien, 1991; Tiddi et al., 2011). Furthermore, female relationships with males may vary in their quality across different female reproductive states. Cycling females, for example, may exhibit preferences for males that are different from those that they would exhibit otherwise. For example, in chimpanzees, the closest male associates of females are typically their maternal brothers, but females dramatically reduce their association patterns with these males once they reach the age of cycling, often by leaving their community (Pusey, 1980). Females may also engage in more promiscuous behavior during early pregnancy in order to confuse paternity, such as occurs in many macaque species (Barbary: Kuester & Paul, 1984, Japanese: Hanby et al., 1971; Eaton, 1972; Takahata, 1980, Rhesus: Bielert et al., 1976, Loy, 1971; Wilson et al., 1982; Chapais, 1983, Stumptail: Slob & Nieuwenhuijsen, 1980; Linnankosky et al., 1981; Nieuwenhuijsen et al., 1986). Research on sexual aversions as a means of inbreeding avoidance should thus focus on behavior that occurs during times when females are more likely to be fertile.

Study species

In white-faced capuchins, females frequently partake in non-conceptive mating (Manson et al., 1997). Despite promiscuity in sexual behavior, however, the species is characterized by high male reproductive skew with alpha males siring the majority of infants (Muniz et al., 2006, 2010; Jack & Fedigan, 2006). The main factor impeding alpha male monopolization of paternity within groups is his relatedness level with the adult females in his group (Muniz et al., 2006, 2010). The Lomas Barbudal population in Costa Rica exhibits inbreeding avoidance between alpha males and their daughters and granddaughters (as demonstrated through genetic paternity assignment). However, it is not yet known what psychological and behavioral mechanisms enable individuals to recognize and avoid mating with kin.

The primary objective of this project is to determine whether early social familiarity is a likely mechanism by which capuchins avoid mating with close relatives. We predict that female capuchins exhibit sexual aversion toward males with which they spent more time during their infancy, and this aversion will be exhibited regardless of the amount of time they generally spend with those males as adults. In capuchins, higher spatial proximity of infants with males is predictive of close relatedness (Godoy, unpublished data), making early social familiarity a good candidate mechanism for kin recognition. However, other cues such as male alpha status during female infancy are also predictive of close relatedness, and so we also seek to test those as possible mechanisms.

Here we first investigate whether dominance rank (of both sexes) and female reproductive state influence female-male association patterns. We then investigate, among likely cycling females, whether they show preferences for males according to relatedness and cues to relatedness even after controlling for the following factors that may influence their preferences or restrict their access to males: male alpha status, female dominance rank, the number of adult males in a group, the number of adult females in a group, male age, and female age. The number of adult males and number of adult females can increase inter-sexual competition for mates, but also increase the likelihood that any one individual will find a mate. Individuals can also be expected to have less competitive ability (i.e. lower dominance) as they age (van Noordwijk & van Schaik, 1987) or to have reduced fertility (Altmann et al, 2010).

Since female-mate guarding is not seen in *Cebus capucinus*, we expect that the high degree of male reproductive skew is the result of female mate choice for alpha males. We thus predict that (1) fine-grained analysis of behavioral data (female-male proximity patterns, responsibility for proximity maintenance, and sexual behavior) will reveal a female preference for alpha males over subordinate males and (2) access to these males will be affected by female dominance rank. We expect that inbreeding avoidance patterns are also the result of female mate choice for unfamiliar males and aversion to males that were in close proximity to them during their infancy and adolescence. We thus predict that females will show behavioral patterns of preference for (1) males that were absent during their infancy and adolescence and (2) among familiar males, a preference for those with which they spent less time during their early development. We analyze our data in terms of female-male proximity patterns, proximity maintenance, and sexual behavior.

METHODS

Field site, study species, and behavioral sampling

Subjects in this study are wild capuchin monkeys (*Cebus capucinus*) from the Lomas Barbudal Biological Reserve and adjacent public and private lands in Guanacaste, Costa Rica. This population of white-faced capuchins has been studied since 1990 with continual monitoring beginning in 2002 (Perry, 2012, Perry et al., 2012). Behavioral data have been collected from this population primarily using focal-animal, scan, and *ad libitum* sampling methods (Altmann, 1974). Subjects were continually monitored during focal-animal sampling, with instantaneous point samples at the beginning of and at every 2.5-minute interval during follows, usually lasting for a period of 10 minutes. At each point sample, the activity of the focal animal was noted as well as whether other monkeys where in contact with, or within one, five, and ten body lengths of the focal. A body length is defined as the average length of an adult male from nose to tail base, which is ~40 cm. Scan samples had the same format as instantaneous point samples. Scan samples were collected at the moment that a monkey was identified and observers rotated through the group attempting to sample as many individuals as possible. A minimum of 10 minutes separate the group scans of any monkey. During follows, we documented whenever the focal came within five body lengths or left that proximity of another monkey, plus which monkey initiated the approach or leave.

Field seasons & study subjects

Behavioral observation occurred during four field seasons when IG and her research assistants were in the field. Fieldwork was concentrated during the conception peak of November through February (Carnegie et al., 2011a). NM group was followed intensively for three months (Dec 2010 - Feb 2011), FF group for four months (Nov 2011 - Feb 2012), RR group for two four-month periods (Nov 2011 - Feb 2012, Nov 2012 - Feb 2013), and AA group for four months (Nov 2013 - Feb 2014). In all four groups alpha males were resident with some adult female kin. All females in the study groups had access to at least one unrelated male.

During these field seasons, AA group, FF group, and RR group each had a stable long-term alpha male. NM group, however, went through a series of alpha rank changes involving two resident males and two migrants from a neighboring habituated group. On January 4, 2011 – after a 1-day observation gap – NM group was found with resident male SM as the new alpha and long-term alpha NM missing. On January 15th NM passively regained his alpha rank after the death of SM, who succumbed to the injuries presumably attained during the original turnover event. NM, who was also nursing injuries, was once again deposed and evicted by three adult males (BK, EZ, OC) from neighboring MK group, two of which (BK, EZ) alternated in being alpha of the group. On February 14th - with BK and OC back in MK group – NM and a coalition of adult females and juveniles evicted EZ. NM remained alpha until the morning of February 22nd when a hostile intergroup encounter occurred between NM group and MK group. BK and EZ jointly evicted NM, and then BK returned back to MK group where he was alpha, leaving EZ as alpha of NM group. EZ remained alpha of NM group for the remainder of the field season, though alpha rank changes continued into the next month. Unless otherwise specified, data presented from NM group come from only those days when NM was the alpha male.

Behavioral data presented in this paper come from 193 dyads comprising 35 females and 21 males. We collected a total of 636 hours of focal follow data and 23 254 group scans on our 56 subjects across 317 field days. We analyzed our data in terms of 'dyad days', i.e. days in which a female-male dyad co-resided in the same group. Our dataset was comprised of 13 785 dyad days across the 4 groups **(Table 1)**.

Table 3-1: Study groups in behavioral analyses.

Study group	Field seasons	Field days	Dyad days	Dyads	Females	Males
NM	2010-2011	32	373	15	5	3
FF	2011-2012	46	1 237	30	10	3
RR	2011-2012, 2012-2013	145	6 384	78	10	8
AA	2013-2014	94	5 791	70	10	7

Early social familiarity measures

For a subset of our females (n=14), we also had 'early spatial proximity' scores from their infancy. These scores were measured as the percentage of all group scans during the female's first year of life during which the female was in proximity to (i.e. within ~4 meters) a particular male. For males that were not present during one of these female's first year of life, we gave them an early spatial proximity score of 0.

Since our early spatial proximity data was limited, we also looked at the length of co-residency during adolescence between dyads. This was measured as the number of years during the female's juvenile period, here defined as the first 5 years of life (i.e. before individuals begin to reproduce) that they spent co-residing with a particular male (range: 0-5 years). Similarly, we also measured the length of co-residency during male adolescence as the number of years (range: 0-5 years) during the male's adolescence that he lived in the same group with a particular female.

Proximity and proximity maintenance

For each dyad in our dataset, we measured whether they were in recorded in close proximity of each other (i.e. within 5 body lengths, ~2 meters) during a group scan or focal follow for either individual. To be included in our analyses, group scans involving dyad partners had to be spaced at least 10 minutes apart.

As a measure of proximity maintenance we used Hinde's Index (Hinde & Atkinson 1970), which was defined as the percentage of approaches into proximity of a male (during a focal follow) that were initiated by the female minus the percentage of leaves initiated by the female. Values are bounded between 100 and -100, with positive values indicating that females are more responsible for proximity maintenance and negative values indicating that males are. We used approaches to within ~2 meters and leaves from that same distance.

Sexual behavior

Courtship dances typically involve maintained eye contact between two capuchins, while one or both members 'duck-face' (akin to the "protruded lips" mentioned in Oppenheimer, 1973), rapidly pace up and down a branch, and make pirouette turns toward their partner

(Manson et al., 1997). The dance is accompanied by vocalizations described as grunts or squeaks (Gros-Louis et al., 2008). The male sometimes, but not always, completes the dance by mounting the female. In our study, we looked at two aspects of female-male courtship. One aspect was whether a male mounted a female during a dyad day. The other aspect was whether or not a female directed a duck face, sex pace, or sex turn toward a male during a dyad day regardless of whether the event culminated in a mount.

Age classification

The ages for 30 (85.7%) of our female and 19 (90.5%) of our male subjects were estimated to be accurate to within two years. The birth dates for individuals first seen as adults were estimated according to the experience of field researchers and assumed to be accurate to within 5 years. Females in this study were all a minimum of 4.5 years of age, and males included in this study were a minimum of 6 years of age.

Dominance ranks

Dominance ranks were assessed using an Elo-rating system (Albers and de Vries, 2001; Neumann et al., 2011) that was originally developed to rank chess players (Elo, 1961, 1978). The 'winners' of dyadic interactions were determined by the direction of avoids, cowers, flees, grimaces, and supplants (Bergstrom & Fedigan, 2010). Initial Elo scores where set to 1 000 for each individual, and the constant *k* was set to 100.

Data on avoids, cowers, flees, grimaces, and supplants were extracted from both focal follow and ad libitum sources during the field seasons described earlier. However, since Elo-rankings require some amount of start-up time before creating reliable dominance hierarchies (Neumann et al., 2011) and since submissive interactions among adult capuchin females occur at low rates (Fedigan, 1993; Perry, 1996; Manson et al., 1999; Bergstrom & Fedigan, 2010), we also used *ad libitum* and focal data from a period of at least two years preceding each field season.

Fecal sample collection and field processing

Fecal samples not contaminated with urine were collected within 10 minutes of an animal defecating and placed in a thermos until stored in a freezer at -20°C at the end of the field day. Samples were later baked at 85°-90°C for at least three hours and then homogenized with mortar and pestle. Visible seeds and insect parts were removed. Dried samples were stored in sealable plastic Whirl Pak© bags on silica until transport to the Max Planck Institute for Evolutionary Anthropology (MPI-EVA) in Leipzig, Germany.

