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ORIGINAL ARTICLE

Inbreeding risk, avoidance and costs in a group-living primate, *Cebus capucinus*

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Abstract Documenting inbreeding and its potential costs in wild populations is a complicated matter. Early infant death before genetic samples can be collected limits the ability of researchers to measure fitness costs, and pedigree information is necessary to accurately estimate relatedness between breeding individuals. Using data from 25 years of research from the Lomas Barbudal Capuchin Monkey Project, and a sample of 109 females that have given birth, we find that despite frequent co-residency of adult opposite-sexed individuals, capuchins produce offspring with close kin (i.e., related at the half-sibling level or higher) less often than would be expected in the absence of inbreeding avoidance. We do not find support for alternative, non-behavioral explanations for this pattern and thus argue for mate choice. Furthermore, we find evidence for fitness costs among inbred animals in the form of delayed female age at first birth but not significantly higher juvenile mortality. Further research is necessary in order to determine the mechanisms by which individuals develop sexual aversion to close kin. Through a combination of demographic records, maternal pedigrees, and genetically determined paternity, this study provides a detailed study of inbreeding and inbreeding avoidance in a well-studied mammal population. This study provides (1) evidence that capuchin monkeys avoid mating with close kin at both the level of parent-offspring and half sibling and (2) evidence of fitness costs to inbreeding in the form of delayed first age at reproduction.

Keywords Inbreeding avoidance · Inbreeding depression · Primates · Capuchin monkeys

Introduction

Ever since Charles Darwin's time, attention has been drawn to the deleterious effects associated with inbreeding (Darwin 1868, 1876). Studies across taxa ranging from angiosperms to birds and mammals have illustrated a range of potential costs that can arise when close kin produce offspring (Charlesworth and Charlesworth 1987; Pusey and Wolf 1996; Crnokrak and Roff 1999; Keller and Waller 2002). For example, a review of breeding records in captive primate colonies found higher infant mortality of inbred offspring in 15 of the 16 colonies investigated (Ralls and Ballou 1982). Studies of wild mammal populations also often show higher costs (e.g., lower juvenile weight or lower juvenile survivorship) than those found in captive populations (Crnokrak and Roff 1999). Inbred white-footed mice, *Peromyscus leucopus noveboracensis*, in a mark-release capture experiment had higher mortality rates than non-inbred individuals, and inbred males showed continual weight loss throughout the experiment even though inbred and non-inbred individuals did not

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differ in weight at the time of their release (Jiménez et al. 1994). In the hermaphroditic land snail, *Arianta arbustorum* (*L.*), inbred and outbred land snails did not differ in their survival when kept in laboratory conditions, but when raised in a garden, inbred offspring suffered significantly higher mortality than outbred offspring (Chen 1993).

In general, inbreeding in the wild has been considered maladaptive (Pusey and Wolf 1996), particularly for mammalian females who because of their greater investment in each offspring bear a higher cost than males if offspring are not viable (Trivers 1972). However, 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 (Parker 1979; Smith 1979; Waser et al. 1986; Lehmann and Perrin 2003; Kokko and Ots 2006; Jamieson et al. 2009; Puurtinen 2011; Lehtonen and Kokko 2015). Thus, evolutionary theory can also predict a tolerance for, or even a preference for, some forms of kin as mating partners. Some studies do show such preferences. For example, Japanese quail, *Coturnix japonica*, prefer unfamiliar first cousins over familiar and unfamiliar siblings, as well as over unfamiliar unrelated partners (Bateson 1982), and African cichlids, *Pelvicachromis taeniatus*, also show mate preferences for unfamiliar close kin over non-kin (Thünken et al. 2007).

