Low paternity skew and the influence of maternal kin in an egalitarian, patrilocal primate

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Levels of reproductive skew vary in wild primates living in multimale groups depending on the degree to which high-ranking males monopolize access to females. Still, the factors affecting paternity in egalitarian societies remain unexplored. We combine unique behavioral, life history, and genetic data to evaluate the distribution of paternity in the northern muriqui (*Brachyteles hypoxanthus*), a species known for its affiliative, nonhierarchical relationships. We genotyped 67 individuals (22 infants born over a 3-y period, their 21 mothers, and all 24 possible sires) at 17 microsatellite marker loci and assigned paternity to all infants. None of the 13 fathers were close maternal relatives of females with which they sired infants, and the most successful male sired a much lower percentage of infants (18%) than reported for the most successful males in other species. Our findings of inbreeding avoidance and low male reproductive skew are consistent with the muriqui's observed social and sexual behavior, but the long delay (≥2.08 y) between the onset of male sexual behavior and the age at which males first sire young is unexpected. The allocation of paternity implicates individual male life histories and access to maternal kin as key factors influencing variation in paternal—and grandmaternal—fitness. The apparent importance of lifelong maternal investment in coresident sons resonates with other recent examinations of maternal influences on offspring reproduction. This importance also extends the implications of the "grandmother hypothesis" in human evolution to include the possible influence of mothers and other maternal kin on male reproductive success in patrilocal societies.

mating system | reproductive strategy | development | molecular ecology | Platyrrhini

In most primates, variance in male reproductive success reflects rank-related differences in access to fertile females (1–3). Paternity analyses have demonstrated that dominant males typically sire a disproportionate number of offspring, consistent with the priority of access that high rank often confers in competition over limited resources, including fertile females (2, 4–7). In hierarchical societies, deviations from rank-biased paternity have been attributed to the mitigating effects of inbreeding avoidance (8) and to demographic, reproductive, and socioecological conditions that affect the number of male competitors, the monopolizability of fertile females, and the accessibility and effectiveness of coalition partners (3, 9–12). However, whether similar factors affect the distribution of paternity in egalitarian societies has not previously been explored. Here we use long-term behavioral and life-history data to evaluate results from a unique genetic analysis of paternity in the northern muriqui (*Brachyteles hypoxanthus*), a critically endangered species distinguished by the tolerant, nonhierarchical relationships among and between males and females in their patrilocal society (13, 14).

Our subjects were members of one wild northern muriqui group (Matão group) that inhabits an Atlantic Forest fragment in Minas Gerais, Brazil, and for which data on maternal kinship and individual life histories have been collected continuously since the onset of systematic observational studies in 1983 (15). The fecal samples used for paternity analyses included the 22 infants born between 2005 and 2007 that survived to ≥2.08 y of age, their 21 mothers (representing diverse ages and histories) (Table S1), and the 24 adult males that were possible sires of at least one infant (Table S2). We considered a male to be a potential sire for an infant if he was >5 y and was known to have completed a copulation before the infant's estimated conception date (birth date minus mean 216.4-d gestation) (16). Although age at sexual maturity for male muriquis can be considerably younger in captivity than in the wild (17), males in our study population become sexually active (i.e., copulate with intromission) between 4.10 and 8.27 y of age, but experience a median delay of 0.69 y before they are sexually mature, as defined by their first complete copulation (i.e., intromission that terminates with ejaculation) at 5.21–8.36 y of age (n = 27) (18). The number of potential sires per infant ranged from 20 to 23 males; the maximum number of possible infants that any given male could have sired ranged from 3 to 22 (Table S2). All 67 individuals were genotyped at 17 variable microsatellite marker loci (Tables S3 and S4). Using these multilocus genotypes, we confirmed the identities of all biological mothers and assigned paternity to all infants with ≥99% confidence (Table S5) (19).