Steroid hormone extraction and assays

Between 12 to 100 mg of dry fecal matter were weighed per sample and combined twice with a 30x volume of 80% methanol according to a standard protocol (Heistermann et al., 1995). After each addition of methanol, the samples were thoroughly shaken for 15 minutes, centrifuged, and then the supernatants decanted. A small sample of methanol was immediately diluted 1:10 and stored at −20 °C until measurement. Pilot work on samples from our population showed that immunoreactive progesterone levels showed more pronounced differences between lactating and pregnant females than did pregnadiol (Deschner, unpublished). As a result, samples were measured via enzyme immunoassays (EIA) of progesterone using the R4859 antibody obtained from Coralie Munro, UC Davis, CA. The inter-assay coefficients of variation (CV) of high and low concentration quality controls were 2.1% and 9.6% respectively. Intra-assay CVs were 10.7% and 15.8% respectively on a sample size of 981 fecal extracts from 13 females for which we had the highest density sampling (one sample every 1-3 days). A small number of samples contained progesterone levels that were lower than the sensitivity level of the assay used. In those few cases (n=2), we assigned the sample the lowest measured concentration of any other sample in our dataset (112 ng/g).

Female reproductive state

Females were considered lactating if their dependent offspring were less than one year of age, and cycling if their offspring were older than one year. Nulliparous females were also classified as cycling if they were at least 5.0 years of age, corresponding to the youngest age at which females in our population are estimated to begin cycling (Perry et al., 2012). We also included a pre-reproductive class of sub-adult females too young to give birth but possibly old enough to cycle (age: 4.5-5.0). In order to cover the range of known gestation lengths for *Cebus capucinus* (Carnegie et al., 2011b), females were classified as 'potentially pregnant' (cycling/pregnant) between 145 and 166 days prior to the estimated birth date of their infants, and as pregnant 144 days onward until the estimated birth date. Females were assumed to be post-reproductive once more than 3.25 years passed without a noted pregnancy, which is a period three standard deviations over the average inter-birth interval in our population (Perry et al., 2012). One female in our dataset (CD, age: 9.45) has never been noted as pregnant and is presumed sterile, but is included as a cycling female because she does regularly show behavioral signs of cycling. Categorization into any reproductive state was refined if immunoreactive progesterone profiles were available for a female. Our youngest and oldest confirmed cycling females were 5.44 and 24.8 years respectively. Our two post-reproductive females were estimated to be 32.9 and 37.8 years old and had not given birth or been noted as pregnant for 5.6 and 7.8 years respectively.

Coefficients of relatedness

Paternity information was available from previous work on this population (Muniz et al., 2006, Godoy et al., unpublished). We used pedigree information to calculate estimated coefficients of relatedness for our 183 dyads using Ed Hagen's DESCENT software (http://itb.biologie.hu-berlin.de/~hagen/Descent/). 22.9% of our females and 20% of our males had full pedigrees back to two generations, meaning we knew their 4 grandparents **(Table 2)**. Since incomplete pedigrees limit our ability to precisely calculate a coefficient of relatedness between individuals, we limit our analyses to four relatedness categories ($r = 0$, $0 < r < 0.25$, $0.25 \leq r < 0.5$ and $r \geq 0.5$) for which we could be more confident as to inclusion.

Table 3-2: Pedigree information for subjects in behavioral analyses.

One generation pedigree	**Females (n=35)**	**Males (n=21)**
Known mother	28 (80.0%)	14 (66.7%)
Known father	30 (85.7%)	13 (61.9%)
2 known parents	26 (74.3%)	13 (61.9%)
1 known parent	6 (17.1%)	1 (4.8%)
0 known parents	3 (8.6%)	7 (33.3%)
Two generation pedigree	**Females (n=35)**	**Males (n=21)**
4 known grandparents	8 (22.9%)	5 (23.8%)
3 known grandparents	1 (2.9%)	0 (0.0%)
2 known grandparents	9 (25.7%)	2 (9.5%)
1 known grandparent	6 (17.1%)	1 (4.8%)
0 known grandparents	11 (31.4%)	13 (61.9%)

Statistics

Statistical analyses were run in R v.3.2.0 (R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/) using the glmer or lmer function from the lme4 package (Bates et al., 2014). To assess the significance of our predictor variables, we ran Generalized Linear Mixed Models (GLMM, Baayen 2008) 1) with binomial error structure and logit link function on all our models involving a binomial response (yes/no) and 2) with

Gaussian error structure for models involving a continuous response. We included random intercepts for female identity, male identity, dyad identity, and group identity in all models. 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 by calculating Variance Inflation Factors (Field, 2005). 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 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 the ‘car’ package of R.

All our models control for the number of adult males in a group, the number of adult females in a group, male age, and female age. All models also either test for or control for male alpha status and female dominance rank and their possible interaction effect.

RESULTS

Factors affecting female-male proximity

Our dataset was composed of 13 767 dyad days, 193 dyads, 35 females, and 21 males. The response variable in our GLMM was whether or not an adult female-male dyad was seen within 5 body lengths (~2 m) of each other on a given day (yes/no). We checked for any effect of female reproductive state, male alpha status, and female dominance rank while controlling for the number of adult males, the number of adult females, male age, and female age. Our full model was significantly different than our null model (χ^2_8=176.54, p<0.0001).

Whether dyads were observed in close proximity was largely explained by female reproductive state and the interaction effect between male alpha status and female dominance rank **(Table 3)**. Cycling, pregnant, and cycling/pregnant females, but not nulliparous or post-reproductive females, were more likely to be in proximity of adult males than were lactating females. Females were also more likely to be in proximity to an alpha male than to subordinate males, and this effect was mediated by female dominance rank. Higher-ranking females were more likely than lower-ranking females to be in close proximity to an alpha male **(Figure 1)**.

Table 3-3: GLMM results for probability of close proximity.

Fixed effect	Estimate	SE	z value	Pr(>|z|)		LRT	Pr(Chi)	
(Intercept)	-0.892	0.446	-2.002	0.0453	*			
Predictor variables								
Female reproductive state						**125.077**	**<0.0001**	***
Cycling [a]	0.484	0.075	6.430	<0.0001	***			
Pregnant [a]	0.853	0.084	10.160	<0.0001	***			
Cycling/Pregnant [a]	0.597	0.133	4.496	<0.0001	***			
Nulliparous [a]	-0.166	0.159	-1.045	0.2960	ns			
Post-reproductive [a]	0.543	0.368	1.475	0.1404	ns			
Alpha status * Fem. dom. rank	-0.268	0.040	-6.629	<0.0001	***	**38.436**	**<0.0001**	***
Male is alpha	2.417	0.333	7.261	<0.0001	***			
Female dominance rank	-0.033	0.022	-1.516	0.1294	ns			
Control variables								
Number of adult females	-0.071	0.023	-3.137	0.0017	**	**9.185**	**0.0024**	**
Number of adult males	0.136	0.048	2.812	0.0049	**	**6.917**	**0.0085**	**
Female age	-0.018	0.010	-1.789	0.0736	.	**3.052**	**0.0806**	**.**
Male age	-0.054	0.021	-2.583	0.0098	**	**4.724**	**0.0297**	*

[a] Reference level is lactating

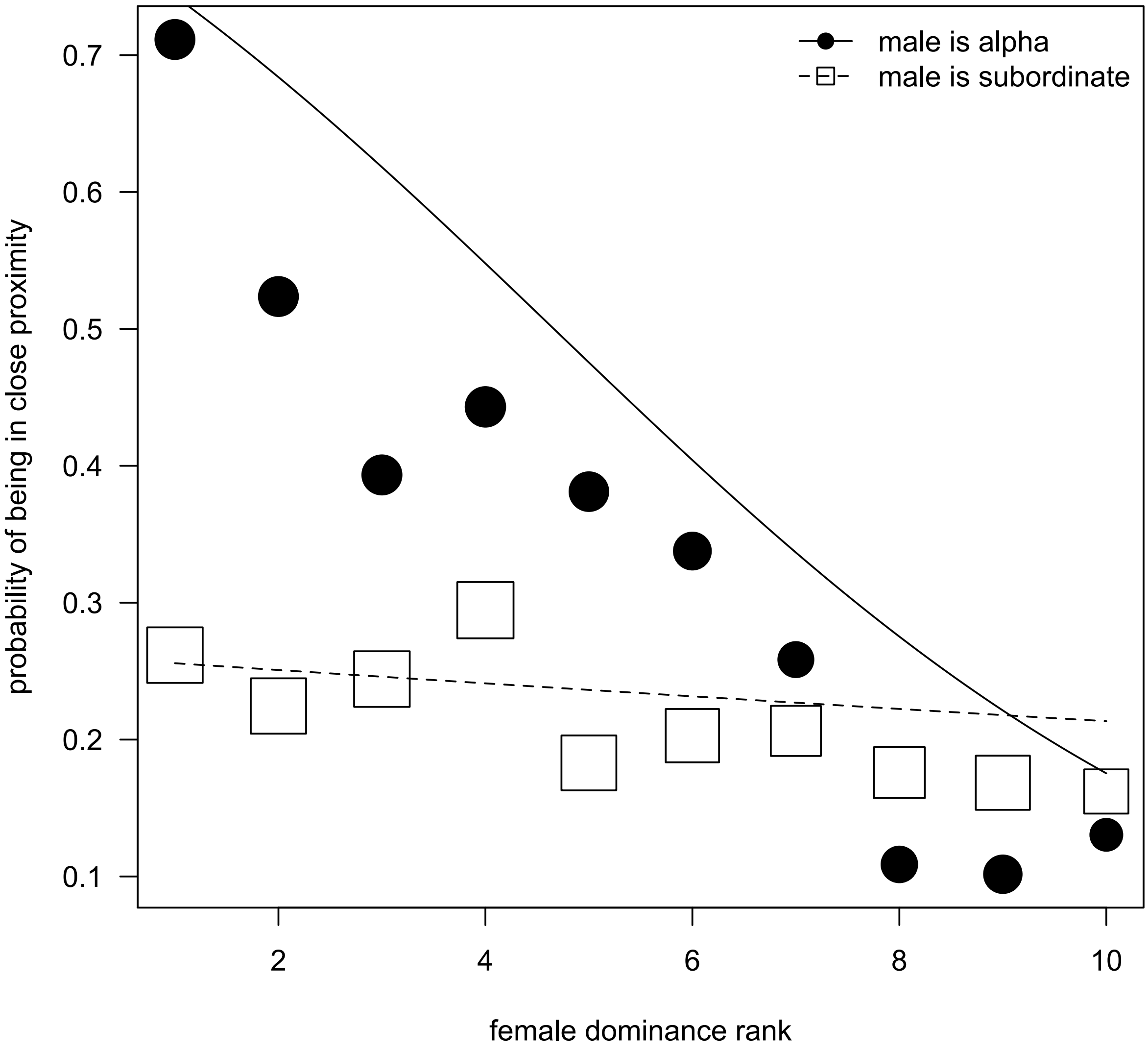

Figure 3-1: Probability of being in close proximity, categorized by male alpha status and female dominance rank. Bubbles represent the proportion of dyad days where females of that rank were in close proximity to an adult male. The size of each bubble represents sample size. Lines showing predicted values control for female reproductive state, the number of adult males, the number of adult females, female age, and male age.

