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1Inbreeding risk, avoidance and costs in a group-living primate, *Cebus capucinus*

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31

32**Abstract:** Documenting inbreeding and its potential costs in wild populations is a
33complicated matter. Early infant death before genetic samples can be collected limits the
34ability of researchers to measure fitness costs, and pedigree information is necessary to
35accurately estimate relatedness between breeding individuals. Using data from 25 years of
36research from the Lomas Barbudal Capuchin Monkey Project, and a sample of 109 females
37that have given birth, we find that despite frequent co-residency of adult opposite-sexed
38individuals, capuchins produce offspring with close kin (i.e. related at the half sibling level
39or higher) less often than would be expected in the absence of inbreeding avoidance. We do
40not find support for alternative, non-behavioral explanations for this pattern and thus
41argue for mate choice. Furthermore, we find evidence for fitness costs among inbred
42animals in the form of delayed female age at first birth, but not significantly higher juvenile
43mortality. Further research is necessary in order to determine the mechanisms by which
44individuals develop sexual aversion to close kin.

45

46**Keywords:** inbreeding avoidance, inbreeding depression, primates, capuchin monkeys

48Significance Statement: Through a combination of demographic records, maternal
 49pedigrees, and genetically determined paternity, this study provides a detailed study of
 50inbreeding and inbreeding avoidance in a well-studied mammal population. This study
 51provides (1) evidence that capuchin monkeys avoid mating with close kin at both the level
 52of daughter-father and half sibling, and (2) evidence of fitness costs to inbreeding in the
 53form of delayed first age at reproduction.

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91

92INTRODUCTION

93 Ever since Charles Darwin's time, attention has been drawn to the deleterious effects
94associated with inbreeding (Darwin 1868, 1876). Studies across taxa ranging from
95angiosperms to birds and mammals have illustrated a range of potential costs that can arise
96when close kin produce offspring (Charlesworth and Charlesworth 1987; Pusey and Wolf
971996; Crnokrak and Roff 1999; Keller and Waller 2002). For example, a review of breeding
98records in captive primate colonies found higher infant mortality of inbred offspring in 15
99of the 16 colonies investigated (Ralls and Ballou 1982). Studies of wild mammal
100populations also often show higher costs (e.g. lower juvenile weight or lower juvenile
101survivorship) than those found in captive populations (Crnokrak and Roff 1999). For
102instance, inbred white-footed mice, *Peromyscus leucopus noveboracensis*, in a mark-release
103capture experiment had higher mortality rates than non-inbred individuals, and inbred
104males showed continual weight loss throughout the experiment even though inbred and
105non-inbred individuals did not differ in weight at the time of their release (Jiménez et al.
1061994). In the hermaphroditic land snail, *Arianta arbustorum* (L.), inbred and outbred land
107snails did not differ in their survival when kept in laboratory conditions, but when raised in
108a garden, inbred offspring suffered significantly higher mortality than outbred offspring
109(Chen 1993).

110 In general, inbreeding in the wild has been considered maladaptive (Pusey and Wolf
1111996), particularly for mammalian females who bear a higher cost than males if offspring
112are not viable, because of their greater initial investment in each offspring (Trivers 1972).
113However, models based on evolutionary theory also predict that there is an optimal degree
114of similarity between parents that helps keep co-adapted genes in a population together

115('optimal outbreeding', Bateson 1983), and that some degree of inbreeding should be
116allowed or tolerated when the inclusive fitness benefits of mating with kin or the costs of
117finding alternative mates outweigh any potential costs to infant fitness (Parker 1979; Smith
1181979; Waser et al. 1986; Lehmann and Perrin 2003; Kokko and Ots 2006; Jamieson et al.
1192009; Puurtinen 2011; Lehtonen and Kokko 2015). Thus, evolutionary theory can also
120predict a tolerance for, or even a preference for, some forms of kin as mating partners. Some
121studies do show such preferences. For example, Japanese quail, *Coturnix japonica*, prefer
122unfamiliar first cousins over familiar and unfamiliar siblings, as well as over unfamiliar
123unrelated partners (Bateson 1982), and African cichlids, *Pelvicachromis taeniatus*, also
124show mate preferences for unfamiliar close kin over nonkin (Thünken et al. 2007).

125 Investigation of the prevalence and impact of inbreeding in wild populations is
126challenging. Pedigree information is often lacking for individuals because of unknown or
127genetically unsampled parents. Though inferences of family relationships via the use of
128microsatellite-derived metrics in the absence of known pedigrees are common, studies
129using these may underestimate the impact of inbreeding depression, because
130microsatellite-derived metrics have a high rate of misclassification of dyadic relationships
131(Pemberton 2004, 2008; Szulkin et al. 2013). Even when relationships can be accurately
132classified, inbreeding avoidance would only be expected in cases where there is a high
133variance in relatedness among potential parent dyads (Szulkin et al. 2013).

134 A further hindrance in estimating the impact of inbreeding in the wild is the large
135proportion of offspring that die before genetic samples can be collected. For example, in
136savannah baboons, 35% of pregnancies end in either miscarriage or early infant death
137(Beehner et al. 2006a, b). In song sparrows, *Melospiza melodia*, offspring produced by close

138kin (i.e. full siblings) are less likely to survive their first year (Keller 1998). If inbred
139offspring are less viable than outbred offspring, early fetal losses and infant deaths before
140genetic sample collection takes place can mask many of the costs to inbreeding, and inflate
141the apparent frequency of inbreeding avoidance.

142 White-faced capuchin monkeys, *Cebus capucinus*, are an excellent species in which to
143study inbreeding avoidance for several reasons. In capuchins, socially dominant alpha
144males achieve a virtual monopoly on reproduction, at least during the early stages of their
145tenures (Jack and Fedigan 2006; Muniz et al. 2006, 2010; Godoy et al. 2016). These males
146also often retain their top rank for tenures exceeding five years, which corresponds to the
147age at which their daughters reach reproductive age. Importantly, long male alpha tenures
148facilitate co-residency of paternal half siblings and full siblings of varied ages, as natal
149males are less likely to migrate out of their group if there is stability in the alpha position
150(Jack et al. 2011) and if their fathers are still present (Perry et al. 2017). Although male
151migration from natal groups decreases the likelihood of inbreeding by siblings, adult and
152sub-adult males often do co-reside with their sexually mature sisters (Godoy 2010), and
153males have been known to become alphas of their own natal groups (Perry et al. 2012).
154Inbreeding avoidance in capuchins has been documented between females and alpha males
155(Muniz et al. 2006, 2010; Godoy et al. 2016), with female relatedness to alpha males (i.e.
156whether they are a daughter or granddaughter) as the largest factor negatively affecting the
157probability that an alpha male is the sire of an infant (Muniz et al. 2010; Godoy et al. 2016).
158Whether inbreeding avoidance extends to more distant kin, however, is still unknown, as
159are the possible fitness costs to inbreeding in the population. The availability of 25 years of
160demographic data, maternal pedigrees, and genetic paternity information from the Lomas

161Barbudal Capuchin Monkey Project allow us to investigate inbreeding and its avoidance in
162this wild primate population.