Results and Discussion

All together, the 22 infants had 13 different fathers, and none were the result of matings between a male and a female who was a close maternal relative (i.e., either his mother or a maternal sibling) or the product of extragroup paternity (Table S2). Males sired zero to four infants each, resulting in very low reproductive skew [Nonacs' B = 0.012, confidence interval (CI) −0.043 to 0.063, P = 0.159] (20). Excluding females' adult sons (known from long-term pedigree records) from the set of potential sires of those female's subsequent offspring did not alter these findings (B = 0.013, CI −0.043 to 0.063, P = 0.148). The B index in muriquis is much lower than that found for gorillas (7) and capuchins (8), and the fact that the lower limit of the 95% CI is less than zero indicates that the muriqui's paternity distribution does not deviate significantly from random expectations. The most successful male in the group sired only 18% of the infants sampled (n = 4); this value is far lower than the percentages reported for the most successful (and typically, high-ranking) males in the hierarchical societies of other patrilocal and matrilocal primates (Table 1). Examination of the genotypes of the males in our set of potential sires and those of their mothers, when available, revealed that the set of potential sires had to have been fathered by a large set of different males. In addition, with few exceptions, adult males who were close in age had to

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Table 1. Maximum paternity percentages for individual males from genetic analyses of wild primates living in multimale-multifemale groups

Species	Paternity assignments (*n*)	Maximum individual paternity success (%)	Residence pattern	Male relationships	Male-female dominance	Reference
Mountain gorilla	48	85	Variable	Hierarchical	M > F	(7)
Yellow baboon	27	81	Matrilocal	Hierarchical	M > F	(2)
White-faced capuchin	41	80	Matrilocal	Hierarchical	M > F	(8, 37)
Chimpanzee	38	67	Patrilocal	Hierarchical	M > F	(9)
Chimpanzee	21	31	Patrilocal	Hierarchical	M > F	(11)
Chimpanzee	34	30	Patrilocal	Hierarchical	M > F	(10)
Bonobo	10	30	Patrilocal	Hierarchical	F ≥ M	(5)
Northern muriqui	22	18	Patrilocal	Egalitarian	F = M	Present study

have been sired by different fathers (Table S6), implying that our findings hold up within and across cohorts.

Age and social experience are known to alter the effects of rank on male reproductive success in other primates (21) and could result in similar reproductive advantages for older male muriquis as well. Behavioral studies (13, 22) have shown that older male muriquis complete a greater proportion of copulations than younger males, are more efficient in completing copulations during conception months than younger males, and are preferred mating partners of reproductively experienced (and unrelated) females. However, paternity success was not related to the frequency of completed copulations during the conception period (Spearman's rank correlation $\rho = 0.27$, $P = 0.196$), and we found no evidence of age-biased paternity in this study. Sires were as likely to be younger ($n = 9$) as they were to be older ($n = 13$) than the median age range (13.05–14.06 y) of the males in the set of possible sires ($P = 0.416$, binomial test, one-tailed), and there was no relationship between sire age and either the age or fecundity of the infant's mother (Fig. S1). Nonetheless, the youngest sire in our study was 8.35 y at the time of the infant's conception, which was 2.08 y after his first complete copulation. Such a delay from the onset of sexual maturity to the onset of reproductive maturity, like that between the onset of sexual activity and sexual maturity in our study population, has implications for interpretations of behavioral development and life histories, and merits further scrutiny under diverse demographic and ecological conditions.

Male philopatry and overlapping generations because of long lifespan have the potential to provide males with life-long access to coalitionary support from both male kin and their mothers (23), and this fact may contribute to the lower degree of reproductive skew seen in patrilocal versus matrilocal primate societies (Table 1). Indeed, support from mothers and other maternal kin can contribute significantly to both offspring and grandoffspring reproductive success in human foraging societies (24). In the bonobo, a species in which females have great social influence, high-ranking mothers enhance their sons' social and mating success through direct interventions in agonistic contests and through the access to unrelated female mates that maternal proximity can provide (3, 25). As in other hierarchical societies, high-ranking male bonobos sire more offspring (5), but maternal presence also has a positive impact on the reproductive opportunities of mid- and low-ranking males (3, 25).