Investigation of the prevalence and impact of inbreeding in wild populations is challenging. Pedigree information is often lacking for individuals because of unknown or genetically unsampled parents. Though inferences of family relationships via the use of microsatellite-derived metrics in the absence of known pedigrees are common, studies using these may underestimate the impact of inbreeding depression, because microsatellite-derived metrics have a high rate of misclassification of dyadic relationships (Pemberton 2004, 2008; Szulkin et al. 2013). Even when relationships can be accurately classified, inbreeding avoidance would only be expected in cases where there is a high variance in relatedness among potential parent dyads (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). In song sparrows, *Melospiza melodia*, offspring produced by close kin (i.e., full siblings) are less likely to survive their first year (Keller 1998). If inbred offspring are less viable than outbred offspring, early fetal losses and infant deaths before genetic sample collection takes place can mask many of the costs to inbreeding and inflate the apparent frequency of inbreeding avoidance.

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 and Fedigan 2006; Muniz et al. 2006, 2010; Godoy et al. 2016). These males also often retain their top rank for tenures exceeding 5 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 (Jack et al. 2011) and if their fathers are still present (SEP 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 (Godoy 2010), and males have been known to become alphas of their own natal groups (Perry et al. 2012). Inbreeding avoidance in capuchins has been documented between females and alpha males (Muniz et al. 2006, 2010; Godoy et al. 2016), with female relatedness to alpha males (i.e., whether they are a daughter or granddaughter) as the largest factor negatively affecting the probability that an alpha male is the sire of an infant (Muniz et al. 2010; Godoy et al. 2016). Whether inbreeding avoidance extends to more distant kin, however, is still unknown, as are the possible fitness costs to inbreeding. The availability of 25 years of demographic data, maternal pedigrees, and genetic paternity information from the Lomas Barbudal Capuchin Monkey Project allow us to investigate inbreeding and its avoidance in this wild primate population.

First, we look at how often breeding-age females reside with adult male kin in order to assess the potential for inbreeding in the population. Second, we investigate whether inbreeding avoidance is limited by the level of relatedness between potential mates. We predict more pronounced inbreeding avoidance at higher levels of relatedness, since costs to inbreeding will presumably be attenuated at lower levels or relatedness. Third, we test alternative non-behavioral explanations for the lower than expected occurrences of inbreeding between alpha males and their female kin in capuchins. If fetal loss or early infant death of non-genotyped inbred infants explained the rarity of close inbreeding events, then one would predict (1) higher infant mortality rates among infants born to females residing in groups where the alpha is a close relative and/or (2) longer inter-birth intervals for females residing in groups where the alpha is a close relative, since miscarriages would increase the time between infant births. Finally, we look for evidence of fitness costs to inbreeding, to test the hypothesis that inbreeding is costly in capuchins. Specifically, we test whether there are higher juvenile mortality rates and/or delayed female age at first birth for inbred versus outbred individuals.

Methods

Field site and study species

The subjects of this study are individually recognized, habituated white-faced capuchin monkeys from the Lomas Barbudal Biological Reserve and adjacent public and private lands in Guanacaste, Costa Rica (hereafter referred to as "Lomas Barbudal"). This wild population has been under observation since 1990 with continuous monitoring since 2002 (Perry 2012; Perry et al. 2012). Behavioral data were available from 11 study groups: four groups were originally habituated, and seven additional groups formed by fissions (Fig. 1). It was not possible to record data blind because our study involved focal animals in the field.

Estimating degrees of relatedness using pedigrees

Paternity information was available from previous work (Muniz et al. 2006; Godoy et al. 2016). Briefly, we have genotyped 334 capuchins from the Lomas Barbudal population using 18 microsatellites (Muniz and Vigilant 2008) and DNA obtained primarily through non-invasively collected fecal samples and occasional sampling of tissue samples from dead capuchins. We have determined paternity for 253 individuals in our study population, and for 248 individuals we knew the identity of both their parents. See Supplementary Information Table S1 for information on the pedigree depth of genotyped individuals from our study groups ($n = 310$).

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; Van Horn et al. 2008). The mean number of alleles per locus in our population is 5.33 (range 3–9) (Godoy et al. 2016). This level of polymorphism even in a population such as the great weed warbler, *Acrocephalus arundinaceus*, with a relatively high variance in relatedness, is estimated to explain only a small proportion of the variance (~0.05) in marker-based relatedness estimates (Csilléry et al. 2006). We therefore used pedigree information to calculate estimated coefficients of relatedness for our dyads using the DESCENT software (https://code.google.com/archive/p/descent/).