163 First, we look at how often breeding-age females reside with adult male kin in order
164to assess the potential for inbreeding in the population. Second, we investigate whether
165inbreeding avoidance is limited by the level of relatedness between potential mates. We
166predict more pronounced inbreeding avoidance at higher levels of relatedness, since costs
167to inbreeding will presumably be attenuated at lower levels of relatedness.

168 Third, we test alternative non-behavioral explanations for the lower than expected
169occurrences of inbreeding between alpha males and their female kin in capuchins. If fetal
170loss or early infant death of non-genotyped inbred infants explained the rarity of close
171inbreeding events, then one would predict (1) higher infant mortality rates among infants
172born to females residing in groups where the alpha is a close relative, and/or (2) longer
173inter-birth intervals for females residing in groups where the alpha is a close relative, since
174miscarriages would increase the time between infant births.

175 Finally, we look for evidence of fitness costs to inbreeding, to test the hypothesis that
176inbreeding is costly in capuchins. Specifically we test whether there are higher juvenile
177mortality rates and/or delayed female age at first birth, for inbred versus outbred
178individuals.

179METHODS

180Field site and study species

181 The subjects of this study are individually recognized, habituated white-faced
182capuchin monkeys from the Lomas Barbudal Biological Reserve and adjacent public and
183private lands in Guanacaste, Costa Rica (hereafter referred to as 'Lomas Barbudal'). This

184wild population has been under observation since 1990 with continuous monitoring since
1852002 (Perry 2012; Perry et al. 2012). Behavioral data were available from 11 study groups:
186four groups were originally habituated, and seven additional groups formed by fissions
187(Fig. 1). It was not possible to record data blind because our study involved focal animals in
188the field.

189**Estimating degrees of relatedness using pedigrees**

190 Paternity information was available from previous work (Muniz et al. 2006; Godoy et
191al. 2016). Briefly, we have genotyped 334 capuchins from the Lomas Barbudal population
192using 18 microsatellites (Muniz and Vigilant 2008) and DNA obtained primarily through
193non-invasively collected faecal samples and occasional sampling of tissue samples from
194dead capuchins. We have determined paternity for 253 individuals in our study population,
195and for 248 individuals we knew the identity of both their parents. See Supplementary
196Information Table S1 for information on the pedigree depth of genotyped individuals from
197our study groups (n=310).

198 Although microsatellite markers can be reliably used to determine parent-offspring
199relationships, they are insufficient for identifying other types of kin relationships, such as
200half-siblings, because of the higher variance in the number of alleles shared per locus
201(Csilléry et al. 2006; Van Horn et al. 2008). The mean number of alleles per locus in our
202population is 5.33 (range: 3-9) (Godoy et al. 2016). This level of polymorphism even in a
203population such as the great weed warbler, *Acrocephalus arundinaceus*, with a relatively
204high variance in relatedness, is estimated to explain only a small proportion of the variance
205(~0.05) in marker-based relatedness estimates (Csilléry et al. 2006). We therefore used

206pedigree information to calculate estimated coefficients of relatedness for our dyads using
207the DESCENT software (<http://itb.biologie.hu-berlin.de/~hagen/Descent/>).

208 When two members of a group are genotyped, we can be confident as to whether or
209not they are a parent-offspring dyad, but all other kinship categories require more
210information on the parentage of the members of the dyad. Since incomplete pedigrees
211(particularly for older natal females born before habituation of their natal groups) limit our
212ability to generate precise coefficients of relatedness, we binned each dyad into one of four
213relatedness categories and treated them as categorical variables (Supplementary
214Information Fig. S1). These included one nonkin category and three categories of kin.

215 Category 0 included all dyads with inferred coefficients of relatedness of 0.
216Immigrant males of unknown origin were considered unrelated to natal females, unless
217genetic paternity assignment showed otherwise. However, some immigrant males that
218were assigned as nonkin of females may in fact have been paternal uncles (or more distant
219kin) of females residing in groups with their alpha father, since male white-faced capuchins
220typically emigrate with natal kin (Jack and Fedigan 2004a,b; Perry et al. 2008, 2012; Perry
2212012; Wikberg et al. 2014).

222 Category 1 included dyads with inferred coefficients of relatedness greater than 0
223but lower than 0.25. Dyads with estimated coefficients of relatedness equal to zero, but
224where both members of the dyad were born in the same natal group, were also
225conservatively binned into this category. This compensates for the tendency to
226miscategorize individuals related at less than the half sibling level as unrelated as a result of
227the use of incomplete pedigrees of fewer than four generations (Csilléry et al. 2006).

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

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

239 **Group composition during infant conception windows**

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

244 Using the known gestation lengths of wild capuchins (avg: 158, std. dev: 8 days,
245 Carnegie et al. 2011), we generated conservative conception windows for births. These
246 windows were three standard deviations (i.e. 24 days) before and after each estimated
247 conception date. Thus, these 49-day windows covered the period 182 to 134 days prior to
248 the known or estimated birth dates for infants. We determined which males were present
249 in a study group during each conception window, and thus which males were available as
250 potential mates for each infant's mother. All males six years of age or older were considered

251 potential sires of infants, since the youngest sire in the Lomas Barbudal population was
252 6.25 years old at the time of his infant's conception (Godoy et al. 2016).

253 **Inbreeding risk**

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

262 **Inbreeding avoidance**

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

267 **Inbreeding costs**

268 ***Juvenile mortality***

269 In a sample of 399 pregnancies, 107 (26.8%) ended either in miscarriage or with
270 infant death before genetic samples could be collected, but only 5.6% (n=6) of these may
271 have died at an age of older than one year. Therefore, we did not consider infants that died
272 during their first year of life in our assessment of juvenile mortality rates. This was in order
273 to avoid potential biases in the dataset due to non-genotyped infants, as well as to avoid

274inclusion of infant deaths due to infanticide after changes of the alpha male. Juvenile
275mortality was instead measured as the proportion of infants that survived from one year of
276age into their fourth year of life (before male migration from groups was likely to bias our
277mortality data).