Consistent with the rarity of within group aggression in northern muriquis, we found no differences in male paternity success based on the number of adult maternal brothers ($n = 0$–3 brothers per possible sire) that males had in the group (Kruskal-Wallis $H = 0.502$, $P = 0.918$; Dunn's multiple comparison post hoc tests, $P > 0.05$ for all pairs; excludes one infant sired by an old male >30 y whose maternal brothers were unknown). Nonetheless, behavioral data have shown that maternal brothers participated in the same affiliative social networks and shared copulations with the same fertile females (17). Under conditions of scramble competition, these fraternal networks could decrease each individual's reproductive opportunities but increase the proportion of paternity shared by kin. Indeed, we found three sets of maternal brothers that each sired as many offspring as the most successful male (and an only son) did so on his own; collectively, these fraternities provided their mothers with comparable numbers of grandoffspring (Fig. 1).

Unlike bonobos (3, 25), there is no evidence that muriqui mothers intervene on behalf of their adult sons' social or sexual interactions, but the strength of spatial associations between muriqui mothers and their adult sons is highly variable. In a prior study (26), only 6 of the 14 mother-adult son dyads exhibited stronger spatial associations than expected by chance, and mothers with more than one adult son associated more often with the youngest one. Not inconsequentially, the sons in those mother-son dyads with the strongest history of associations were among the most reproductively successful during the present study (Fig. 1). Thus, if proximity with their mothers provides younger sons with greater access to females than they would otherwise have, then maternal social influence could exert a leveling effect on the reproductive success of individual sons while increasing the concentration of paternity within her family.

If close associations between muriqui mothers and their young adult sons are mutually advantageous, then the presence of other

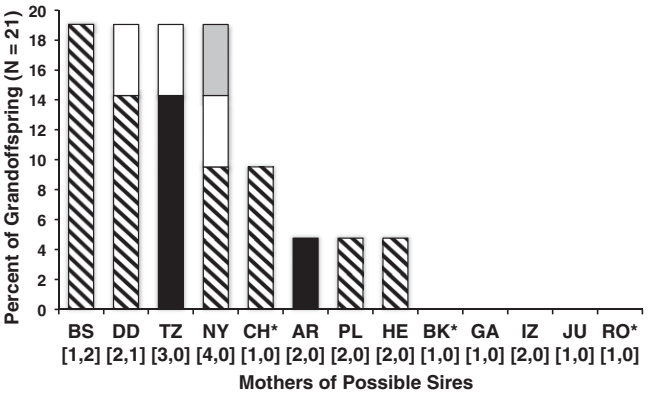

Fig. 1. Females' "grandmaternal" success through sons, based on the percentage of 21 infants sired. Excludes one infant sired by an old male (IV, >30 y) whose mother was unlikely to be alive and therefore not among the females sampled. Bars are the mothers of potential sires in this study; asterisks indicate mothers who had died before their grandoffspring were conceived (Table S2). Segmented bars represent the percent of offspring sired by different sons. Thus, BS gained the same number of grandoffspring from her only son as DD, TZ, and NY gained from the two to three of their sons that sired offspring. Numbers of resident adult sons and daughters, respectively, are noted in brackets for each mother. Hatched segments indicate offspring sired by six males whose mothers had previously maintained unusually strong spatial associations with them (26).