When two members of a group are genotyped, we can be confident as to whether or not they are a parent-offspring dyad, but all other kinship categories require more information on the parentage of the members of the dyad. Since incomplete pedigrees (particularly for older natal females born before habituation of their natal groups) limit our ability to generate precise coefficients of relatedness, we binned each dyad into one of four relatedness categories and treated them as categorical variables (Supplementary Information Fig. S1). These included one non-kin category and three categories of kin.

Category 0 included all dyads with inferred coefficients of relatedness of 0. Immigrant males of unknown origin were considered unrelated to natal females, unless genetic paternity assignment showed otherwise. However, some immigrant males that were assigned as non-kin of females may in fact have been paternal uncles (or more distant kin) of females residing in groups with their alpha father, since male white-faced capuchins typically emigrate with natal kin (Jack and Fedigan 2004a, b; Muniz 2008; Perry et al. 2012; Perry 2012; Wikberg et al. 2014).

Category 1 included dyads with inferred coefficients of relatedness greater than 0 but lower than 0.25. 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 this category. This compensates for the tendency to miscategorize individuals related at less than the half-sibling level as unrelated as a result of the use of incomplete pedigrees of fewer than four generations (Csilléry et al. 2006).

Category 2 included dyads with inferred coefficients of relatedness greater than or equal to 0.25 but lower than 0.5. Half sibling identification requires some parentage information for a dyad (two generation pedigree), while identification of grandparents, grandoffspring, full nephew/nieces, full uncles/aunts, and double full first cousins requires some information on grandparents (three generation pedigree). We do note that we have yet to detect any double first full cousins in our population.

Category 3 included dyads with inferred coefficients of relatedness equal to or greater than 0.5. This category includes parent-offspring and full sibling dyads. Parent-offspring identification requires only that both members of a dyad are genotyped (one generation pedigree), while full sibling identification requires some parentage information for a dyad (two-generation pedigree).

Group composition during infant conception windows

For dates prior to July 2006, census data were extracted from the daily behavioral data files of observers who were in the field. Starting in July 2006, observers systematically kept census records of which individuals were present in a group during an observation day and noted any wounds, suspected pregnancies, and births.

Using the known gestation lengths of wild capuchins (average 158, SE 8 days, Carnegie et al. 2011), we generated conservative conception windows for births. These windows were three standard errors (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 determined which males were

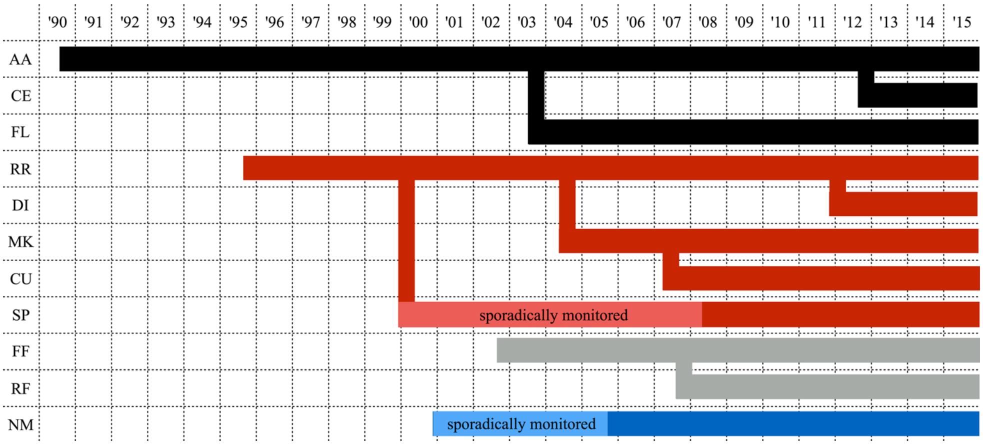

Fig. 1 Study groups. Shown are four groups and their seven fission products

present in a study group during each conception window, and thus which males were available as potential mates for each infant's mother. All males 6 years of age or older were considered potential sires of infants, since the youngest sire in the Lomas Barbudal population was 6.25 years old at the time of his infant's conception (Godoy et al. 2016).