Proximity with cycling females

Looking at our subset of dyads formed with cycling females (not including those that fell into the category of cycling/pregnant), we looked at the effect of relatedness on probability of close female-male proximity, while controlling for the number of adult females, the number of adult males, female age, male age, and the interaction effect of male alpha male status and female dominance rank. The dataset consisted of 134 dyads formed between 25 females and 21 males from 4 social groups across 4 890 dyad days. Our full model, however, was not significantly different from our null model (χ^2_3=5.401, p=0.1447).

Using the same dataset and same control variables, we looked at the effect on male-female proximity of three cues to relatedness: (1) male alpha status during female infancy, (2) years of co-residency during female adolescence (range: 0-5), and (3) years of co-residency during male adolescence (range: 0-5) - on the probability of close proximity. Our full model was marginally different from our null model (χ^2_3=8.304, p=0.0581).

Male alpha status during female infancy, but not years of residency during female adolescence or years of co-residency during male adolescence, had significant effects on the probability of close proximity **(Table 4)**. Dyads were more likely to be in close proximity if the male was alpha during the female's infancy.

Table 3-4: Final GLMM results for probability of close proximity (cycling females only).

Fixed effect	Estimate	SE	LRT	Pr(Chi)	
(Intercept)	0.556	0.679			
Predictor variables					
Male alpha status during female infancy	0.693	0.310	4.651	0.0310	*
Years of co-residency during female adolescence	0.021	0.046	0.194	0.6594	ns
Years of co-residency during male adolescence	-0.078	0.046	2.636	0.1045	ns
Control variables					
Alpha status * Female dominance rank	-0.304	0.058	25.645	<0.0001	***
Male is currently alpha	2.406	0.451			
Female dominance rank	-0.047	0.034			
Number of adult females	-0.107	0.051	4.201	0.0404	*
Number of adult males	0.059	0.075	0.509	0.4758	ns
Female age	0.002	0.015	0.017	0.8976	ns
Male age	-0.091	0.030	5.992	0.0144	*

For the subset of cycling females (n=8) for which we had spatial proximity data from their first year of life, we looked for the effect on male-female proximity of (1) their infancy spatial proximity scores, (2) their years of co-residency during male adolescence, (3) male alpha status during the females' infancies, and (4) years of co-residency during male adolescence. The interaction term for alpha male rank and female dominance was not significant and was removed from the final model (χ^2_1=1.506, p=0.2197). Our full model was significantly different from our null model (χ^2_4=14.859, p=0.0050).

There was a significant effect of female early spatial proximity to males, male alpha status during female infancy, and years of co-residency during male adolescence, but not of male absence during female adolescence **(Table 5)**. Dyads were more likely to be in close proximity if the males were alpha during the females' infancies, and if females had spent more time with the males during their first year of life, though the effect size was small. Dyads were less likely to be in close proximity the longer a female had been present during a male's adolescence.

Table 3-5: Final GLMM results for probability of close proximity (cycling females only), according to early social familiarity.

Fixed effect	Estimate	SE	LRT	Pr(Chi)	
(Intercept)	3.926	1.938			
Predictor variables					
Co-residency during female adolescence (yes)	0.353	0.345	1.034	0.3092	ns
Spatial proximity during female infancy	0.056	0.019	8.220	0.0041	**
Male alpha status during female infancy	0.831	0.376	5.054	0.0246	*
Years of co-residency during male adolescence	-0.357	0.124	7.332	0.0068	**
Control variables					
Male is currently alpha	1.812	0.492	6.612	0.0101	*
Female dominance rank	-0.203	0.104	2.373	0.1234	ns
Number of adult females	-0.374	0.088	28.288	<0.0001	***
Number of adult males	-0.001	0.108	0.069	0.7929	ns
Female age	0.042	0.164	0.486	0.4859	ns
Male age	-0.169	0.043	13.027	0.0003	***

Factors affecting proximity maintenance

Proximity maintenance was problematic to assess because many dyads were never recorded approaching or leaving within five body lengths of each other. For example, out of 134 possible dyads formed between adult males and cycling females, 17 were never recorded approaching or leaving proximity of each other. Furthermore, out of the remaining 117 dyads, only 79 had a total of 10 or more approaches or leaves – the minimum number used to calculate Hinde's index in previous work on this population (Perry, 1997).

The response variable in our GLMM was the calculated Hinde's Index for each dyad. The dataset was comprised of 204 Hinde's Indices for 144 dyads (n=34 females, n=20 males). Some dyads had more than one Hinde's Index because the reproductive state of the female changed across the field seasons. We looked for effects on Hinde's Index of (1) female reproductive state and (1) an interaction effect of male alpha status and female reproductive state, while controlling for the total amount of approaches and leaves used to calculate each Hinde's Index. Our interaction term was not significant and thus was dropped from our final mode (χ^2_1=1.025, p=0.3113). Our final full model was significantly different from our null model (χ^2_7=24.817, p=0.0008).

There were significant effects of male alpha status, female dominance rank, and female reproductive state on Hinde's indices **(Table 6)**. Hinde's indices were higher (i.e. females were more responsible for maintaining proximity) for dyads formed with alpha males than for those formed with subordinate males **(Figure 2)**. Hinde's indices were also higher for higher-ranking females. Hinde's indices where negative in 153 out of 204 cases, meaning that males were more responsible for proximity maintenance in 75% of cases. Of the 47 cases where Hinde's indices were positive, 20 (42.6%) involved alpha males. Few associations between female reproductive state and Hinde's Index were found. Post-reproductive females, but not other females, had higher Hinde's indices as compared to lactating females **(Figure 3)**.

Table 3-6: Final GLMM results for factors affecting proximity maintenance.

Fixed effect	Estimate	SE	t value	LRT	Pr(Chi)	
(Intercept)	-11.158	7.251	-1.539			
Predictor variables						
Female reproductive state				**11.408**	**0.0439**	*
Cycling [a]	-3.099	4.411	-0.702			
Pregnant [a]	-3.086	4.805	-0.642			
Cycling/Pregnant [a]	2.064	6.921	0.298			
Nulliparous [a]	2.778	7.063	0.393			
Post-reproductive [a]	34.689	12.677	2.736			
Male is alpha	17.368	6.800	2.554	**5.910**	**0.0151**	*
Female dominance rank	-1.520	0.666	-2.285	**5.152**	**0.0232**	*
Control variables						
Total approaches and leaves	-0.021	0.047	-0.441	**0.193**	**0.6608**	**ns**
Female age	-0.235	0.288	-0.817	**0.656**	**0.4179**	**ns**
Male age	0.170	0.541	0.314	**0.098**	**0.7548**	**ns**

[a] Reference level is lactating

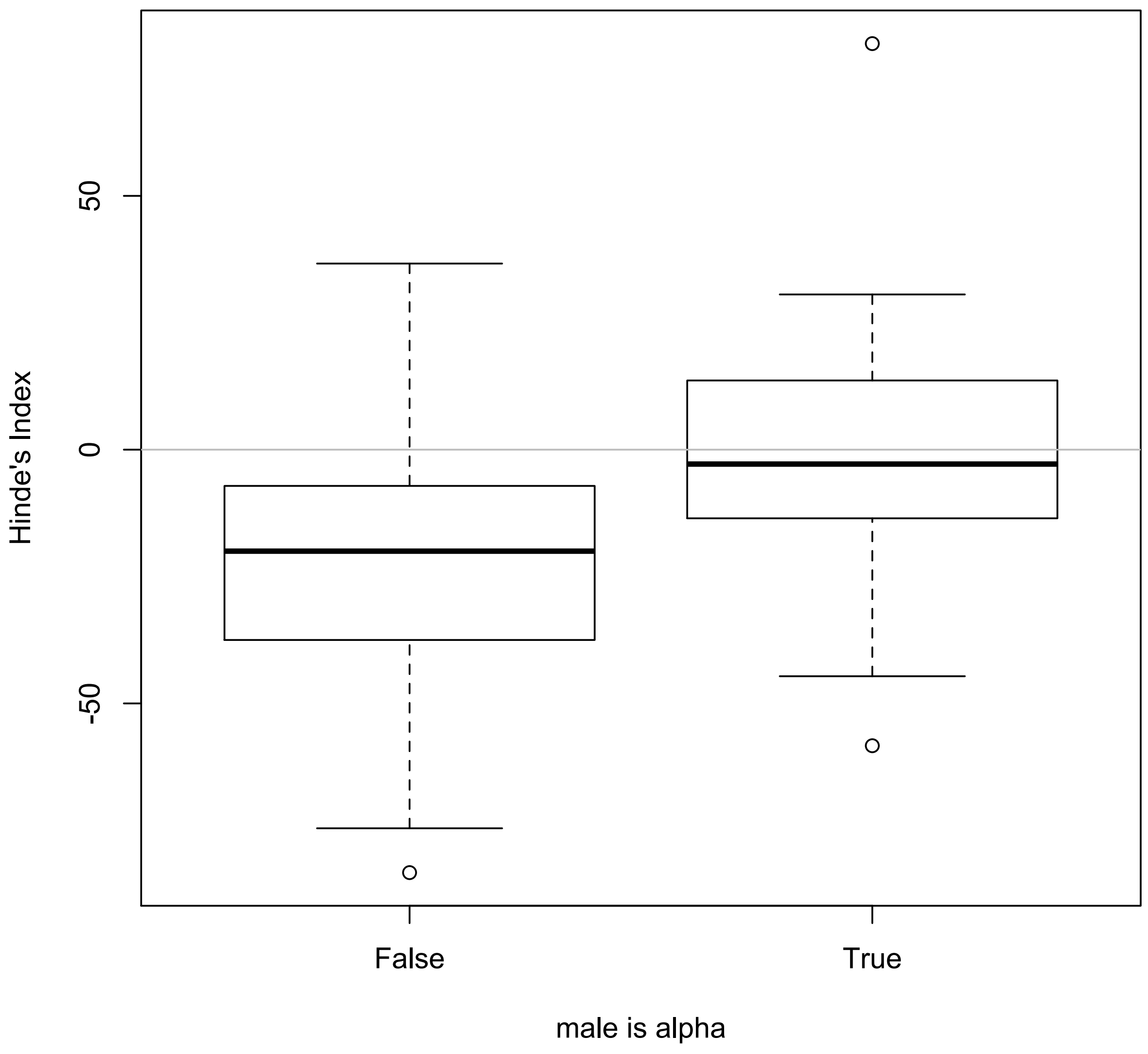

Figure 3-2: Hinde's indices, categorized by male alpha status. Positive values indicate that females were more responsible for proximity maintenance.