closely related female kin, such as maternal sisters, could provide similar advantages. However, in patrilocal societies female dispersal usually precludes coresidence between adult females and both their mothers and male siblings, and likely results in a lower average genetic relatedness among females compared with males, at least in small groups (27). Females in our study population typically dispersed from their natal groups at a median age of 6.19 y (updated from ref. 15). Nonetheless, of the three (of 34) females that have remained and reproduced in their natal group, two are the maternal sisters of the most successful sire in this study and the other is the maternal sister of a pair of equally successful maternal brothers. Indeed, the sons of females with greater than or equal to three adult offspring resident in the group, whether those offspring were all sons (for mothers TZ and NY) or a combination of sons and daughters (for mothers BS and DD), collectively sired more infants than the sons of other females (Fig. 1). Although our sample size is limited (n = 13 females with any adult sons among the set of possible sires) (Fig. 1), grandmaternal success through sons was more strongly correlated with the number of resident adult offspring of both sexes (Spearman's rank correlation $\rho = 0.82$, $P < 0.001$) than with the number of adult sons only (Spearman's rank correlation $\rho = 0.52$, $P = 0.066$). This finding suggests that considerations of reproductive skew among male primates living in patrilocal societies might be more appropriately examined from the perspective of their mothers (25), and also taking into account the potential influence of maternally related kin.

In matrilocal baboons, social bonds among females contribute to infant survivorship, and thus to female reproductive success (28). These effects, which can extend into the offspring's adulthood, have been linked to the strength of a female's social bonds with her mother, adult daughters, and maternal sisters (29). We suggest that similar benefits from associations with familiar maternal female kin could accrue in patrilocal societies through the retention of daughters in their natal groups, which occurs at similar (10%) or higher rates (50%) in some chimpanzee populations (30) than in muriquis (8%). Additional opportunities for associations with unfamiliar maternal kin can arise from the immigration of maternal granddaughters, but whether they are recognized as kin and thus avoided as mates is not yet known. Nonetheless, in patrilocal societies, the mechanisms by which extended female kin bonds enhance female reproductive success may revolve more around their impact on the reproductive success of sons. This theory would be consistent with the benefits of high maternal investment and its effects on life histories in primates, and extends the implications of the grandmother hypothesis in human evolution (24, 31) to include the influence of mothers and other maternal kin on male reproductive success in patrilocal societies.

Methods

Study Population. The study was conducted at Reserva Particular do Patrimônio Natural Feliciano Miguel Abdala (previously known as the Estação Biológica de Caratinga) in Minas Gerais, Brazil (19°50′S, 41°50′W), a 957-ha forest known to support one of the largest remaining populations of northern muriquis (32). The >300 individuals that comprise the current population are distributed among four mixed-sex groups. Our study group (Matão group, >100 individuals at present) is the largest in the population and has been the focus of an ongoing long-term study of ecology and behavior since 1982 (15). Northern muriquis have distinctive facial, pelage, and body features (e.g., mottled faces, conspicuous genitals, variation in body size and fur color) that allow experienced fieldworkers to recognize them individually. Individual-based life-history data have been maintained on all members of this group since 1983. Females give birth at roughly 3-y intervals, and births are usually concentrated during the dry season months, from May to October (33).

The 22 infants in our sample for paternity analysis were born between May 2005 and October 2007 and correspond to three annual birth cohorts. We did not include the seven other infants born during this period because these infants died at <2.09 y, after which mortality rates declined to a negligible level (i.e., only one of the infants has since died, at 3.50 y of age). Our sample thus consisted of 76% of all offspring born during the study period, and 100% of animals that survived their critical years, which is consistent with other studies of male primate reproductive skew (7). Near daily observations provided birthdate estimates to within a median of 5 d (range: 0–23 d, based on the number of days between sightings of a mother without a new infant and with a new infant).

Duplicate fecal samples (from two distinct defecations) were collected noninvasively from 65 of the 67 study subjects (mothers, offspring, and potential sires) during fieldwork between July and August 2009 (Tables S1 and S2). Between 2 and 4 mL of fresh scat were collected immediately after defecation and mixed with an approximately equal volume of the nucleic acid stabilization buffer RNALater (Ambion). Additionally, we used fecal samples collected in 2006 from two adult males (DI and IV) who died before July 2009 and were possible fathers of at least some of the infants. These samples were stored in desiccating silica gel at an approximate ratio of 1:4 of feces to silica. Samples were stored at −20 °C before DNA extraction. Research was conducted with permission from Conselho Nacional de Desenvolvimento Científico e Tecnológico, Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis/Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and Preserve Muriqui, and in compliance with all institutional animal care and use guidelines and United States and Brazilian regulations.