Inbreeding risk

We assembled group composition data on 391 conceptions, 343 of which occurred during periods with no turnover at the alpha male position (i.e. during stable alpha tenures). These datasets were used to determine the availability of male kin for females during the conception windows of their infants. Because only the relationship between the mother and potential mates was of interest for assessing paternity risk, our analysis was not constrained by whether or not infants were genotyped. We used this dataset to determine the availability of male kin during the first half of the female reproductive career to see how frequently adult females reside with close adult male kin.

Inbreeding avoidance

There were 193 genotyped infants of known parentage that were conceived during periods of stability at the alpha male position. We used this information to determine the effect of categorical relatedness on the probability that an alpha male is the father of an infant, and on the probability that a subordinate male is the father of an infant.

Inbreeding costs

Juvenile mortality

In a sample of 399 pregnancies, 107 (26.8 %) ended either in miscarriage or with infant death before genetic samples could be collected, but only 5.6 % ($n = 6$) of these may have died at an age of older than 1 year. Therefore, we did not consider infants that died during their first year of life in our assessment of juvenile mortality rates. This was in order to avoid potential biases in the dataset due to non-genotyped infants, as well as to avoid inclusion of infant deaths due to infanticide after changes of the alpha male. Juvenile mortality was instead measured as the proportion of infants that survived from 1 year of age into their fourth year of life (before male migration from groups was likely to bias our mortality data).

Our dataset consisted of 186 infants born before 2011 that survived their first year of life and for which we knew the identity of their father and mother. We used this data to test for higher mortality in inbred juveniles.

Female age at first birth

We had a sample of 58 females for which we could estimate age at first birth with an accuracy of plus or minus 90 days. We used this dataset to look for costs of inbreeding in the form of delayed age at first reproduction.

Generalized linear mixed models

Statistical analyses were run in R v.3.2.0 (R Core Team 2015) 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") or (2) with Gaussian error structure on models involving a continuous response. 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 (VIF) (Field 2005), which measure the degrees to which variance of the estimated regression coefficients are inflated compared to when the predictor variables are not collinear. 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 and Schielzeth 2011) using a likelihood ratio test (Dobson and 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

Prevalence of male kin during the first half of the female reproductive career

Co-residence with male kin

Of the 95 females for which we had group composition data during their fifth year of life, 42.1 % still lived with their fathers at age 5 years, while 31.6 % lived with at least one adult paternal half brother (Supplementary Information Table S2). Even at 10 years of age, 20.3 % of females still co-resided with their father and 42.3 % with a paternal half brother. 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.

Co-residence with alpha male kin

Because alpha males sire the majority of infants in capuchin groups, we looked at how often females (during the early part of their reproductive careers) resided with alpha males that were related to them. We found that a large proportion of the females at Lomas Barbudal had the potential to breed with related alpha males, particularly fathers and paternal half brothers (Supplementary Information Table S3). For example, at 5 years of age, 30.1 % of females lived with an alpha father and 9.5 % with an alpha paternal half brother. Co-residency with alpha fathers decreased over time, while co-residency with alpha paternal half brothers remained relatively constant and co-residency with unrelated alpha males increased through the first half of the female reproductive career (i.e., ages 5–15).

Distribution of male kin during conceptions

Most conceptions occurred while related ($r > 0$) adult males were co-resident with the females; out of 391 conceptions for which we had group composition data, 290 (74.2 %) occurred when the mother had adult male kin in the group. Females resided with at least one paternal half brother in 30.2 % of cases and with their father in 16.4 % (Table 1, column a).