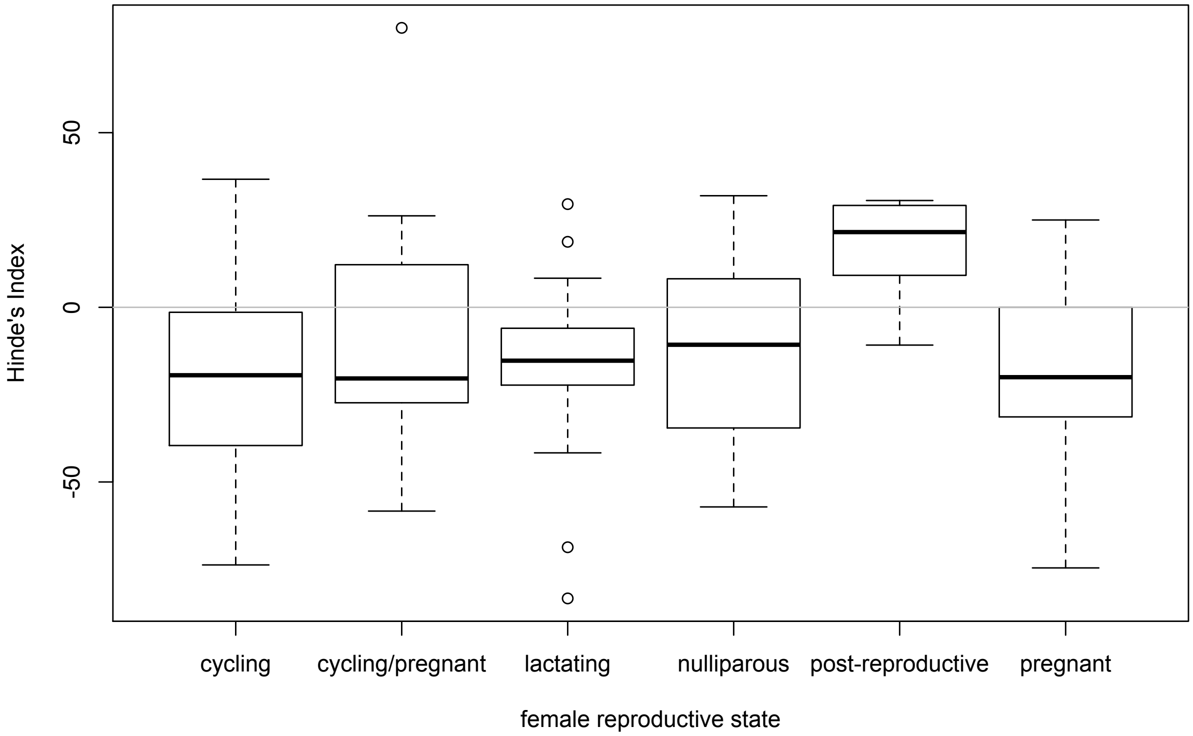

Figure 3-3: Hinde's indices, categorized by female reproductive state. Positive values indicate that females were more responsible for proximity maintenance.

Sexual mounts

A total of 94 sexual mounts by a male were observed over 83 days **(Table 7)**. The mounts involved 49 dyads, 20 females, and 20 males. Six mounts (n=4 females) involved the alpha male of the group, with four occurring with the alpha female of a group and the remaining two with a beta female. Four of the mounts involved females while they were cycling and the remaining two involved pregnant females during their first trimester.

Table 3-7: Sexual mounts documented.

Reproductive state	N (dyad days)	Dyad days	r=0	0 <r<0.25	0.25≤r<0.5	r≥0.5
Cycling	43 (38)	4 665	22	11	10	0
Pregnant	45 (42)	2 732	22	8	11	4
Cycling/Pregnant	2 (1)	394	0	0	0	2
Lactating	1 (1)	3 928	0	0	1	0
Nulliparous	3 (1)	1 029	3	0	0	0
Post-reproductive	0 (0)	430	0	0	0	0

GLMM results for factors affecting likelihood copulation

Our dataset was comprised of 13 776 dyad days, 193 dyads, 35 females, and 21 males. Our response variable was whether or not an adult male was seen mounting an adult female (yes/no) at any point during a field day. Our predictor variables were female reproductive state and an interaction between male alpha status and female dominance rank. Our control variables were the number of adult males, the number of adult females, male age, and female age. Our full model was significantly different from our null model (χ^2_8=65.813, P<0.0001).

There was a significant effect of female reproductive state and an interaction effect between male alpha status and female dominance rank on the probability a mount **(Table 8)**. Sexual mounts were more likely to be seen involving cycling and pregnant females as compared to lactating females. Alpha males, compared to subordinate males, were more likely to mount the highest-ranking females but less likely to mount lower-ranking females **(Figure 4)**.

Table 3-8: Probability of observing a sex mount on a dyad day.

Reproductive state	**Estimate**	**SE**	**z value**	**Pr(>|z|)**		**LRT**	**Pr(Chi)**	
(Intercept)	-7.366	1.501	-4.908	<0.0001	***			
Predictor variables								
Female reproductive state						**55.027**	**<0.0001**	***
Cycling [a]	3.301	1.136	2.907	0.0037	**			
Pregnant [a]	3.995	1.133	3.527	0.0004	***			
Cycling/Pregnant [a]	2.137	1.561	1.369	0.1710	ns			
Nulliparous [a]	1.581	1.603	0.986	0.3240	ns			
Post-reproductive [a]	-13.589	[b]	-0.006	0.9954	ns			
Male is alpha * Fem. dom. rank	-1.400	0.795	-1.760	0.0785	.	**11.389**	**0.0007**	***
Male is alpha	2.842	1.463	1.943	0.0520	.			
Female dominance rank	0.028	0.061	0.466	0.6409	ns			
Control variables								
Number of adult females	-0.022	0.099	-0.222	0.8240	ns	**0.054**	**0.8161**	**ns**
Number of adult males	-0.109	0.102	-1.065	0.2868	ns	**1.178**	**0.2777**	**ns**
Female age	0.034	0.024	1.377	0.1686	ns	**2.004**	**0.1568**	**ns**
Male age	-0.073	0.049	-1.492	0.1356	ns	**2.983**	**0.0842**	**.**

[a] Reference level is lactating

[b] Standard error not shown because it is meaningless as a result of complete separation (i.e. no sexual mounts were documented involving post-reproductive females)

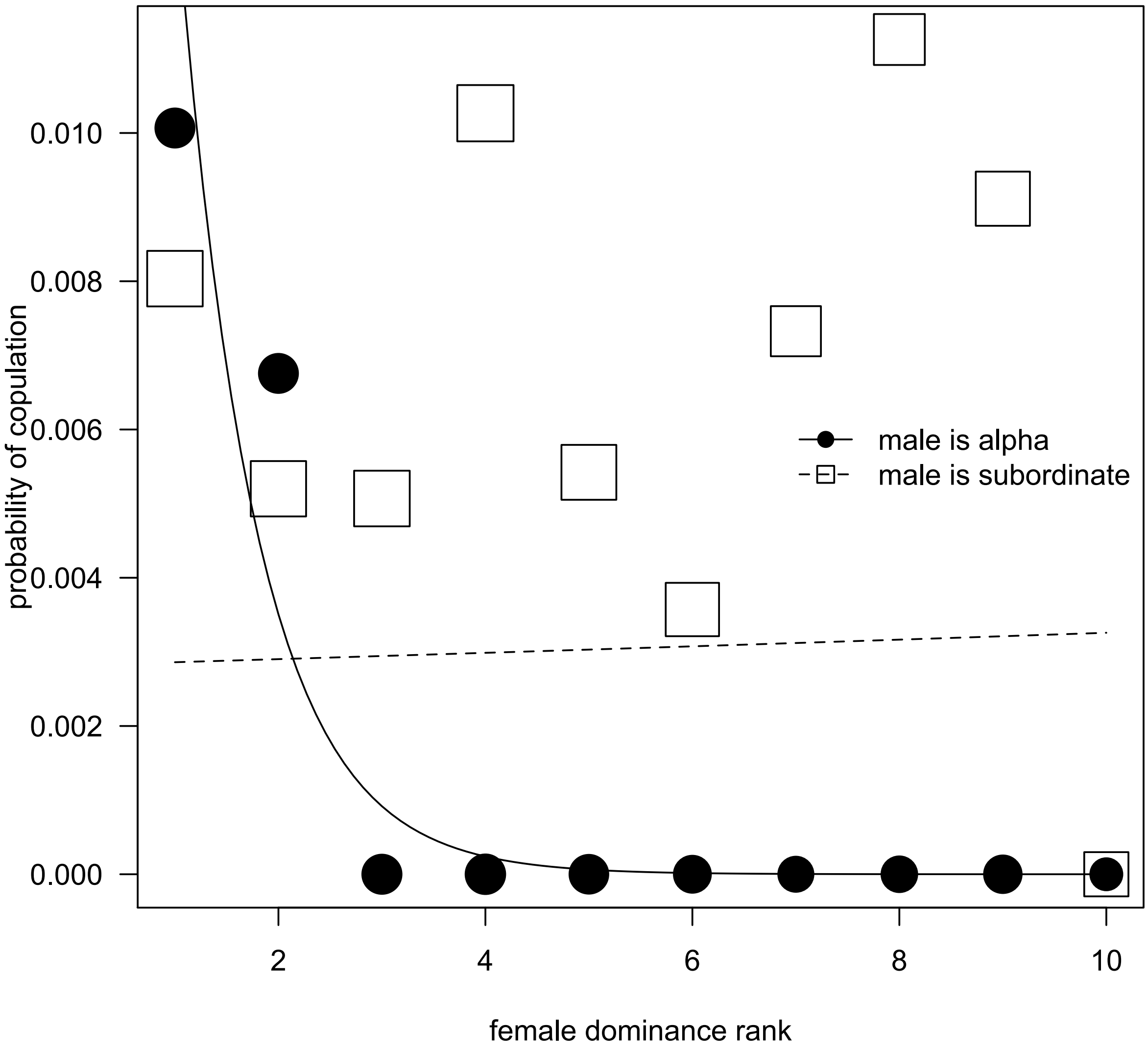

Figure 3-4: Likelihood of a sex mount, categorized by male alpha status and female dominance rank. Bubbles represent the proportion of dyad days for which mounts were seen for females at a particular dominance rank. The size of each bubble represents sample size. Predicted lines control for female reproductive state, the number of adult females, the number of adult males, female age, and male age.

GLMM results for factors affecting likelihood of mounts with cycling females

Our dataset involved 134 dyads formed between 25 cycling females and 21 males. The dataset was comprised of 4 894 dyad days across 4 groups. Our response variable was whether a dyad was observed engaged in sexual mount on a given day (yes/no). We ran two models. The first model looked at the effect of relatedness on the probability of observing a sexual mount on a dyad day. The second model looked at the effect on the probability of sexual mounts of three cues to relatedness: 1) male alpha status during female infancy, 2) years of co-residency during female adolescence, and 3) years of co-residency during male adolescence. Both models controlled for the number of adult females, the number of adult males, female age, male age, and the interaction effect of male alpha status and female dominance rank. Neither full model was significantly different from their null model (Model 1: χ^2_3=1.911, P=0.5911, Model 2: χ^2_2=0.900, P=0.8253).