DNA Extraction, Quantification, and PCR. Total genomic DNA was extracted using the QIAamp DNA Stool Mini Kit (Qiagen) following the "Isolation of DNA from Stool for Human DNA Analysis" protocol (July 2007, pp. 22–25) with the following modifications: (*i*) 250 μL of the fecal slurry (or ∼150 mg of dry feces) were incubated in ASL buffer for 1 h at 56 °C, vortexing every 15–20 min, before proceeding to step 3 of the protocol; (*ii*) in step 11, we incubated the solution for 30 min instead of 10 min, vortexing it every 10 min; (*iii*) in step 19, we first added 100 μL of buffer AE heated to 70 °C to the spin column and incubated it at room temperature for 30 min; following centrifugation, the elution step was repeated with 50 μL of buffer AE without changing the 1.5 mL collection tube.

Nuclear DNA quantifications were performed using an iQ5 Real-Time PCR Detection System (BioRad) following ref. 34. Quantitative PCR (qPCR) reactions contained 7.5 μL of 2× iQ5 SYBR Green Supermix, 1.5 μL of 10× BSA, 1.5 μL of DNA template, 3.9 μL of H_2O, and 3.0 pmol each of forward and reverse primers (34). We included 1 ng/μL and 10 ng/μL human DNA standards in all qPCR reactions to derive the regression equation used to calculate the concentration of unknown DNA extracts. For accuracy, each DNA extract was quantified twice, and an average concentration obtained from these two replicates was used as a working value. The correlation between the two replicate quantifications was very high (r = 0.93, n = 67 subjects, $P <$ 0.0001), and the average concentration for 91% of samples (61 of 67) was over 0.5 ng/μL (Table S3). Cycling conditions for the qPCR assays were as follows: initial denaturation at 95 °C for 3 min, 50 cycles of 95 °C for 15 s (denaturation step) and 59 °C for 30 s (coupled annealing and extension step), and 81 cycles of 55 °C for 10 s, increasing 0.5 °C every cycle (melting-curve step).

We first tested a set of 52 published and unpublished microsatellite marker loci identified as potentially suitable for New World monkeys. Eight DNA extracts were tested for most of these 52 loci before we were able to identify 17 loci that were variable in our study subjects. This set of 17 loci was then amplified for each of the total sample set of 67 individuals using a combination of six multiplex PCR reactions (Fig. S2). Genotyping PCR reactions were carried out in a total volume of 5.0 μL and included 2.5 μL of 2× Qiagen multiplex PCR master mix, 0.04–0.22 μM of each primer, and roughly 1.0 ng of DNA template. Either the forward or the reverse primer was labeled with a fluorescent dye for automated capillary electrophoretic analysis. PCR fragments were separated and visualized on an ABI 3730 DNA Analyzer using the GeneScan 500 ROX size standard (Applied Biosystems) for allele size estimates. Automated allele calling was carried out using the GENEMAPPER 3.7 software (Applied Biosystems) with all allele calls subsequently confirmed by eye and checked for consistency across replicate PCRs of the same sample or from the same individual. Although the DNA extracts contained sufficient amounts of template overall (34), 1,058 genotypes (93%) were replicated four or more times and all homozygous genotypes were replicated at least three times each (Table S3) to minimize possible genotyping errors due to allelic dropout (34, 35). Maternity for all infants (n = 22) and for 17 adult males with mothers still resident in the group was initially assigned based on the pedigrees derived from the long-term observational data.