Risk of inbreeding with alpha males

Of the 391 conceptions in our dataset, 343 (87.7 %) occurred during stable alpha tenures. Of these conceptions, 37.9 % (130 of 343) occurred when the female was related to the alpha male (Table 1, column b). Since alpha males are the primary breeding males in capuchins, this means that approximately one in every three conceptions during stable alpha tenures had the potential to result in an inbred offspring. Furthermore, for 31.5 % ($n = 41$) of the situations where females were related to the alpha male, there were no unrelated ($r = 0$) adult males available to females.

Effect of categorical relatedness on probability that an alpha male is the father of an infant

Having established that females commonly have adult male kin available in their groups, we next used our dataset of 193 conceptions during stable alpha tenures and for which the infants were genotyped to investigate the share of paternities to alpha males when the mother is a relative or not. Alpha males sired 141 (73.1 %) of the 193 genotyped infants that were conceived during stable periods, including 90.1 % (109 of 121) of offspring born to unrelated females. For infants born to related females, the percentage sired was less and varied by categorical relatedness (Table 2). In 40.6 % ($n = 13$ of 32) of the cases of inbreeding between females and alpha males, there were no unrelated males available for the female to choose from.

Furthermore, we used a GLMM to explore the significance of categorical relatedness on the probability of an alpha male being the sire of an offspring. Our dataset was comprised of conceptions involving 69 mothers and 23 alpha males from nine groups. 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 full model was significantly different from the null model, which consisted of only control variables and random effects ($\chi^2_3 = 46.747$, $P < 0.0001$).

Relative to the $r = 0$ relatedness category, alpha males sired significantly fewer offspring with females in the $r \geq 0.5$ and $0.25 \leq r < 0.5$ categories (Table 3). Alpha males were not significantly less likely to sire offspring with females in the

Table 1 Availability of adult male kin during conception windows and the risk of inbreeding between females and alpha males. The table shows (a) the number of conceptions (from a total pool of $n = 391$) for which females had at least one adult male available that fit into a particular relatedness or kinship category and (b) conceptions during stable alpha tenures ($n = 343$), categorized by categorical relatedness and kinship between mothers and alpha males

Relatedness or kinship	No. of conceptions (%)	
	Availability of male kin	Inbreeding risk with alpha
Relatedness category		
0, $r = 0$	349 (89.3)	213 (62.1)
1, $0 < r < 0.25$	203 (51.9)	41 (12)
2, $0.25 \leq r < 0.5$	173 (44.2)	42 (12.2)
3, $r \geq 0.5$	123 (31.5)	47 (13.7)
Kinship category		
Non-kin	349 (89.3)	213 (62.1)
Grandfather	6 (1.5)	5 (1.5)
Paternal half brother	118 (30.2)	32 (9.3)
Maternal half brother	41 (10.5)	2 (0.6)
Full brother	30 (7.7)	0 (0)
Son	48 (12.3)	2 (0.6)
Father	64 (16.4)	45 (13.1)

$0 < r < 0.25$ category than they were to sire infants with unrelated females.

Effect of categorical relatedness on probability that a subordinate is the father of an infant

Since subordinate males also sire offspring, we investigated the pattern of conceptions by females and subordinate males. 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. There was no inbreeding between females and subordinate males related at the level of $r \geq 0.5$ (Table 4), though there were 20 such dyads ($n = 14$ unique) in our dataset (sons $n = 8$, fathers $n = 2$, full brothers $n = 10$).

We used a GLMM to explore the significance of categorical relatedness on the probability of a subordinate male being the sire of an offspring. From our 52 subordinate-sired infants, we generated a dataset of 313 dyads formed between 30 females and 59 subordinate adult males. The response variable was whether or not a subordinate male was the father of an infant (yes/no). The identities of the mothers, subordinate males, and infants were included as random effects. 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 full model was significantly different from the null model, which consisted of only control variables and random effects ($\chi^2_3 = 10.557$, $P < 0.0144$).

Relative to the $r = 0$ relatedness category, subordinate males sired significantly fewer offspring with females in the $r \geq 0.5$ and $0.25 \leq r < 0.5$ categories, after controlling for the number of adult males and adult females in the group (Table 5). 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.