Finally, we also looked at our subset of cycling females for which we had proximity data from their first year of life. The dataset was comprised of 1 764 dyad days, 53 dyads, 8 females, and 18 males. We tested the significance of (1) a female's infancy spatial proximity scores with a male, (2) male absence during the female's entire adolescence, (3) male alpha status during the female's infancy, and (4) years of co-residency during male adolescence. The interaction term was not significant (χ^2_1=0.996, P=0.3183) and was removed from the final model. The final full model was not significantly different from the null model (χ^2_4=4.955, P=0.2920). There were only 14 dyad days where a sexual mount was recorded with this subset of females.

Courtship

We observed 178 events where a female directed a sexual display towards a male over 120 dyad days. These involved 73 dyads formed between 25 females and 19 males **(Table 9)**.

Table 3-9: Female courtship of males.

Reproductive state	N (dyad days)	Dyad days	r = 0	0 < r < 0.25	0.25 ≤ r < 0.5	r ≥ 0.5
Cycling	98 (58)	4 665	70	14	13	1
Pregnant	54 (48)	2 732	42	7	4	1
Cycling/Pregnant	15 (5)	394	8	2	0	5
Lactating	7 (7)	3 928	3	1	3	0
Nulliparous	4 (2)	1 029	3	0	1	0
Post-reproductive	0 (0)	430	0	0	0	0

GLMM results for factors affecting likelihood of female courtship

Our response variable was whether or not a female was observed directing a courtship display toward an adult male at any point during a dyad day (yes/no). Our predictor variables were female reproductive state and the interaction between male alpha status and female dominance rank. Our control variables were the number of adult females, the number of adult males, female age, and male age. Our interaction term was not significant and was thus dropped from our final model (χ^2_1=0.516, P=0.4727). Our final model was significantly different from our null model (χ^2_5=67.729, P<0.0001).

There was a significant effect of female reproductive state on the probability of documenting courtship between a dyad **(Table 10)**. Courtship was more likely to be seen for cycling, pregnant, and cycling/pregnant females, but not nulliparous or post-reproductive females, as compared to lactating females. There was no significant effect of male alpha status or female dominance rank.

Table 3-10: Probability of observing female courtship.

Reproductive state	Estimate	SE	z value	Pr(>|z|)		LRT	Pr(Chi)	
(Intercept)	-8.109	1.013	-8.001	<0.0001	***			
Predictor variables								
Female reproductive state						**67.729**	**<0.0001**	***
Cycling [a]	2.015	0.425	4.744	<0.0001	***			
Pregnant [a]	2.454	0.432	5.688	<0.0001	***			
Cycling/Pregnant [a]	1.815	0.610	2.974	0.0029	**			
Nulliparous [a]	0.107	0.871	0.122	0.9026	ns			
Post-reproductive [a]	-14.710	[b]	-0.010	0.9920	ns			
Male is alpha	-0.143	0.565	-0.253	0.8004	ns	**0.063**	**0.8024**	**ns**
Female dominance rank	-0.038	0.052	-0.733	0.4637	ns	**0.539**	**0.4629**	**ns**
Control variables								
Number of adult females	0.111	0.085	1.311	0.1898	ns	**1.717**	**0.1901**	**ns**
Number of adult males	-0.055	0.099	-0.560	0.5754	ns	**0.297**	**0.5858**	**ns**
Female age	0.007	0.021	0.342	0.7321	ns	**0.119**	**0.7299**	**ns**
Male age	0.076	0.043	1.777	0.0756	.	**2.625**	**0.1052**	**ns**

[a] Reference level is lactating

[b] Standard error not shown because it is meaningless as a result of complete separation (i.e. no post-reproductive females were observed courting males)

GLMM results for factors affecting likelihood of female courtship by cycling females

Our dataset involved 134 dyads formed between 25 cycling females and 21 males. The dataset was comprised of 4 894 dyad days across 4 groups. Our response variable was whether a female directed a courtship display toward a male on a given day (yes/no). We ran two models. The first model looked at the effect of relatedness on the probability of female courtship. The second model looked at the effect on the probability of female courtship of two cues to relatedness: (1) male alpha status during female infancy and (2) years of co-residency during female adolescence - on the probability of female courtship. Both models controlled for current male alpha status, female dominance rank, the number of adult females, the number of adult males, female age, and male age. Both of our final models were significantly different from their null models (Model 1: χ^2_3=17.924 P=0.0005, Model 2: χ^2_2=9.259, P=0.0098).

Relatedness was a significant predictor of the probability of courtship **(Table 11)**. Females were less likely to direct courtship behavior toward related males ($0 < r < 0.25$, $0.25 \leq r < 0.5$, and $r \geq 0.5$) as compared to unrelated males ($r=0$).

Table 3-11: GLMM results for probability of courtship according to relatedness.

Fixed effects	**Estimate**	**S.E.**	**z value**	**Pr(>|z|)**		**LRT**	**Pr(Chi)**	
(Intercept)	-3.475	1.304	-2.665	0.0077	**			
Predictor variables								
Relatedness						**17.924**	**0.0005**	***
$r \geq 0.5$ [a]	-3.024	1.158	-2.611	0.0090	**			
$0.25 \leq r < 0.5$ [a]	-1.237	0.516	-2.398	0.0165	*			
$0 < r < 0.25$ [a]	-1.508	0.505	-2.985	0.0028	**			
Control variables								
Male is currently alpha	1.436	0.557	2.576	0.0100	**	**4.981**	**0.0256**	*
Female dominance rank	0.070	0.094	0.748	0.4546	ns	**0.615**	**0.4330**	**ns**
Number of adult females	0.020	0.135	0.149	0.8817	ns	**0.093**	**0.7607**	**ns**
Number of adult males	-0.088	0.165	-0.536	0.5919	ns	**1.091**	**0.2962**	**ns**
Female age	-0.029	0.035	-0.831	0.4058	ns	**0.852**	**0.3561**	**ns**
Male age	-0.016	0.041	-0.402	0.6878	ns	**0.103**	**0.7478**	**ns**

[a] Reference level is $r = 0$

Length of co-residency during female adolescence and former male alpha status had significant effects on the likelihood of female courtship **(Table 12)**. Females were less likely to court a male the longer he had been present during her adolescence and females showed a trend to be additionally less likely to court a male if he had been alpha during her first year of life.

Table 3-12: GLMM results for probability of courtship, according to cues to relatedness.

Fixed effects	**Estimate**	**S.E.**	**LRT**	**Pr(Chi)**	
(Intercept)	-3.675	1.358			
Predictor variables					
Male alpha status during female infancy	-1.920	1.165	4.053	0.0441	*
Years of co-residency during female adolescence	-0.282	0.116	5.205	0.0225	*
Control variables					
Male is currently alpha	1.097	0.637	2.130	0.1444	ns
Female dominance rank	0.087	0.099	0.816	0.3664	ns
Number of adult females	0.002	0.135	0.099	0.7527	ns
Number of adult males	-0.143	0.138	0.138	0.2860	ns
Female age	-0.067	0.041	2.760	0.0966	.
Male age	0.047	0.044	0.876	0.3493	ns

We further analyzed a subset of cycling females (n=8) for which we had spatial proximity data from their first year of life. This dataset was comprised of 1 766 dyad days in 3 groups and involving 53 dyads formed with 18 males. We tested for the effect of female-male spatial proximity during female infancy, male absence during female adolescence, and former male alpha status. Spatial proximity during female infancy was a significant predictor of the likelihood of courtship, as was male absence during female adolescence **(Table 13)**. Cycling females were less likely to court familiar versus unfamiliar males, and were less likely to court males with which they spent more time during their infancy, even after accounting for the preference for unfamiliar males (i.e. males that were absent during the female's entire adolescence) **(Figure 5)**.

Table 3-13: GLMM results for probability of courtship, according to early social familiarity.

Fixed effects	**Estimate**	**S.E.**	**LRT**	**Pr(Chi)**	
(Intercept)	1.175	3.119			
Predictor variables					
Co-residency during female adolescence (yes)	-1.274	0.623	4.803	0.0284	*
Spatial proximity during female infancy	-0.223	0.126	5.322	0.0211	*
Male alpha status during female infancy	0.131	1.554	0.007	0.9331	ns
Control variables					
Male is currently alpha	1.354	1.146	1.378	0.2405	ns
Female dominance rank	-0.261	0.175	2.489	0.1146	ns
Number of adult females	-0.061	0.138	0.198	0.6560	ns
Number of adult males	-0.002	0.211	0.001	0.9914	ns
Female age	-0.391	0.206	3.050	0.0807	.
Male age	-0.007	0.066	0.012	0.9112	ns

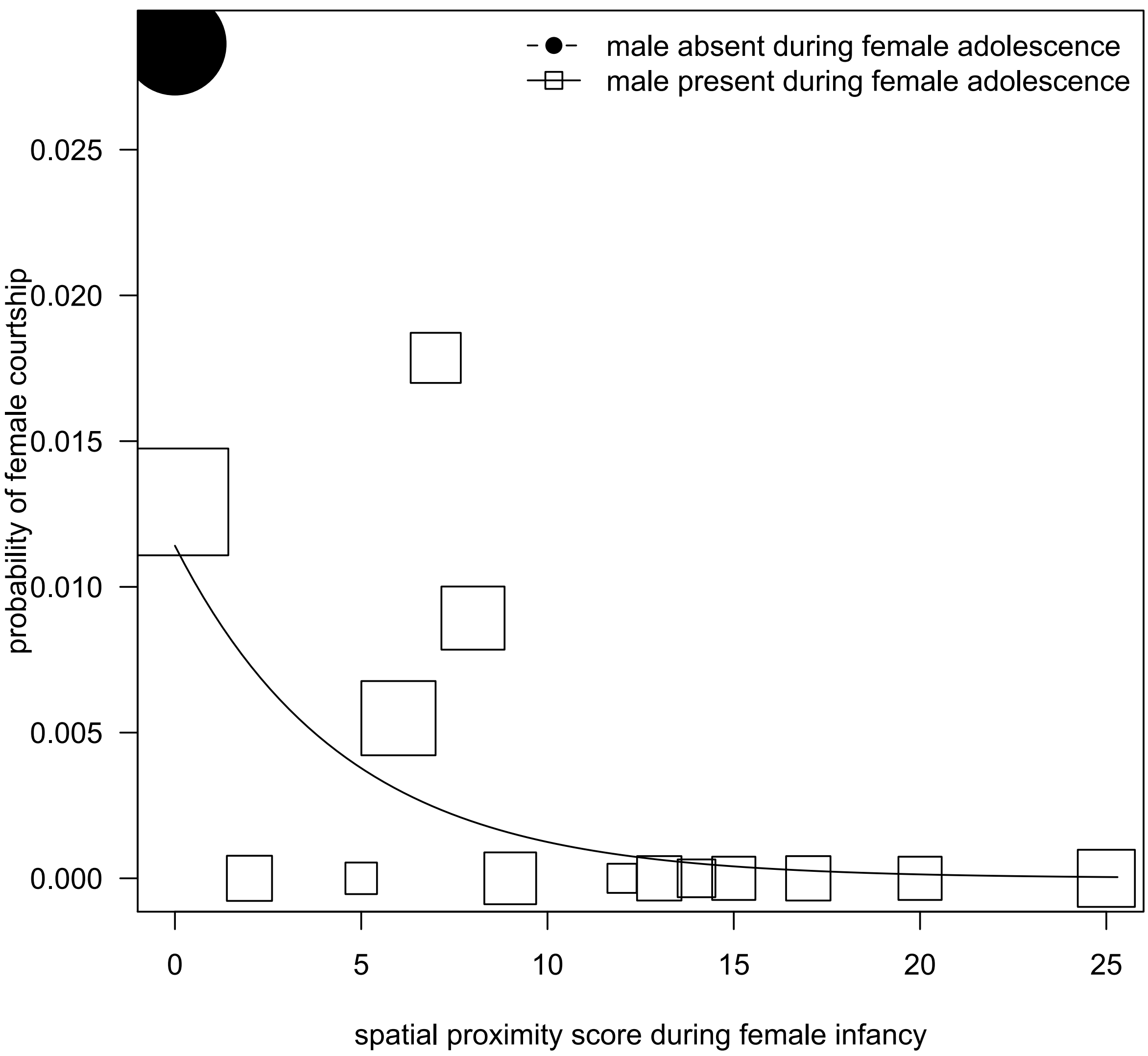

Figure 3-5: Probability of female courtship, according to early social familiarity. The line showing the predicted values controls for absence during female adolescence, former alpha status, current alpha status, female age, male age, the number of adult males, and the number of adult females.