278 Our dataset consisted of 186 infants born before 2011 that survived their first year
279of life and for which we knew the identity of their father and mother. We used this data to
280test for higher mortality in inbred juveniles.

281*Female age at first birth*

282 We had a sample of 58 females for which we could estimate age at first birth with an
283accuracy of plus or minus 90 days. We used this dataset to look for costs of inbreeding in
284the form of delayed age at first reproduction.

285**Generalized linear mixed models**

286 Statistical analyses were run in R v.3.2.0 (R Core Team 2015) using the `glmer` or `lmer`
287function from the `lme4` package (Bates et al. 2014). To assess the significance of our
288predictor variables, we ran Generalized Linear Mixed Models (GLMM, Baayen 2008) 1) with
289binomial error structure and logit link function on all our models involving a binomial
290response ('yes'/'no') or 2) with Gaussian error structure on models involving a continuous
291response. We included random slopes where possible. We confirmed model stability by
292excluding all levels of all random effects one by one and comparing the estimates with
293estimates derived from the model based on the full data set. We checked for the presence of
294strong collinearity between our predictor variables by calculating Variance Inflation Factors
295(Field 2005), which measure the degrees to which variance of the estimated regression
296coefficients are inflated compared to when the predictor variables are not collinear. The

297highest VIF in any model was 1.478 suggesting no problems. In order to establish the
298significance of the test predictors, we conducted a full versus null model comparison
299(Forstmeier and Schielzeth 2011) using a likelihood ratio test (Dobson and Barnett 2008).
300The null comprised all terms in the full model except the test predictors. P-values for
301individual predictors were also obtained using likelihood ratio tests.

302RESULTS

303Prevalence of male kin during the first half of the female reproductive career

304*Co-residence with male kin*

305 Of the 95 females for which we had group composition data during their fifth year of
306life, 42.1% still lived with their fathers at age five years, while 31.6% lived with at least one
307adult paternal half brother (Supplementary Information Table S2). Even at 10 years of age,
30820.3% of females still co-resided with their father and 42.3% with a paternal half brother.
309During the early part of their breeding careers (ages 5-15), females continued to live with
310adult male kin, particularly males related to them at the half sibling level.

311*Co-residence with alpha male kin*

312 Because alpha males sire the majority of infants in capuchin groups, we looked at
313how often females (during the early part of their reproductive careers) resided with alpha
314males that were related to them. We found that a large proportion of the females at Lomas
315Barbudal had the potential to breed with related alpha males, particularly fathers and
316paternal half brothers (Supplementary Information Table S3). For example, at five years of
317age, 30.1% of females lived with an alpha father and 9.5% with an alpha paternal half
318brother. Co-residency with alpha fathers decreased over time, while co-residency with
319alpha paternal half brothers remained relatively constant and co-residency with unrelated

320alpha males increased through the first half of the female reproductive career (i.e ages 5-
32115).

322**Distribution of male kin during conceptions**

323 Most conceptions occurred while related ($r > 0$) adult males were co-resident with
324the females; out of 391 conceptions for which we had group composition data, 290 (74.2%)
325occurred when the mother had adult male kin in the group. Females resided with at least
326one paternal half brother in 30.2% of cases and with their father in 16.4% (Table 1, column
327a).

328**Risk of inbreeding with alpha males**

329 Of the 391 conceptions in our dataset, 343 (87.7%) occurred during stable alpha
330tenures. Of these conceptions, 37.9% (130 of 343) occurred when the female was related to
331the alpha male (Table 1, column b). Since alpha males are the primary breeding males in
332capuchins, this means that approximately one in every three conceptions during stable
333alpha tenures had the potential to result in an inbred offspring. Furthermore, for 31.5% (n
334= 41) of the situations where females were related to the alpha male, there were no
335unrelated ($r = 0$) adult males available to females.

336**Effect of categorical relatedness on probability that an alpha male is the father of an** 337**infant**

338 Having established that females commonly have adult male kin available in their
339groups, we next used our dataset of 193 conceptions during stable alpha tenures and for
340which the infants were genotyped to investigate the share of paternities to alpha males
341when the mother is a relative or not. Alpha males sired 141 (73.1%) of the 193 genotyped
342infants that were conceived during stable periods, including 90.1% (109 of 121) of

343 offspring born to unrelated females. For infants born to related females, the percentage
344 sired was less and varied by categorical relatedness (Table 2). In 40.6% (n=13 of 32) of the
345 cases of inbreeding between females and alpha males, there were no unrelated males
346 available for the female to choose from.

347 Furthermore, we used a GLMM to explore the significance of categorical relatedness
348 on the probability of an alpha male being the sire of an offspring. Our dataset was
349 comprised of conceptions involving 69 mothers and 23 alpha males from nine groups. The
350 response variable was whether or not an alpha male was the father of an infant ('yes'/'no').
351 The identities of the mother and alpha male were included as random effects. We included
352 random slopes where possible. The predictor variables were whether or not the mothers of
353 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
354 ≥ 0.5 . The number of adult males and number of adult females in a group were included as
355 control variables in our model because previous research had shown the possible influence
356 of each variable on alpha paternity (Muniz et al. 2010). However, due to a limited dataset in
357 the Muniz et al. study, both variables could not be included in the same model. The full
358 model was significantly different from the null model, which consisted of only control
359 variables and random effects ($\chi^2_3=46.747$, $P<0.0001$).

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

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

366 Since subordinate males also sire offspring, we investigated the pattern of
367 conceptions by females and subordinate males. We analyzed data for only those
368 conceptions during stable alpha periods where a subordinate male was the sire of the
369 infant (n=52 infants) and we excluded the alpha males from the analysis. There was no
370 inbreeding between females and subordinate males related at the level of $r \geq 0.5$ (Table 4),
371 though there were 20 such dyads (n=14 unique) in our dataset (sons: n=8, fathers: n=2, full
372 brothers: n=10).