Alternative, non-behavioral explanations for paternity patterns

The significantly lower occurrence of offspring produced by relatives can be explained as an outcome of inbreeding avoidance or, alternatively, a scenario in which matings between kin

Table 2 Percentage of offspring sired by alpha males, categorized by categorical relatedness between infants' mothers and alpha males. Data come from 193 conceptions during stable alpha tenures

Relatedness category	Percentage	Number	Inbreeding events where females did not have unrelated subordinate males available
0, $r = 0$	90.1	109 of 121	–
1, $0 < r < 0.25$	78.9	15 of 19	6 of 15 (40.0 %)
2, $0.25 \leq r < 0.5$	65.0	13 of 20	7 of 13 (53.9 %)
3, $r \geq 0.5$	12.1	4 of 33	0 of 4 (0 %)

Table 3 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
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					
No. of adult males	−0.381	0.161	1	4.595	*0.0321*
No. of adult females	−0.168	0.170	1	0.971	0.3244

Significant effects are shown in *italics*

SE standard error, *LRT* likelihood ratio test

do occur, but resultant progeny are less fit and die either during gestation or soon after birth before genetic samples can be collected for paternity determination. This scenario predicts that age at first birth should be higher and inter-birth intervals longer for females residing with a related alpha male as compared to when the alpha male is unrelated, as a result of higher incidences of miscarriages resulting from inbreeding events. Furthermore, first-year infant mortality rates should be higher for cases in which females were co-resident with a related alpha male (i.e., the primary breeding male) as compared to when the alpha male is unrelated. Such a result would suggest higher infant mortality rates for inbred offspring (before genetic samples could be collected). However, we found no support for any of these three possibilities and thus no support for the alternative (non-behavioral) explanation for paternity patterns (See Supplementary Information Tables S4, S5, and S6).

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) was the product of some degree of inbreeding (Table 6). For 52 out of 53 of the inbred offspring, we had information on the group composition around the time of their conception. In 44.2 % (n = 23) of the inbreeding cases, the mothers did not have any unrelated (r = 0) males available in their group. For the remaining 29 cases, 20 of the infants were sired by the alpha of the group (69.0 %) and the remaining 9 were sired by males that were either more distantly related to the mother (n = 8) or as equally related to the mother (n = 1) as was the alpha male.

Table 4 Percentage of offspring sired by subordinate males, categorized by the categorical relatedness between infants' mothers and subordinate males. Data come from 52 conceptions during stable alpha tenures where a subordinate male was the sire of the infant

Relatedness category	Percentage	Number
0, $r = 0$	65.4	34 of 52
1, $0 < r < 0.25$	17.3	9 of 52
2, $0.25 \leq r < 0.5$	15.4	8 of 52
3, $r \geq 0.5$	0.0	0 of 52

Table 5 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, $0.25 \leq r < 0.5$	−1.579	0.572	1	7.688	*0.0056*
3, $r \geq 0.5$	−17.087	[a]	1	5.742	*0.0166*
Control variables					
No. of adult males	−0.275	0.133	1	3.824	0.0505
No. of adult females	−0.077	0.114	1	0.449	0.5026

Significant effects are shown in *italics*

SE standard error, *LRT* likelihood ratio test

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

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 or likely to have been the alpha during the infant conception window. There was one case of mother-son inbreeding. It involved a male that migrated into and became the alpha of

Table 6 Genotyped infants, categorized by kinship and relatedness between their parents

	Number of infants	Percentage
Relatedness category of parents		
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 of parents		
Non-kin	195	78.6
Other kin	25	10.1
Full niece-uncle	1	0.4
Full aunt-nephew	0	0.0
Granddaughter-grandfather	0	0.0
Paternal half siblings	22	8.9
Maternal half siblings	0	0.0
Full siblings	0	0.0
Mother-son	1	0.4
Daughter-father	4	1.6

a fission product of his natal group where his mother still resided. The four cases of father-daughter inbreeding involved two dyads, which each produced offspring twice.