DISCUSSION

Female-male close proximity was largely explained by female reproductive state and an interaction effect between alpha male status and female dominance rank. Females higher in the dominance hierarchy were more likely to be in close proximity to alpha males than were lower ranking females. These findings are similar to those found in *Cebus apella nigritus*, where alpha males are the preferred partners of females, but with higher-ranking females having stronger affiliation with alpha males than lower-ranking females (Tiddi et al., 2011). Cycling, pregnant, and potentially pregnant females (but not nulliparous or post-reproductive females) were also more likely to be in proximity of adult males as compared to lactating females.

Among our cycling females, actual relatedness did not have a significant effect on close proximity. However, years of co-residency during male adolescence and former male alpha status during female infancy, but not years of co-residency during female adolescence, had significant effects. Females were more likely to be in close proximity to a male if he was alpha during her first year of life, and less likely to be in close proximity to him the longer the female was present during the male's adolescence. When we looked at the subset of cycling females for which we had proximity information from their infancy, we found that the amount of time a female spent around a male when she was young had a slightly positive impact on her likelihood of proximity with that male when she was older and cycling.

Males were generally responsible for proximity maintenance except for two exceptions. The first occurred with post-reproductive females, where females where more responsible than males. The second occurred with alpha males, where proximity maintenance was more equally balanced. Given the general pattern of male responsibility for proximity, it may not be surprising that female cues to relatedness had a mixed effect on close proximity to cycling females. Male cues to relatedness (co-residency during their adolescence) had the only significant negative impact. Further investigation of male sexual preferences will be necessary to better understand the role they play in determining inbreeding avoidance patterns in capuchins.

The likelihood of female-male sexual behavior in capuchins was largely dependent on female reproductive state. Almost all documented sexual mounts (95.2%) and courtship events (94.8%) involved pregnant or cycling females. These results are in line with other work on *Cebus capucinus* (Manson, 1997; Perry 1997; Carnegie et al., 2006) showing that pregnant females engage in high rates of matings with males. The likelihood of a mount and of female courtship toward males was significantly higher for cycling and pregnant females as compared to lactating females. An interaction effect between male alpha status and female dominance rank also played a role in the likelihood of a mount, but not in the likelihood of female courtship. Alpha males, compared to subordinate males, were more likely to mount higher-ranking females, but less likely with lower-ranking females. However, alpha males were no more likely than subordinate males to be courted by females.

Among cycling females, we found no effects of either relatedness or cues to relatedness on the probability of a mount. These behaviors, however, were not common as we documented only 43 events across 38 dyad days with cycling females.

On the other hand, the probability of courtship by cycling females toward males was affected by both relatedness and cues to relatedness. Females were less likely to court related males ($r \geq 0.5$, $0.25 \leq r < 0.5$, and $0 < r < 0.25$) as compared to unrelated males. When we looked at female cues to relatedness, we found that females were less likely to court males that were alpha during the female's infancy (even despite our finding of a slight bias for close proximity to these males). Females were also less likely to court males that were present for longer periods of the female's adolescence. When we looked at only the subset of cycling females for which we had proximity data from their first year of life, we found that early spatial proximity had a significant negative effect on their probability of courtship. Females were less likely to court males that they spent more time around when the females were infants, even after accounting for their general preference for unfamiliar males. That is, females were more likely to court unfamiliar males (i.e. males not present at any point during the female's adolescence) and familiar males with which the female had spent less time during their first year of life. Reproductive females in many species also show preferences for unfamiliar (i.e. non-natal) males over familiar males: baboons (*Papio cynocephalus Anubis*) (Bercovitch, 1991), ringtailed lemurs (*Lemur catta*) (Pereira & Weiss, 1991), the mandarin vole (*Microtus mandarinus*) (Fadao et al., 2000), and even the habitually inbreeding naked mole rat (*Heterocephalus glaber)* (Clarke & Faulkes, 1999). Overall, we find that our data support the hypothesis that early social familiarity is a mechanism by which female, and perhaps males, develop sexual aversion toward opposite-sexed individuals. Future work focusing on natal male preferences for females will be necessary to understand the role that early social familiarity plays in determining the frequency and intensity with which males court females. Our current dataset involved too few natal males for which we had spatial proximity data during their infancy.

Our findings that only 6 of 94 copulations involved an alpha male, though alpha males typically sire most offspring in this species (Jack & Fedigan, 2006; Muniz et al., 2006, 2010), suggest that the observed mounts may not be a representative sample of the copulations that actually result in conception. Furthermore, close relatedness had negative effects on female courtship but not on general patterns of female-male proximity. This may indicate that if proximity avoidance as a means to inbreeding avoidance occurs, it may occur specifically during periods of highest female fertility. Previous work on *Cebus capucinus* in the wild has shown that males appear capable of detecting the female peri-ovulatory period (5-day window: Carnegie et al., 2005; 7-day window: Schoof et al., 2014). Future work in the Lomas population of capuchins will look at even more fine-grained behavioral analyses of female-male associations between periovulatory versus non-periovulatory periods within cycling females.

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	
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

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	
*	0:30	40
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.

Offspring ID	Loci typed	First parent non-exclusion probability	Second parent non-exclusion probability	Mother ID	Loci typed	Pair loci compared	Pair loci mismatching	Pair LOD score	Candidate father ID	Loci typed	Pair loci compared	Pair loci mismatching	Pair LOD score	Pair Delta	Pair confidence	Trio loci compared	Trio loci mismatching	Trio LOD score	Trio Delta	Trio confidence
AJ	18	1.24E-02	3.80E-05	VU	18	18	0	7.27E+00	DU	18	18	0	4.02E+00	0.00E+00		18	0	8.12E+00	5.01E+00	*
AS	17	1.11E-02	1.52E-03	CG	18	17	0	1.17E+01	BA	18	17	0	4.56E+00	4.56E+00	*	17	0	1.00E+01	1.00E+01	*
AV	18	5.19E-03	6.37E-04	CT	18	18	0	1.04E+01	OD	18	18	0	9.29E+00	9.29E+00	*	18	0	9.50E+00	9.50E+00	*
AY	17	3.99E-03	4.72E-08	FA	18	17	0	4.24E+00	MS	18	17	0	1.23E+01	1.16E+01	*	17	0	1.69E+01	1.69E+01	*
AZ	18	5.98E-03	3.22E-04	MF	18	18	0	7.93E+00	PW	18	18	0	4.55E+00	1.58E-01	*	18	0	6.70E+00	6.70E+00	*
BH	17	3.33E-02	1.06E-04	BO	18	17	0	7.35E+00	HE	18	17	0	5.81E+00	5.81E+00	*	17	0	1.05E+01	1.05E+01	*
BI	18	2.21E-02	8.72E-04	MM	18	18	0	5.79E+00	TO	18	18	0	2.81E+00	2.81E+00	*	18	0	7.57E+00	7.57E+00	*
BJ	18	1.72E-02	2.09E-03	LL	18	18	0	9.07E+00	NM	18	18	0	4.47E+00	4.47E+00	*	18	0	6.63E+00	6.63E+00	*
BM	18	2.38E-03	4.67E-04	BV	18	18	0	9.07E+00	PW	18	18	0	5.45E+00	5.45E+00	*	18	0	7.76E+00	7.76E+00	*
BT	17	1.61E-03	4.68E-05	OP	18	17	0	9.10E+00	TO	18	17	0	7.17E+00	7.17E+00	*	17	0	1.11E+01	1.11E+01	*
BW	18	7.72E-03	1.58E-07	BO	18	18	0	3.15E+00	QJ	18	18	0	1.02E+01	1.02E+01	*	18	0	1.55E+01	1.55E+01	*
CF	18	1.89E-03	3.54E-06	CU	18	18	0	6.49E+00	PW	18	18	0	6.88E+00	6.88E+00	*	18	0	1.13E+01	1.13E+01	*
CI	18	7.00E-05	8.67E-06	CM	18	18	0	1.25E+01	FZ	18	18	0	1.28E+01	1.11E+01	*	18	0	1.24E+01	1.13E+01	*
CX	18	2.57E-02	3.57E-03	CM	18	18	0	7.04E+00	OD	18	18	0	6.18E+00	6.18E+00	*	18	0	8.01E+00	8.01E+00	*
CZ	18	6.31E-06	1.16E-08	SC	18	18	0	9.45E+00	MO	18	18	0	1.50E+01	1.50E+01	*	18	0	1.78E+01	1.78E+01	*
DG	18	2.20E-02	1.78E-04	DD	18	18	0	3.99E+00	TO	18	18	0	4.08E+00	4.08E+00	*	18	0	8.73E+00	8.73E+00	*
DL	18	3.31E-02	1.98E-03	DN	18	18	0	6.97E+00	OD	18	18	0	3.97E+00	3.97E+00	*	18	0	7.85E+00	7.85E+00	*
DM	18	1.70E-03	9.28E-07	DN	18	18	0	8.03E+00	FZ	18	18	1	4.02E+00	4.02E+00	*	18	1	9.52E+00	9.52E+00	*
DP	18	2.69E-02	5.40E-03	DD	18	18	0	6.78E+00	DU	18	18	0	-1.01E	0.00E+00		18	0	2.51E+00	2.51E+00	*