373 We used a GLMM to explore the significance of categorical relatedness on the
374 probability of a subordinate male being the sire of an offspring. From our 52 subordinate-
375 sired infants, we generated a dataset of 313 dyads formed between 30 females and 59
376 subordinate adult males. The response variable was whether or not a subordinate male was
377 the father of an infant ('yes'/'no'). The identities of the mothers, subordinate males, and
378 infants were included as random effects. The predictor variables were whether or not the
379 mothers of infants were related to the subordinate male at the level of a) $0 < r < 0.25$, b)
380 $0.25 \leq r < 0.5$, or c) $r \geq 0.5$. The number of adult males and number of adult females in a
381 group were included as control variables. Random slopes were included where possible.
382 The full model was significantly different from the null model, which consisted of only
383 control variables and random effects ($\chi^2_3=10.557$, $P<0.0144$).

384 Relative to the $r = 0$ relatedness category, subordinate males sired significantly fewer
385 offspring with females in the $r \geq 0.5$ and $0.25 \leq r < 0.5$ categories, after controlling for the
386 number of adult males and adult females in the group (Table 5). Subordinate males were
387 not significantly less likely to sire offspring with females in the $0 < r < 0.25$ category than
388 they were to sire infants with unrelated females, but there was a trend in that direction.

389 **Alternative, non-behavioral explanations for paternity patterns**

390 The significantly lower occurrence of offspring produced by relatives can be
 391 explained as an outcome of inbreeding avoidance or, alternatively, a scenario in which
 392 matings between kin do occur, but resultant progeny are less fit and die either early during
 393 gestation or soon after birth before genetic samples can be collected for paternity
 394 determination. This scenario predicts that age at first birth should be higher and inter-birth
 395 intervals longer for females residing with a related alpha male as compared to when the
 396 alpha male is unrelated, as a result of higher incidences of miscarriages resulting from
 397 inbreeding events. Furthermore, first year infant mortality rates should be higher for cases
 398 in which females were co-resident with a related alpha male (i.e the primary breeding
 399 male) as compared to when the alpha male is unrelated. Such a result would suggest higher
 400 infant mortality rates for inbred offspring (before genetic samples could be collected).
 401 However, we found no support for these three possibilities and thus no support for the
 402 alternative (non-behavioral) explanation for paternity patterns (See Supplementary
 403 Information Table S4, S5, and S6).

404 **Inbreeding in the population**

405 Looking at all genotyped individuals (regardless of alpha status or group stability)
 406 for whom we knew their father and mother (n=248 infants), 21.4 % (n=53) were the
 407 product of some degree of inbreeding (Table 6). For 52 out of 53 of the inbred offspring, we
 408 had information on the group composition around the time of their conception. In 44.2%
 409 (n=23) of the inbreeding cases, the mothers did not have any unrelated ($r = 0$) males
 410 available in their group. For the remaining 29 cases, 20 of the infants were sired by the
 411 alpha of the group (69.0%) and the remaining 9 were sired by males that were either more

412distantly related to the mother (n=8) or as equally related to the mother (n=1) as was the
413alpha male.

414 Out of 22 known instances of inbreeding between paternal half siblings, 63.6%
415(n=14) were cases where the brother was also the alpha male of the group at some point
416during the infant conception window. Similarly, all five parent-offspring inbreeding events
417involved a male who was confirmed or likely to have been the alpha during the infant
418conception window. There was one case of mother-son inbreeding. It involved a male that
419migrated into and became the alpha of a fission product of his natal group where his
420mother still resided. The four cases of father-daughter inbreeding involved two dyads,
421which each produced offspring twice.

422 We have documented only one instance of extra-group paternity in Lomas Barbudal.
423Even in this case, the father of her infant was a familiar paternal half brother (he emigrated
424from her natal group) that was the alpha male in a nearby group. Thus, it appears that
425extra-group paternity is extremely rare at Lomas Barbudal and does not constitute an
426alternative female reproductive strategy for preventing inbreeding.

427**Potential costs to inbreeding**

428***Mortality in inbred versus non-inbred juveniles***

429 With our sample of 186 infants of known parentage, we tested for higher mortality
430in inbred versus non-inbred individuals. We found that mortality rates doubled for
431juveniles in the $0.25 \leq r < 0.5$ and $r \geq 0.5$ categories compared to the $r=0$ category, but that
432mortality rates for the $0 < r < 0.25$ were comparable to those of the $r=0$ category (Table 7).
433However, the numbers of individuals dying before the age of four were small and a GLMM
434incorporating the identity of each infant's mother as a random effect revealed only a

435 marginal effect of relatedness on mortality between ages one and four when comparing $r \geq$
 436 0.25 to $r < 0.25$ ($\chi^2_1=2.916$, $P=0.0877$).

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

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

446 **DISCUSSION**

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

451 Alpha males co-residing with close adult female kin (i.e. at the half sibling level and
 452 higher) sired far fewer offspring with them than would be expected in the absence of some
 453 form of behavioral inbreeding avoidance (see also Muniz et al. 2006, 2010; Godoy et al.
 454 2016). The same results were found when looking at subordinate males. Only 2% of
 455 genotyped infants were a product of inbreeding at the $r \geq 0.5$ level. Co-resident kin at the
 456 level of $0.25 \leq r < 0.5$ (i.e. half sibling level) also produced fewer offspring than expected by
 457 chance, but this effect was weaker than inbreeding avoidance at the $r \geq 0.5$ (i.e. father-

458daughter) level. In over a third of the cases of inbreeding, the females had no non-kin adult
459male groupmates available as potential mates. Age at first birth did not vary as a function of
460female relatedness to the alpha male, and extra-group paternity was extremely rare,
461suggesting that neither delaying reproduction nor mating outside the group were viable
462alternative female strategies. Co-resident male-female pairs related at $0 < r < 0.25$ bred less
463often than unrelated pairs, but this difference was not significant.

464 In collared flycatchers, *Ficedula albicollis*, inbreeding pairs have lower hatching rates
465than outbreeding pairs, and the offspring that are produced have lower fledging skeletal
466weight and higher post-fledging mortality rates than outbred offspring (Kruuk et al. 2002).
467In theory, the reduced viability, early mortality and consequent absence of inbred offspring
468in a population may lead to the inference that such individuals are not produced at all,
469potentially leading to the inference of behavioral inbreeding avoidance by related parents.
470If matings between close kin do occur at higher than apparent frequencies in capuchins, but
471result in either early stage fetal loss or early infant death (i.e. before genetic samples can be
472collected), then higher infant mortality rates and markers for miscarriages should be
473evident among potentially inbreeding pairs. However, we found that infant mortality rates
474in stable groups (i.e. where no alpha turnover took place) did not significantly vary
475according to the relatedness between mothers and alpha males. Additionally, both (1)
476female age at first birth and (2) the lengths of inter-birth intervals for females living with
477their alpha male relatives did not differ from those of females living with non-kin alphas.
478These results are consistent with those from a smaller sample analyzed in Muniz et al.
479(2006). These findings together provide further evidence against apparent inbreeding

480avoidance patterns being the result of fetal loss or early infant mortality, and instead are
481suggestive of mate choice.