We have documented only one instance of extra-group paternity in Lomas Barbudal. Even in this case, the father of her infant was a familiar paternal half brother (he emigrated from her natal group) that was the alpha male in a nearby group. Thus, it appears that extra-group paternity is extremely rare at Lomas Barbudal and does not constitute an alternative female reproductive strategy for preventing inbreeding.

Potential costs to inbreeding

Mortality in inbred versus non-inbred juveniles

With our sample of 186 infants of known parentage, we tested for higher mortality in inbred versus non-inbred individuals. We found that mortality rates doubled for juveniles in the $0.25 \leq r < 0.5$ and $r \geq 0.5$ categories compared to the $r = 0$ category but that mortality rates for the $0 < r < 0.25$ were comparable to those of the $r = 0$ category (Table 7). However, the numbers of individuals dying before the age of four were small and a GLMM incorporating the identity of each infant's mother as a random effect revealed only a marginal effect of relatedness on mortality between ages one and four when comparing $r \geq 0.25$ to $r < 0.25$ ($\chi^2_1 = 2.916$, $P = 0.0877$).

Delayed age at first birth in inbred versus non-inbred females

With our sample of 58 females with accurate estimates of their ages at first birth, we tested for older ages at first birth in inbred females compared to outbred females. To do this, we ran a GLMM with female age as the response variable. Since our sample sizes were small, our test variable was relatedness at any level between the parents of inbred offspring. The identity of each female's group of residence was added in as a random effect. The full model was significantly different from the null model ($\chi^2_1 = 7.046$, $P = 0.0079$). In other words, inbred females ($\text{age}_{avg} = 6.73$, SE = 0.177, $n = 12$) gave birth significantly later than did non-inbred females ($\text{age}_{avg} = 6.246$, SE = 0.08, $n = 46$) (Fig. 2).

Discussion

Overall, we find that females in the Lomas Barbudal population of capuchins frequently co-reside with close adult male kin, that behavioral avoidance of close inbreeding occurs between individuals related at the half-sibling and higher level, and that there is a cost associated with inbreeding.

Table 7 Juvenile mortality by categorical relatedness of parents

Relatedness category	Deaths	Number	Mortality (%)
0, $r = 0$	17	135	12.6
1, $0 < r < 0.25$	3	25	12.0
2, $0.25 \leq r < 0.5$	6	22	27.3
3, $r \geq 0.5$	1	4	25.0

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; Godoy et al. 2016). 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 fewer 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. Co-resident male-female pairs related at $0 < r < 0.25$ bred less often than unrelated pairs, but this difference was not significant.

In collared flycatchers, *Ficedula albicollis*, inbreeding pairs have lower hatching rates than outbreeding pairs, and the offspring that are produced have lower fledging skeletal weight and higher post-fledging mortality rates than outbred offspring (Kruuk et al. 2002). In theory, the reduced viability, early mortality, and consequent absence of inbred offspring in a population may lead to the inference that such individuals are not produced at all, potentially leading to the inference of behavioral inbreeding avoidance by related parents. If matings between close kin do occur at higher than apparent

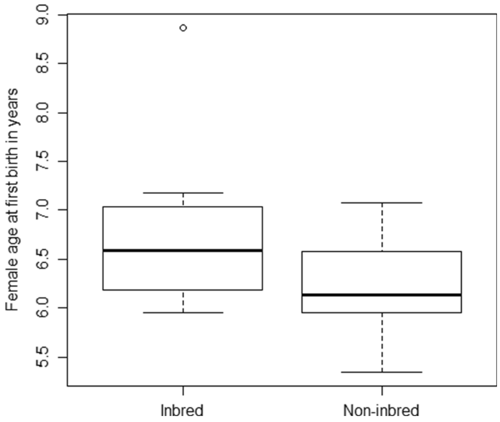

Fig. 2 Female age at first birth, categorized by whether or not females are inbred. The *boxes* plot the first, second (median), and third quartiles. The *whiskers* indicate the minimum and maximum values falling within 1.5 times the inter-quartile range

frequencies in capuchins but result in either early stage fetal loss or early infant death (i.e., before genetic samples can be collected), then higher infant mortality rates and markers for miscarriages should be evident among potentially inbreeding pairs. However, we found that infant mortality rates in stable groups (i.e., where no alpha turnover took place) 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 apparent 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 makes sense in this particular population, given than over 42.1 % 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 was 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 also engages in father-daughter inbreeding avoidance in the wild (Vigilant et al. 2015).