													+00							
DS	18	1.55E-02	5.32E-07	DI	18	18	0	4.86E+00	MO	18	18	0	8.80E+00	7.42E+00	*	18	0	1.44E+01	1.44E+01	*
DT	18	7.19E-03	3.12E-06	DD	18	18	0	2.40E+00	TO	18	18	0	8.59E+00	8.59E+00	*	18	0	1.48E+01	1.48E+01	*
DV	18	1.43E-02	3.67E-08	EI	18	18	0	1.08E+00	QJ	18	18	0	1.08E+01	1.08E+01	*	18	0	1.77E+01	1.77E+01	*
DY	18	7.13E-04	2.80E-06	DH	18	18	0	6.73E+00	AR	18	18	0	9.22E+00	9.22E+00	*	18	0	1.44E+01	1.44E+01	*
DZ	18	7.65E-03	1.07E-04	DI	18	18	0	7.13E+00	MO	18	18	0	5.19E+00	1.05E+00	*	18	0	8.40E+00	8.40E+00	*
EB	18	3.80E-03	5.37E-06	CH	18	18	0	8.60E+00	PW	18	18	0	5.58E+00	5.58E+00	*	18	0	1.09E+01	1.09E+01	*
EC	18	1.10E-02	1.30E-05	DW	18	18	0	5.69E+00	MO	18	18	0	6.10E+00	6.10E+00	*	18	0	8.47E+00	8.47E+00	*
EI	18	3.88E-03	2.19E-04	EE	18	18	0	1.15E+01	HE	18	18	0	4.83E+00	4.83E+00	*	18	0	8.62E+00	8.62E+00	*
EQ	18	1.91E-03	1.96E-08	MI	18	18	0	4.34E+00	QJ	18	18	0	1.17E+01	1.17E+01	*	18	0	1.81E+01	1.81E+01	*
ER	18	4.95E-03	1.89E-04	PY	18	18	0	8.18E+00	SM	18	18	0	4.94E+00	4.68E+00	*	18	0	1.01E+01	1.01E+01	*
EV	17	8.88E-03	1.64E-03	EE	18	17	0	7.09E+00	HE	18	17	0	3.62E+00	3.62E+00	*	17	0	5.97E+00	5.97E+00	*
FE	18	5.09E-02	1.30E-02	TH	18	18	0	9.18E+00	OD	18	18	0	3.06E+00	3.06E+00	*	18	0	6.46E+00	6.46E+00	*
FG	18	1.13E-02	5.27E-06	TD	18	18	0	8.86E+00	BK	17	17	0	7.42E+00	7.42E+00	*	17	0	1.28E+01	1.28E+01	*
GI	17	7.45E-03	3.08E-03	KY	18	17	0	9.29E+00	EO	18	17	0	6.64E+00	6.64E+00	*	17	0	8.31E+00	8.07E+00	*
GR	17	6.31E-02	3.41E-04	MW	18	17	0	2.86E+00	AL	18	17	0	5.28E+00	5.28E+00	*	17	0	9.65E+00	9.65E+00	*
GS	17	4.14E-02	3.29E-06	GE	18	17	0	2.53E+00	MO	18	17	0	6.82E+00	6.82E+00	*	17	0	1.14E+01	1.14E+01	*
GY	18	5.09E-02	2.22E-03	GL	18	18	0	6.04E+00	NM	18	18	0	6.10E+00	6.10E+00	*	18	0	6.96E+00	6.96E+00	*
HB	18	1.35E-02	2.87E-06	MH	18	18	0	3.48E+00	MO	18	18	0	8.58E+00	4.52E+00	*	18	0	1.19E+01	1.19E+01	*
HC	18	1.05E-02	4.35E-05	SC	18	18	0	4.67E+00	BB	18	18	0	7.55E+00	7.55E+00	*	18	0	1.07E+01	1.07E+01	*
HK	18	1.50E-02	3.57E-03	DR	18	18	0	1.02E+01	OD	18	18	0	4.28E+00	4.28E+00	*	18	0	7.31E+00	7.31E+00	*
HL	18	7.54E-03	3.55E-08	GE	18	18	0	2.92E+00	MO	18	18	0	1.19E+01	1.19E+01	*	18	0	1.77E+01	1.77E+01	*
HV	17	4.99E-03	7.16E-05	CH	18	17	0	5.62E+00	PW	18	17	0	4.13E+00	4.13E+00	*	17	0	7.46E+00	7.46E+00	*
IC	18	3.82E-03	4.00E-04	CG	18	18	0	1.03E+01	GB	18	18	0	4.18E+00	4.18E+00	*	18	0	8.01E+00	8.01E+00	*
IE	18	3.72E-	2.12E-	BO	18	18	0	3.92E	QJ	18	18	0	1.11E	1.11E	*	18	0	1.59E	1.59E	*

		03	07					+00					+01	+01				+01	+01	
IK	18	7.66E-04	6.77E-04	LR	18	18	1	3.89E+00	YA	18	18	0	6.33E+00	6.33E+00	*	18	1	9.74E+00	9.74E+00	*
IO	18	1.71E-03	1.67E-04	SY	18	18	0	1.24E+01	AL	18	18	0	5.03E+00	3.79E+00	*	18	0	9.28E+00	9.28E+00	*
IZ	18	1.02E-02	1.65E-07	MB	18	18	0	5.20E+00	BE	18	18	0	1.10E+01	1.10E+01	*	18	0	1.76E+01	1.57E+01	*
JH	18	1.28E-02	6.02E-05	MH	18	18	0	6.23E+00	MO	18	18	0	4.91E+00	0.00E+00		18	0	8.70E+00	8.70E+00	*
JP	18	5.98E-03	2.91E-04	OP	18	18	0	8.39E+00	DU	18	18	0	2.91E+00	2.91E+00	*	18	0	6.45E+00	6.45E+00	*
JU	18	3.13E-03	5.71E-07	JJ	18	18	0	4.83E+00	HE	18	18	1	3.08E+00	3.08E+00	*	18	1	9.69E+00	9.69E+00	*
KB	18	1.83E-03	1.02E-06	CU	18	18	0	1.05E+01	AR	18	18	0	8.92E+00	8.92E+00	*	18	0	1.51E+01	1.51E+01	*
KD	18	2.64E-03	5.86E-04	CT	18	18	0	9.34E+00	OD	18	18	0	9.65E+00	9.65E+00	*	18	0	9.11E+00	9.11E+00	*
KE	17	3.90E-03	1.01E-07	PL	18	17	0	3.24E+00	MS	18	17	0	1.40E+01	1.40E+01	*	17	0	1.73E+01	1.73E+01	*
KF	18	3.16E-03	1.18E-07	KK	18	18	0	5.76E+00	MS	18	18	0	1.17E+01	1.17E+01	*	18	0	1.61E+01	1.61E+01	*
KG	18	2.32E-03	1.12E-03	KK	18	18	0	5.82E+00	BA	18	18	0	8.22E+00	8.22E+00	*	18	0	8.95E+00	8.95E+00	*
KH	18	7.47E-02	2.23E-04	VU	18	18	0	4.65E+00	DU	18	18	0	2.41E+00	2.41E+00	*	18	0	6.74E+00	6.74E+00	*
KM	18	3.68E-03	2.78E-04	FY	18	18	0	1.05E+01	TO	18	18	0	7.83E+00	7.83E+00	*	18	0	9.20E+00	9.20E+00	*
KX	18	1.16E-02	4.12E-04	RH	18	18	1	-1.88E+00	AL	18	18	0	8.88E+00	8.88E+00	*	18	1	1.05E+01	1.05E+01	*
LB	17	2.46E-02	1.58E-03	LR	18	17	0	8.81E+00	BA	18	17	0	5.13E+00	5.13E+00	*	17	0	8.45E+00	8.45E+00	*
LD	18	1.70E-03	4.64E-07	ME	18	18	0	9.20E+00	QJ	18	18	0	1.19E+01	1.19E+01	*	18	0	1.51E+01	1.51E+01	*
LG	18	1.10E-02	2.50E-04	LA	18	18	0	4.83E+00	BA	18	18	0	8.73E+00	8.73E+00	*	18	0	1.13E+01	1.13E+01	*
LH	18	7.80E-03	6.35E-05	LL	18	18	0	9.75E+00	NM	18	18	0	7.56E+00	7.56E+00	*	18	0	1.08E+01	1.08E+01	*
LI	18	4.71E-03	6.73E-07	LU	18	18	0	9.32E+00	PH	18	18	0	9.61E+00	0.00E+00		18	0	1.50E+01	1.50E+01	*
LN	18	1.03E-02	3.75E-06	MI	18	18	0	2.75E+00	HE	18	18	0	8.75E+00	8.75E+00	*	18	0	1.34E+01	1.34E+01	*
LO	18	1.05E-02	3.81E-05	DA	18	18	0	4.58E+00	DU	18	18	0	4.41E+00	2.70E+00	*	18	0	9.54E+00	6.36E+00	*
LU	18	1.13E-03	1.04E-07	KK	18	18	0	2.86E+00	MS	18	18	0	1.28E+01	1.28E+01	*	18	0	1.58E+01	1.58E+01	*
LZ	17	1.77E-02	5.94E-04	LR	18	17	0	4.89E+00	BA	18	17	0	6.63E+00	6.63E+00	*	17	0	9.12E+00	9.12E+00	*

ML	18	4.85E-03	1.08E-07	ME	18	18	0	5.94E+00	HE	18	18	1	4.20E+00	4.20E+00	*	18	1	1.14E+01	1.14E+01	*
MP	18	1.32E-02	6.81E-04	MJ	18	18	0	5.54E+00	SM	18	18	0	7.18E+00	7.18E+00	*	18	0	9.69E+00	9.69E+00	*
MR	18	5.14E-03	2.34E-05	CK	18	18	0	7.37E+00	TO	18	18	0	5.74E+00	5.74E+00	*	18	0	1.13E+01	1.13E+01	*
MU	18	6.07E-03	7.41E-04	MB	18	18	0	9.03E+00	BB	18	18	0	6.95E+00	1.45E+00	*	18	0	8.05E+00	6.54E+00	*
MX	18	5.33E-03	7.06E-06	ME	18	18	0	6.73E+00	HE	18	18	1	1.77E+00	1.77E+00	*	18	1	6.88E+00	6.88E+00	*
MZ	18	1.57E-02	5.89E-05	MM	18	18	0	5.83E+00	TO	18	18	0	5.70E+00	5.70E+00	*	18	0	1.05E+01	1.05E+01	*
NA	18	1.32E-02	2.87E-04	LL	18	18	0	9.65E+00	NM	18	18	0	6.49E+00	6.49E+00	*	18	0	8.97E+00	8.97E+00	*
NE	18	6.43E-03	1.36E-04	FY	18	18	0	1.12E+01	DU	18	18	0	1.77E+00	1.77E+00	*	18	0	7.31E+00	7.31E+00	*
NH	18	7.43E-05	1.46E-05	GL	18	18	0	1.00E+01	NM	18	18	0	1.09E+01	1.09E+01	*	18	0	1.19E+01	1.19E+01	*
NY	18	1.02E-02	1.44E-03	TH	18	18	0	6.44E+00	OD	18	18	0	6.07E+00	6.07E+00	*	18	0	8.14E+00	8.14E+00	*
OA	17	1.28E-03	1.40E-05	OP	18	17	0	7.77E+00	DU	18	17	0	5.96E+00	1.90E+00	*	17	0	1.00E+01	1.00E+01	*
OE	18	1.24E-02	5.03E-06	MH	18	18	0	4.13E+00	MO	18	18	0	7.89E+00	7.89E+00	*	18	0	1.16E+01	1.16E+01	*
OJ	18	1.96E-03	1.48E-05	SN	18	18	0	6.11E+00	BK	17	17	0	8.31E+00	8.31E+00	*	17	0	1.14E+01	1.14E+01	*
OK	18	2.58E-03	5.70E-08	TX	18	18	0	5.11E+00	MS	18	18	0	1.07E+01	1.07E+01	*	18	0	1.66E+01	1.66E+01	*
ON	17	6.53E-03	1.08E-04	DD	18	17	0	6.19E+00	DU	18	17	0	2.93E+00	2.93E+00	*	17	0	7.61E+00	7.61E+00	*
OS	18	4.24E-02	2.85E-05	VV	18	18	0	3.34E+00	DU	18	18	0	5.72E+00	5.72E+00	*	18	0	9.68E+00	9.68E+00	*
OT	18	4.37E-04	1.02E-04	CB	18	18	1	3.67E+00	AL	18	18	0	1.02E+01	3.27E+00	*	18	1	1.07E+01	1.07E+01	*
PC	18	3.49E-02	7.21E-04	DA	18	18	0	4.84E+00	DU	18	18	0	1.93E+00	1.93E+00	*	18	0	5.90E+00	5.90E+00	*
PD	18	5.75E-03	1.27E-06	MH	18	18	0	5.40E+00	MO	18	18	0	9.12E+00	9.12E+00	*	18	0	1.33E+01	1.33E+01	*
PE	18	8.12E-03	4.10E-05	CS	18	18	0	4.77E+00	PW	18	18	0	5.21E+00	5.21E+00	*	18	0	8.61E+00	8.61E+00	*
PV	18	2.45E-03	2.31E-09	VV	18	18	0	3.54E+00	BX	18	18	0	1.50E+01	1.50E+01	*	18	0	2.06E+01	2.06E+01	*
PX	18	2.07E-03	2.74E-05	MF	18	18	0	7.07E+00	AL	18	18	0	8.92E+00	2.36E+00	*	18	0	1.22E+01	1.22E+01	*
QH	18	1.51E-02	7.84E-04	FY	18	18	0	7.40E+00	DU	18	18	0	2.17E+00	1.58E+00	*	18	0	5.99E+00	5.99E+00	*
QM	18	9.70E-03	1.78E-04	VD	18	18	0	6.78E+00	DU	18	18	0	3.18E+00	3.18E+00	*	18	0	6.55E+00	6.55E+00	*