482 That there would be mechanisms in place to prevent inbreeding between father-
483daughter pairs makes sense in this particular population, given that over 42.1% of our
484females resided with their fathers at the age when they reached sexual maturity (i.e. in their
485fifth year of life). Furthermore, selection may be particularly strong for father-daughter
486inbreeding avoidance in capuchins because if no mechanism were in place, multiple-
487generations of inbreeding could occur given that in some cases adult females are also
488resident with their grandfathers. Indeed, another primate with high male reproductive
489skew toward one dominant and long dominance tenures is the mountain gorilla (*Gorilla*
490*beringei beringei*), and this species also engages in father-daughter inbreeding avoidance in
491the wild (Vigilant et al. 2015).

492 Inbreeding at the level of paternal half siblings (8.2% of births) and more distantly
493related kin (10.2%) was more common than inbreeding at the full-sibling level (2%). Dyads
494related at $0.25 \leq r < 0.5$ appeared to avoid inbreeding, but to a more limited degree than
495parent-offspring and full sibling dyads, whereas the dyads related at $0 < r < 0.25$ did not
496differ significantly from unrelated dyads. While this may reflect an inability to accurately
497detect more distant kin categories, it may also reflect a reduced cost to inbreeding at these
498lower coefficients of relatedness. In the house mouse, *Mus musculus domesticus*, the
499offspring of full-sibling pairs showed lowered resistance to experimentally induced
500*Salmonella* infections compared to outbred offspring, having higher mortality and lower
501bacterial clearance; interestingly though, the offspring of full first cousin pairs did not differ

502 from outbred individuals in their resistance to *Salmonella* infection, at least not while under
503 laboratory conditions (Ilmonen et al. 2008).

504 If parent-offspring matings produce less viable young, then father-daughter
505 inbreeding avoidance may be a form of reproductive concession that, while reducing the
506 overall level of reproductive skew toward dominant males, does not negatively impact
507 overall alpha male reproductive success. This would, however, be a larger reproductive
508 trade-off for alpha males less closely related to the females in their group, since (1) any
509 costs of inbreeding would theoretically be lower and (2) males would have less inclusive
510 fitness benefits from the offspring born to more distantly related females. Alpha males may
511 also benefit from not inbreeding with their daughters because of the added benefit of
512 having reproductively available females as incentives for male allies to remain in the group
513 (Perry 2012).

514 Our current data suggest that there is a cost to inbreeding, as inbred females have a
515 later age at first birth than do non-inbred females. Delayed age at first birth in inbred
516 females has also been documented in captive Barbary sheep (*Ammotragus lervia*
517 *sahariensis*) (Cassinello and Alados 1996). Contrastingly, in semi-free ranging mandrills
518 (*Mandrillus sphinx*) age at first conception is accelerated, not delayed, in inbred females
519 (Charpentier et al. 2006). To our knowledge, our results are the first evidence of delayed
520 female reproduction as a consequence of inbreeding in non-human primates. In the
521 hermaphroditic land snail, the number of eggs laid by outbred and inbred pairs (full-sibling
522 pairs) do not differ significantly, but the proportion of eggs that hatch and the number of
523 hatchlings produced is significantly lower for inbreeding pairs (Chen 1993). It may be that
524 in capuchins, inbred and outbred females do not differ in when they first become pregnant,

525but instead differ in the likelihood of a successful pregnancy. Whether the reproductive
526delay in inbred capuchins is the result of slowed sexual maturation, or the result of early
527miscarriages is unknown. Future research comparing the interbirth intervals of inbred
528versus non-inbred females would help differentiate between the two possibilities, as would
529hormonal monitoring of female reproductive states. At present we do not have sufficient
530data on interbirth intervals or the onset of cycling in inbred females to address these issues.

531 Although not statistically significant, our findings give some suggestion of more
532severe costs to inbreeding in the form of higher juvenile mortality for inbred offspring.
533Interestingly, in wild cactus finches, *Geospiza scandens*, inbred individuals show lower
534juvenile survivorship compared to noninbred individuals, but only when looking at years
535with low rainfall (low food availability) or large population sizes (higher competition)
536(Keller et al. 2002). Other studies have also found environmental-specific costs to
537inbreeding (e.g. Jiménez et al. 1994; Keller et al. 1994; Henry et al. 2003). The population
538growth dynamics of wild capuchins are known to be susceptible to environmental stressors
539such as rainfall deficits accompanying El Niño events (Campos et al. 2015). Future models
540of inbreeding depression in capuchins may benefit from the incorporation of measures of
541environmental stressors.

542 To date, genetic analyses of paternity in our population are indicative of avoidance of
543close inbreeding, particularly at the level of parent-offspring, and perhaps a tolerance for,
544but not preference for, inbreeding with more distant kin. Admittedly though, our ability to
545generate accurate estimated coefficients of relatedness below the level of half siblings is
546limited. Future research analyzing the mate preferences of dyads with deeper known
547pedigrees may help shed light on the precise limits to inbreeding avoidance in this

548population. Furthermore, researching potential mechanisms of kin recognition in capuchins
549will also help establish a clearer picture of why matings between certain categories of kin
550(i.e. paternal half siblings) is more common than others.

551

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559**Ethical Approval:** All applicable international, national, and/or institutional guidelines for
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561Committee (IACUC), known as the Chancellor's Animal Research Committee (ARC),
562approved the protocol (ARC # 2005-084).