Paternity and Skew Analyses. We used the software CERVUS 3.0 (19) to derive standard summary statistics, test for deviation from expected genotype frequencies under Hardy–Weinberg equilibrium, and estimate the frequency of null alleles for each locus (Table S4). Before the paternity analysis, we conducted a confirmatory maternity analysis allowing CERVUS to choose any of the 21 females as the most likely mother for each of the 22 offspring and adult males with mothers still resident in the group to ensure the effectiveness of these loci to assign parent-offspring relationships; these analyses confirmed field-assigned maternities.

Confidence in paternity inference is substantially improved when the genotype of a known parent can be included in the analysis both because it increases the exclusionary power and reduces the likelihood of a false positive (19). Thus, paternity was assigned using the maximum likelihood method implemented in CERVUS, incorporating the genotypes of the known mothers to increase confidence. We ran 10,000 simulated offspring, and all males were considered equally likely to have sired each of the 22 infants. To be conservative and allow for the possibility that unsampled males (e.g., males from an adjacent social group) could have sired some offspring, we assumed that our sample included only 80% of potential sires, and we used a 1% rate of genotyping error. Because five loci had a positive estimated frequency of null alleles, we also analyzed the data excluding these five loci to check for consistency of the results (Table S5). The exclusionary power of the 17-locus dataset was 0.9953 if no information on maternal genotype was used and 0.9999 if prior information on maternity was incorporated. The exclusionary power of the smaller 12-locus dataset was 0.9869 and 0.9996, respectively. For each of the 22 infants, CERVUS assigned most-likely paternity to the same male at the ≥99% confidence level regardless of whether the full 17-locus genotype dataset or the smaller 12-locus subset was used.

For two of the loci in our panel (*LL113* and *LL1110*), some of the alleles differed in size from one another by a single base pair rather than always by integer multiples of the microsatellite repeat motif, likely indicating insertion/deletion mutations in the DNA sequence flanking the microsatellite (Table S3). Allele calls at these loci were consistent across replicates (including those for individuals who were heterozygotes for alleles differing in size by a single base pair), all mother-offspring pairs shared at least one allele at each of these loci, and genotype frequencies for these loci did not differ significantly from Hardy–Weinberg expectations (Table S4). Still, to be conservative, we reran all paternity analyses excluding these two loci. For the larger dataset (now 15 loci), our results were unchanged: all paternities were assigned to the same adult male as in the full 17-locus dataset with ≥99% confidence, as in previous analyses. For the smaller dataset (now 10 loci), 20 of 22 assigned most-likely sires were the same as in all of the other analyses at the ≥99% confidence level, and one additional assigned most-likely sire was the same as in previous analyses, but the confidence level in this assignment dropped to ≥95% (Table S5). The one remaining paternity was assigned to a different male at the ≥95% confidence level, with the second most-likely sire being the male confidently assigned paternity in all earlier analyses. The genotypes of both of these males were perfectly compatible with that of the offspring, and the change in the assignment is almost certainly a result of discarding valuable information from seven variable loci. Additionally, the young age of the newly assigned male at the time of the infant's conception argues strongly against the possibility that he could have been the sire. These results suggest that paternities assigned with both the 17-locus and 12-locus datasets are accurate and robust.

Nonacs' *B* index of reproductive skew was calculated using the SKEW CALCULATOR software (20) to test for unequal distribution of paternity among possible sires. The program outputs the *B* index (and associated *P*-value), which usually varies from −1 to 1, a 95% CI, the minimum *B* value possible (i.e., if paternities were distributed equally among all sires), and the maximum *B* value possible (i.e., if all paternities were monopolized by a single individual). If the CI includes zero, then the distribution of paternity among males cannot be concluded to be significantly different from random. When the equal sharing value (minimum *B*) falls within the lower CI, then an equal distribution of paternities among males cannot be excluded, while if the upper CI equals the maximum *B*, then the possibility of complete reproductive skew (i.e., one male being responsible for all paternities) cannot be rejected.