QN	18	7.76E-03	1.19E-05	CS	18	18	0	5.96E+00	PW	18	18	0	5.08E+00	5.08E+00	*	18	0	1.03E+01	1.03E+01	*
QT	18	2.06E-03	2.02E-04	KT	18	18	1	1.36E+00	AL	18	18	0	6.55E+00	6.55E+00	*	18	1	1.00E+01	1.00E+01	*
QV	18	2.21E-02	1.33E-04	VU	18	18	0	4.47E+00	DU	18	18	0	2.07E+00	2.07E+00	*	18	0	6.78E+00	6.78E+00	*
RB	18	1.31E-02	2.43E-04	RH	18	18	0	5.07E+00	AL	18	18	0	9.26E+00	3.04E+00	*	18	0	1.06E+01	1.06E+01	*
RD	17	1.34E-02	2.13E-05	DW	18	17	0	6.10E+00	GM	18	17	0	7.02E+00	1.66E+00	*	17	0	1.15E+01	7.33E+00	*
RE	18	6.24E-03	3.24E-04	RF	18	18	0	8.94E+00	AL	18	18	0	6.00E+00	6.00E+00	*	18	0	9.04E+00	9.04E+00	*
RG	18	2.77E-02	3.37E-03	RY	18	18	0	5.17E+00	PP	18	18	0	5.10E+00	1.65E+00	*	18	0	6.04E+00	5.28E+00	*
RK	18	2.04E-03	2.98E-07	ME	18	18	0	7.35E+00	QJ	18	18	0	1.12E+01	1.12E+01	*	18	0	1.50E+01	1.50E+01	*
RN	17	3.50E-02	6.51E-04	TX	18	17	0	5.28E+00	BA	18	17	0	5.63E+00	5.63E+00	*	17	0	9.67E+00	9.67E+00	*
RP	18	1.52E-03	2.65E-07	LR	18	18	0	5.16E+00	MS	18	18	0	9.68E+00	9.68E+00	*	18	0	1.41E+01	1.41E+01	*
RS	17	3.19E-02	2.34E-05	RF	18	17	0	4.77E+00	FZ	18	17	0	5.26E+00	1.92E+00	*	17	0	1.00E+01	7.27E+00	*
RW	18	1.12E-02	6.36E-05	CU	18	18	0	8.05E+00	PW	18	18	0	3.61E+00	3.61E+00	*	18	0	8.38E+00	8.38E+00	*
SB	18	5.23E-02	5.04E-04	CE	18	18	0	3.54E+00	TO	18	18	0	4.42E+00	1.34E+00	*	18	0	8.09E+00	8.09E+00	*
SS	18	3.69E-03	4.68E-05	SN	18	18	0	6.25E+00	AR	18	18	0	7.64E+00	7.64E+00	*	18	0	1.08E+01	1.08E+01	*
ST	18	7.36E-03	6.93E-05	SD	18	18	0	5.62E+00	FZ	18	18	0	7.16E+00	5.24E+00	*	18	0	9.48E+00	6.91E+00	*
TB	18	7.80E-03	9.15E-04	TA	18	18	0	7.47E+00	OD	18	18	0	4.20E+00	4.20E+00	*	18	0	8.30E+00	8.30E+00	*
TE	18	5.79E-03	1.73E-03	TA	18	18	0	7.43E+00	OD	18	18	0	3.92E+00	0.00E+00		18	0	7.06E+00	7.06E+00	*
TG	18	1.43E-02	1.44E-03	PL	18	18	0	6.16E+00	BA	18	18	0	6.28E+00	6.28E+00	*	18	0	9.22E+00	9.22E+00	*
TN	18	5.87E-03	1.87E-06	TA	18	18	0	6.00E+00	FZ	18	18	0	9.88E+00	3.58E+00	*	18	0	1.45E+01	9.74E+00	*
TP	18	1.27E-02	5.76E-05	LL	18	18	0	1.04E+01	NM	18	18	0	6.75E+00	6.75E+00	*	18	0	1.07E+01	1.07E+01	*
TS	18	2.07E-03	1.54E-06	DI	18	18	0	7.03E+00	YA	18	18	0	1.01E+01	6.59E+00	*	18	0	1.47E+01	1.47E+01	*
UB	18	1.10E-02	3.59E-04	FY	18	18	0	1.11E+01	DU	18	18	0	1.46E+00	0.00E+00		18	0	6.46E+00	6.46E+00	*
UH	18	1.60E-02	1.28E-05	RT	18	18	0	2.82E+00	FU	18	18	0	7.27E+00	7.27E+00	*	18	0	1.14E+01	1.14E+01	*
US	18	5.04E-03	2.59E-06	UU	18	18	0	4.76E+00	AR	18	18	0	8.18E+00	8.18E+00	*	18	0	1.39E+01	1.39E+01	*

VL	18	7.43E-03	2.55E-05	VV	18	18	0	5.47E+00	TO	18	18	0	6.95E+00	6.95E+00	*	18	0	1.21E+01	1.21E+01	*
VM	18	1.13E-02	1.47E-03	CE	18	18	0	5.33E+00	DU	18	18	0	2.35E+00	2.35E+00	*	18	0	4.45E+00	4.45E+00	*
VR	18	1.68E-02	3.26E-04	VV	18	18	0	6.88E+00	DU	18	18	0	2.44E+00	2.44E+00	*	18	0	6.24E+00	6.24E+00	*
WB	18	1.86E-03	1.88E-07	WW	18	18	0	6.59E+00	AR	18	18	0	1.06E+01	1.06E+01	*	18	0	1.71E+01	1.71E+01	*
WG	18	2.49E-03	1.25E-05	WW	18	18	0	7.60E+00	AR	18	18	0	8.07E+00	8.07E+00	*	18	0	1.31E+01	1.31E+01	*
WK	18	4.62E-03	3.76E-04	MF	18	18	0	8.27E+00	AL	18	18	0	9.65E+00	3.63E+00	*	18	0	1.00E+01	1.00E+01	*
WS	18	1.14E-02	1.59E-04	WW	18	18	0	7.48E+00	GF	18	18	0	4.31E+00	4.31E+00	*	18	0	9.92E+00	9.92E+00	*
YB	18	8.81E-03	1.44E-04	CS	18	18	0	8.24E+00	PW	18	18	0	5.17E+00	5.17E+00	*	18	0	7.86E+00	7.86E+00	*
YD	18	1.63E-03	2.97E-04	LR	18	18	0	1.05E+01	BA	18	18	0	6.65E+00	6.65E+00	*	18	0	1.01E+01	1.01E+01	*
YH	18	7.27E-05	3.47E-08	CG	18	18	0	9.39E+00	MS	18	18	0	1.39E+01	1.39E+01	*	18	0	1.79E+01	1.79E+01	*
YJ	18	8.34E-04	1.66E-08	MI	18	18	0	3.80E+00	QJ	18	18	0	1.31E+01	1.31E+01	*	18	0	1.86E+01	1.86E+01	*
YN	18	5.43E-04	7.62E-05	CB	18	18	1	1.63E+00	AO	18	18	0	8.28E+00	8.28E+00	*	18	2	6.93E+00	6.93E+00	*
YU	18	2.39E-03	8.00E-04	CM	18	18	0	1.13E+01	OD	18	18	0	4.66E+00	4.66E+00	*	18	0	7.99E+00	7.99E+00	*
YY	18	2.74E-02	1.03E-04	LU	18	18	0	8.13E+00	YA	18	18	0	3.26E+00	3.26E+00	*	18	0	1.02E+01	1.02E+01	*
GL	18	2.13E-02	2.13E-02		0	0	0	0.00E+00	NM	18	18	0	2.13E+00	2.13E+00	*	0	0	0.00E+00	0.00E+00	
JY	18	5.60E-02	5.60E-02		0	0	0	0.00E+00	NM	18	18	0	6.43E+00	6.43E+00	*	0	0	0.00E+00	0.00E+00	
MJ	18	1.71E-03	1.71E-03		0	0	0	0.00E+00	NM	18	18	0	7.07E+00	7.07E+00	*	0	0	0.00E+00	0.00E+00	
PY	18	4.94E-02	4.94E-02		0	0	0	0.00E+00	NM	18	18	0	6.61E+00	6.61E+00	*	0	0	0.00E+00	0.00E+00	

Table S6: GLMM results for probability of close relatedness (r ≥ 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)	0.181	0.742				
Test variables						
Male is alpha	9.178	2.574	1	13.576	0.0002	***
Spatial proximity	0.970	0.179	1	13.576	0.0002	***
Age proximity	-2.166	0.544	1	10.384	0.0013	**
Control variables						
# of adult males	-0.056	0.213	1	0.062	0.8031	ns
# of adult females	0.858	0.231	1	6.751	0.0094	**
Infant is male	-0.308	0.273	1	1.064	0.3024	ns

Table S7: GLMM results for probability of close relatedness (r ≥ 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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