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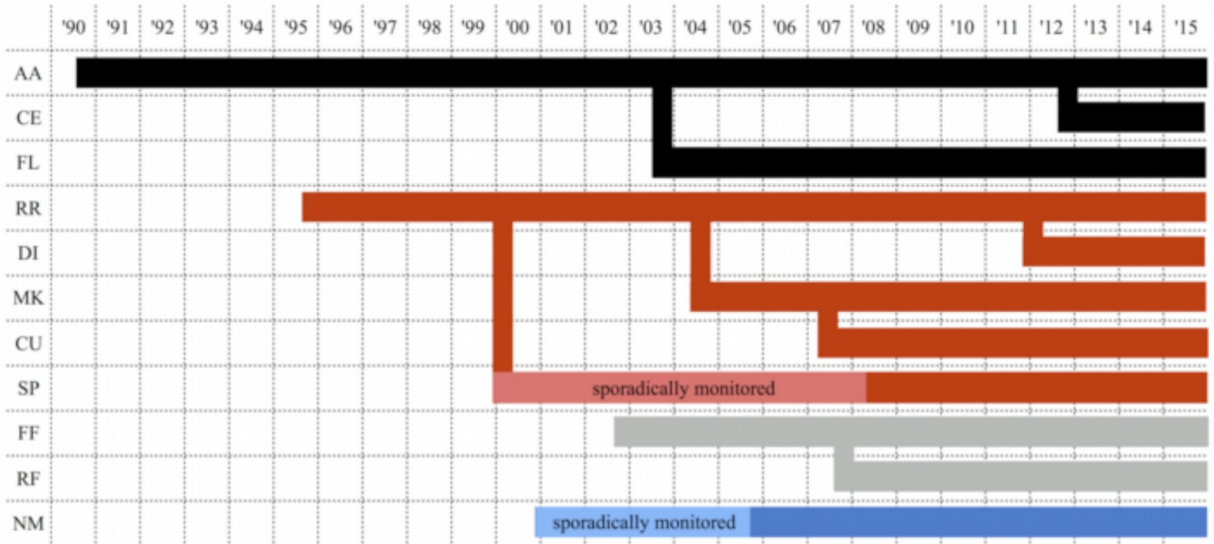
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702 **FIGURES**

703

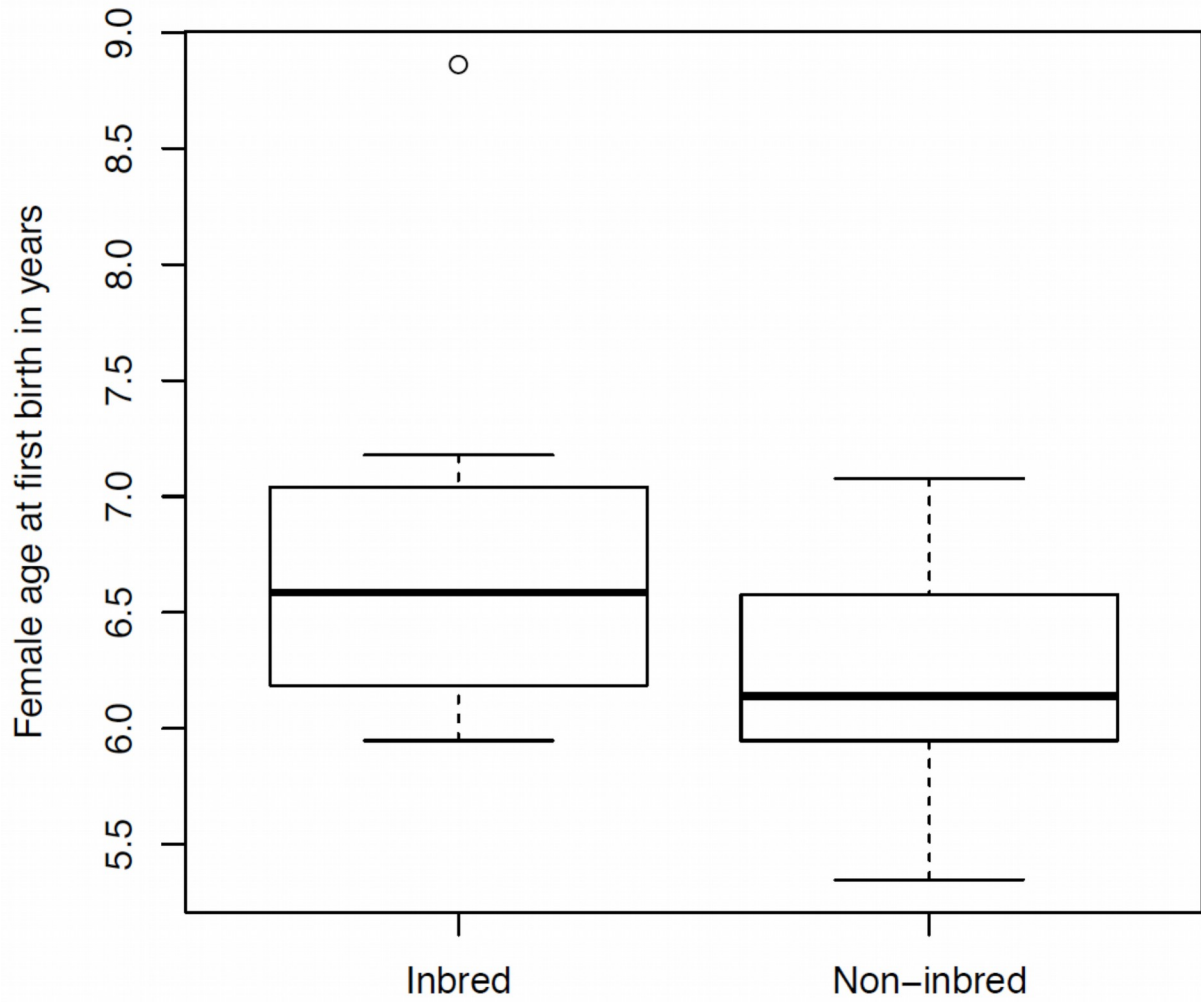
704 **Fig. 1 Study groups.** Shown are four groups and their seven fission products



705

706

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



710

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 (%)	
	(a) Availability of male kin	(b) 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)

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	N	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 %)

720**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					
# of adult males	-0.381	0.161	1	4.595	0.0321
# of adult females	-0.168	0.170	1	0.971	0.3244

721 Significant effects are shown in boldface.

722

723**Table 4** Percentage of offspring sired by subordinate males, categorized by the categorical

724 relatedness between infants' mothers and subordinate males. Data come from 52 conceptions

725 during stable alpha tenures where a subordinate male was the sire of the infant

Relatedness category	Percentage	N
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

726

727

729

730 **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					
# of adult males	-0.275	0.133	1	3.824	0.0505
# of adult females	-0.077	0.114	1	0.449	0.5026

731^a Standard error not shown because it is meaningless as a result of complete separation

732 Significant effects are shown in boldface.

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

Relatedness category of parents	# of infants	Percentage
0: $r = 0$	195	78.6
738 1: $0 < r < 0.25$	25	10.1
739 2: $0.25 \leq r < 0.5$	23	9.3
3: $r \geq 0.5$	5	2.0
Kinship category of parents	# of infants	Percentage
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