Inbreeding at the level of paternal half siblings (8.2 % of births) and more distantly related kin (10.2 %) was more common than inbreeding at the full-sibling level (2 %). Dyads related at $0.25 \leq r < 0.5$ appeared to avoid inbreeding, but to a more limited degree than parent-offspring and full sibling dyads, whereas 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. In the house mouse, *Mus musculus domesticus*, the offspring of full-sibling pairs showed lowered resistance to experimentally induced *Salmonella* infections compared to outbred offspring, having higher mortality and lower bacterial clearance; interestingly though, the offspring of full first cousin pairs did not differ from outbred individuals in their resistance to *Salmonella* infection, at least not while under laboratory conditions (Ilmonen et al. 2008).

If parent-offspring matings produce less viable young, then father-daughter inbreeding avoidance may be a form of reproductive concession that, while reducing the overall level of reproductive skew toward dominant males, 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. 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).

Our current data suggest that there is a cost to inbreeding, as inbred females have a later age at first birth than do non-inbred females. Delayed age at first birth in inbred females has also been documented in captive Barbary sheep (*Ammotragus lervia sahariensis*) (Cassinello and Alados 1996). Contrastingly, 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. In the hermaphroditic land snail, the number of eggs laid by outbred and inbred pairs (full-sibling pairs) do not differ significantly, but the proportion of eggs that hatch and the number of hatchlings produced is significantly lower for inbreeding pairs (Chen 1993). It may be that in capuchins, inbred and outbred females do not differ in when they first become pregnant, but instead differ in the likelihood of a successful pregnancy. Whether the reproductive delay in inbred capuchins is the result of slowed sexual maturation or the result of early miscarriages is unknown. Future research comparing the inter-birth intervals of inbred versus non-inbred females would help differentiate between the two possibilities, as would hormonal monitoring of female reproductive states. At present, we do not have sufficient data on inter-birth intervals or the onset of cycling in inbred females to address these issues.

Although not statistically significant, our findings give some suggestion of more severe costs to inbreeding in the form of higher juvenile mortality for inbred offspring. Interestingly, in wild cactus finches, *Geospiza scandens*, inbred individuals show lower juvenile survivorship compared to non-inbred individuals, but only when looking at years with low rainfall (low food availability) or large population sizes (higher competition) (Keller et al. 2002). Other studies have also found environmental specific costs to inbreeding (e.g., Jiménez et al. 1994; Keller et al. 1994; Henry et al. 2003). The population growth dynamics of wild capuchins are known to be susceptible to environmental stressors such as rainfall deficits accompanying El Niño events (Campos et al. 2015). Future models of inbreeding depression in capuchins may benefit from the incorporation of measures of environmental stressors.

To date, genetic analyses of paternity in our population are indicative of avoidance of close inbreeding, particularly at the level of parent-offspring, and perhaps a tolerance for, but not preference for, inbreeding with more distant kin. Admittedly though, our ability to generate accurate estimated coefficients of relatedness below the level of half siblings is limited. Future research analyzing the mate preferences of dyads with deeper known pedigrees may help shed light on the precise limits to inbreeding avoidance in this population. Furthermore, researching potential mechanisms of kin recognition in capuchins will also help establish a clearer picture of why matings between certain categories of kin (i.e., paternal half siblings) are more common than others.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The UCLA Institutional Animal Care and Use Committee (IACUC), known as the Chancellor's Animal Research Committee (ARC), approved the protocol (ARC # 2005-084).

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