Table 7 Juvenile mortality, by categorical relatedness of parents

Relatedness category	Deaths	N	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 %

SUPPLEMENTARY INFORMATION

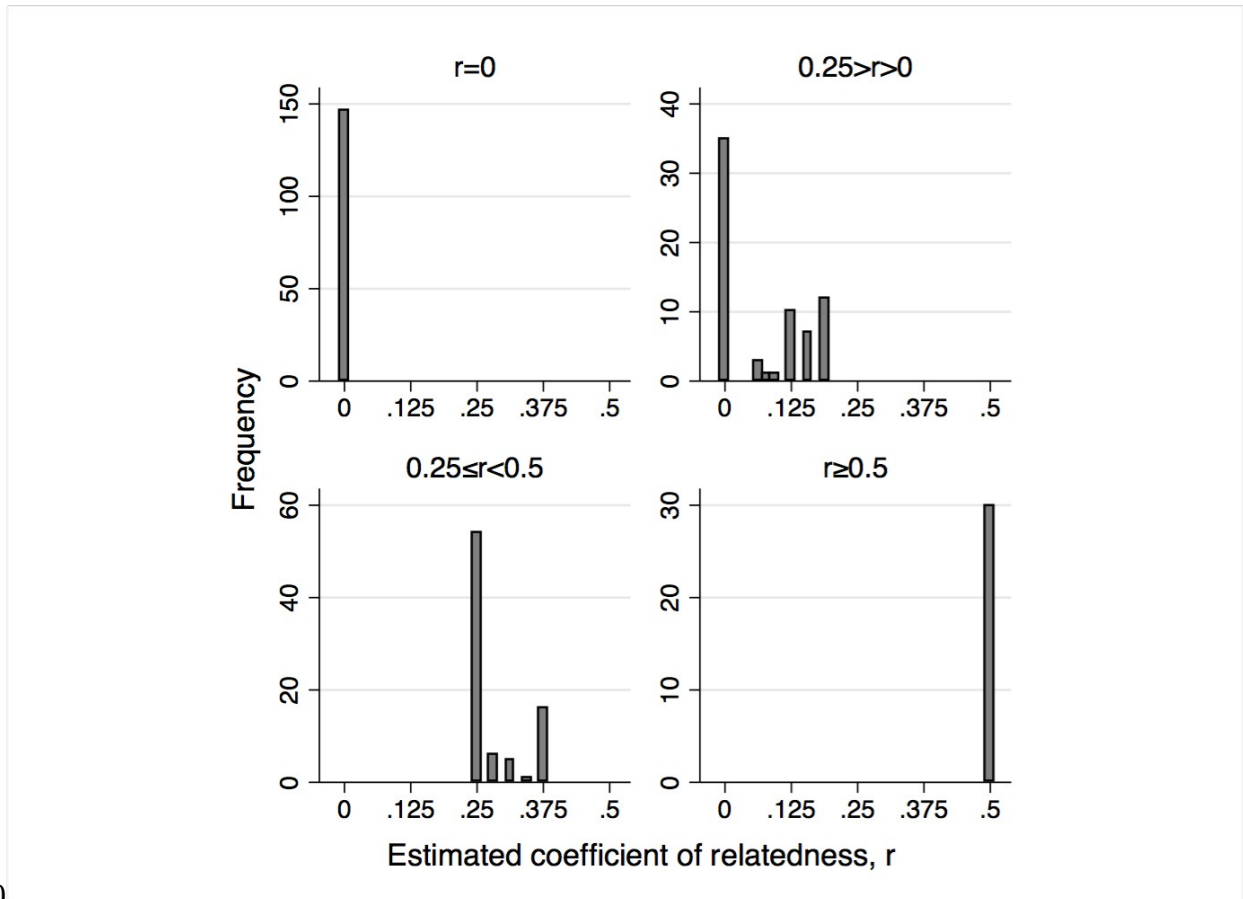
Table S1 Pedigree information for genotyped individuals of known sex.

Information is not shown for 6 infants

who died before their sexes were determined.

No. of known ancestors	Females (n=137)		Males (n=173)	
	No.	%	No.	%
Parents				
0	11	8.0	39	22.5
1	14	10.2	4	2.3
2	112	81.8	130	75.1
Grandparents				
0	37	27.0	68	39.3
1	23	16.8	18	10.4
2	39	28.5	30	17.3
3	8	5.8	12	6.9
4	30	21.9	45	26.0
Great-grandparents				
0	79	57.7	110	63.6
1	36	26.3	33	19.1
2	16	11.7	25	14.5
3	5	3.6	2	1.2
4	0	0	3	1.7
5	1	0.7	0	0
6-8	0	0	0	0

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751 **Figure S1** Distribution of the estimated coefficients of relatedness in a sample of 327
752 unique dyads, which are binned into four relatedness categories. Incomplete pedigrees
753 mean that the actual coefficients of relatedness can be higher than the estimated values.
754 The dyads represented in this figure come from the data used in the analyses seen in Tables
755 2-5. Note that there are several cases in the $0.25 > r > 0$ category, where dyads were
756 estimated to have a coefficient of relatedness equal to zero because of incomplete
757 pedigrees; these dyads were cases where both individuals were born into the same natal
758 group.

759

Table S2 Male kin availability across the first half of the female breeding career. The table shows the number of females of each age who was co-resident with at least one adult male kin from a particular kinship category

Kinship Category	Female age in years										
	5	6	7	8	9	10	11	12	13	14	15
	N=95	N=89	N=74	N=69	N=64	N=59	N=52	N=43	N=34	N=29	N=22
Non-kin ($r = 0$)	86 90.5%	82 92.1%	70 94.6%	64 92.8%	60 93.8%	58 98.3%	52 100%	43 100%	34 100%	28 96.6%	21 95.5%
Distant kin ($r < 0.25$)	33 34.7%	37 41.6%	24 32.4%	28 40.6%	27 42.4%	24 40.7%	19 36.5%	15 34.9%	15 44.1%	13 44.8%	5 22.7%
Grandfather	3 3.2%	3 3.4%	2 2.7%	2 2.9%	1 1.6%	1 1.7%	1 1.9%	1 2.3%	0 0%	0 0%	0 0%
Paternal half brother	30 31.6%	35 39.3%	35 47.3%	30 43.5%	33 51.6%	25 42.4%	20 38.5%	13 30.2%	11 32.4%	9 31%	7 31.8%
Maternal half brother	4 4.2%	3 3.4%	1 1.4%	3 4.3%	6 9.4%	7 11.9%	5 9.6%	5 11.6%	4 11.8%	3 10.3%	4 18.2%
Full brother	6 6.3%	3 3.4%	2 2.7%	7 10.1%	9 14.1%	9 15.3%	6 11.5%	5 11.6%	6 17.6%	4 13.8%	3 13.6%
Son	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	3 7%	5 14.7%	10 34.5%	6 27.3%
Father	40 42.1%	33 37.1%	21 28.4%	18 26.1%	15 23.4%	12 20.3%	7 13.5%	5 11.6%	4 11.8%	3 10.3%	2 9.1%

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767**Table S3** Availability of alpha male kin across the first half of the female breeding career.

768Table shows the number of females at each age that lived in a group where an alpha male

769fell into a particular kinship category

Kinship Category	Female age in years										
	5	6	7	8	9	10	11	12	13	14	15
	N=95	N=89	N=74	N=69	N=64	N=59	N=52	N=43	N=34	N=29	N=22
Non-kin ($r = 0$)	51 53.7%	50 56.2%	45 60.8%	45 65.2%	44 68.8%	44 74.6%	39 75%	31 72.1%	28 82.4%	25 86.2%	19 86.4%
Distant kin ($r < 0.25$)	10 10.5%	12 13.5%	8 10.8%	9 13%	8 12.5%	4 6.8%	4 7.7%	2 4.7%	0 0%	0 0%	0 0%
Grandfather	2 2.1%	2 2.2%	1 1.4%	1 1.4%	1 1.6%	1 1.7%	0 0%	0 0%	0 0%	0 0%	0 0%
Paternal half brother	9 9.5%	9 10.1%	6 8.1%	7 10.1%	9 14.1%	8 13.6%	9 17.3%	6 14%	5 14.7%	4 13.8%	4 18.2%
Maternal half brother	1 1.1%	1 1.1%	1 1.4%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%
Full brother	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%
Son	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%	0 0%
Father	29 30.5%	23 25.8%	17 23%	12 17.4%	11 17.2%	7 11.9%	5 9.6%	5 11.6%	4 11.8%	3 10.3%	1 4.5%

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773 **Alternate, non-behavioral explanations for paternity patterns**

774 ***Female-alpha relatedness and female age at first birth***

775 We looked at a small subset of females (n=37) whose age at first birth was known to
 776 be accurate to within 3 months, and who lived in a group containing a stable alpha from age
 777 4.5 (presumably before commencing cycling) through to their first infant's conception
 778 (Table S4). We ran a GLMM to assess whether categorical relatedness between females and
 779 the alpha males of their groups positively impacted the age at which females had their first-
 780 born offspring (i.e. delayed age at first birth). Such a result would suggest that inbreeding
 781 does occur but that pregnancies result in miscarriage. Our dataset included data on 13
 782 alpha males from seven social groups. Our response variable was each female's age at first
 783 birth. Our test variables were the levels of relatedness between the infants' mothers and the
 784 alpha males; $0 < r < 0.25$, $0.25 \leq r < 0.5$, and $r \geq 0.5$. The identities of the alphas, females,
 785 and groups of residence were included as random effects. The full model was not
 786 significantly different from the null model ($\chi^2_3=2.657$, $P=0.4477$). In other words, we did
 787 not find evidence for miscarriages. Similar results were found when condensing all $r > 0$
 788 categories together (i.e. a kin versus non-kin comparison) ($\chi^2_1=0.299$, $P=0.5843$).

789

790 **Table S4** 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]

791

792Female-alpha relatedness and inter-birth intervals

793 To further investigate the possibility of miscarriages driving our results of apparent
794inbreeding avoidance, we also analyzed a subset of inter-birth intervals (n=91), for which
795the following criteria were met; 1) the first infant survived its first year of life, 2) the alpha
796male, during the conception window of the subsequent infant, was the same male that was
797alpha during the first infant's conception window, and 3) the IBI estimate was accurate to
798within 3 months (**Table S2**). We dropped one IBI outlier, which was more than 5 standard
799deviations higher than the population mean (mean: 749 days, st.dev: 145, Perry et al.
8002012).

801 We ran a GLMM to test for a positive effect of categorical relatedness between
802females and alpha males on the inter-birth intervals for females (i.e. longer inter-birth
803intervals). Such a result would suggest that inbreeding occurs but that pregnancies end in
804miscarriage. Our dataset comprised 52 mothers and 14 alpha males from nine social
805groups. Our test variables were the levels of relatedness between the infants' mothers and
806the alpha males; $0 < r < 0.25$, $0.25 \leq r < 0.5$, and $r \geq 0.5$. We included the identities of
807females, alphas, and groups of residence as random effects. The full model was not
808significantly different from the null model ($\chi^2_3=4.339$, $P=0.2271$), meaning we found no
809evidence for miscarriages. Similar results were found when condensing all $r > 0$ categories
810together and comparing kin versus non-kin ($\chi^2_1=0.0985$, $P=0.7536$).

811

812

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814**Table S5** 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]

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818Female-alpha relatedness and probability of infant death

819 There was a sample of 246 births (105 of which were not genotyped) where the
820alpha male position remained stable from the estimated conception window of the infant
821through to either 1) the end of the infant's first year of life or 2) the infant's death (**Table**
822**S3**). Inclusion of ungenotyped infants allowed for us to avoid possible sample bias if inbred
823offspring died more often before genetic samples could be collected from them. We ran a
824GLMM to test the effect of relatedness between infants' mothers to the alpha male on the
825probability of an infant dying during early infancy. A positive relationship (i.e. higher infant
826mortality) would suggest that inbreeding does occur but that the offspring are less viable.
827Our dataset was comprised of 89 mothers and 24 alpha males from 11 social groups. Our
828response variable was whether an infant died before reaching the age of one (yes/no). Our
829test variables were the levels of relatedness between the infants' mothers and the alpha
830males: $0 < r < 0.25$, $0.25 \leq r < 0.5$, and $r \geq 0.5$. The identities of mothers, alphas, and groups
831of residence were included as random effects. The full model was not significantly different
832from the null model ($\chi^2_3=1.860$, $P=0.6020$). Similar results were found when combining all
833 $r > 0$ categories and comparing kin versus non-kin ($\chi^2_1=0.591$, $P=0.4419$). Thus, we found
834no evidence for our inbreeding avoidance patterns actually being the result of a prevalence
835of inbred offspring that died before genetic sample collection.

836

837

838**Table S6** 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 %

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