The *B* index has the advantage over other skew indices in that it allows us to adjust the proportion of paternity that each adult male could possibly have relative to each male's reproductive tenure. For instance, if a particular male was observed copulating with ejaculate only in 2005, his total contribution to the offspring pool would only be evaluated relative to infants conceived during and after 2005 and would exclude those conceived earlier (e.g., in 2004). In addition, if adult females are known to avoid incestuous liaisons with their adult sons, these adult sons can be excluded as potential sires of their mother's offspring. Finally, because Nonacs' *B* index has been used in other studies of reproductive skew in primates, our results can be compared across species.

We calculated *B* indices for our samples in two ways. First, we considered males as potential sires of each infant only if the male was at least 5 y old and was observed copulating either on or before the estimated conception date of a particular infant. In a second analysis, we used the same criteria, but we also excluded adult sons as potential sires of their mother's subsequent offspring (Table S2) because, based on behavioral observations and corroborated by our paternity results, copulations between adult sons and their mothers are extremely rare (13, 36). For both of these analyses, the resultant Nonacs' *B* index values were close to zero and nonsignificant. In addition, the 95% CI (from −0.043 to +0.063 in both analyses) allows us to exclude a scenario of monopoly (Nonacs' Max. *B* was 0.907 and 0.908, respectively), whereas the random distribution (95% CI overlaps with zero) and equal sharing (95% CI includes the equal sharing value, i.e., Nonacs' Min. $B = -0.043$) scenarios cannot be rejected.

As a final analysis, we conducted a limited examination of patterns of paternity and reproductive skew in the past using DADSHARE v4 (http://www.zoo.cam.ac.uk/zoostaff/amos.htm). This Excel macro uses maternal and offspring genotypes to infer paternal alleles and then uses a Monte Carlo simulation procedure to determine the minimum number of sires required to generate a progeny set and to identify sets of offspring that could have been fathered by the same male. Based on the genotypes of the 24 males in the set of potential sires and of those males' mothers, when available, a minimum of nine males would have been needed to father the potential sires included in our sample, and in only three cases could potential sires who were born less than two years apart have themselves been fathered by the same male (Table S6). Because DADSHARE does not exhaustively search for compatible paternal sibling sets, the input order for progeny genotypes could potentially affect the outcome. Nonetheless, our DADSHARE analysis returned identical sets of possible paternal siblings when the order in which the progeny sets of different females and the order of male offspring within each female's progeny set were varied.

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Supporting Information

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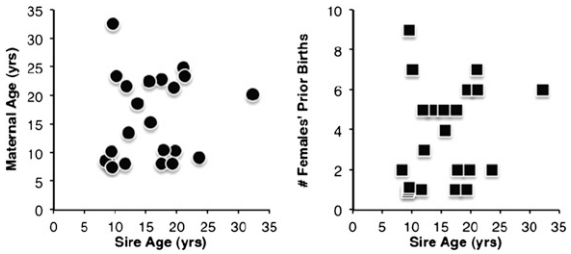

Fig. S1. Sire age vs. maternal age and reproductive history. Data are depicted at the time the offspring in this study were conceived. There was no relationship between sire age and either maternal age (Spearman's rank correlation $\rho = 0.265$, $n = 22$, $P = 0.234$) or maternal fecundity (Spearman's rank correlation $\rho = 0.310$, $n = 22$, $P = 0.161$).

A. Overview of the marker loci, primer concentrations, and thermal cycling profile used in each multiplex reaction.

Primer Set	Loci	Primer Concentrations (μM)	Cycling Conditions
Multiplex 1	LL1118, D5S111, D8S260	0.10 - 0.10 - 0.10	PCR 1
Multiplex 2	SB38, LL1115, LL157	0.08 - 0.14 - 0.08	PCR 1
Multiplex 3	D8S165, LL113, LL1110	0.04 - 0.04 - 0.22	PCR 1
Multiplex 4	SB30, D17S804, LEON15	0.13 - 0.11 - 0.06	PCR 1
Multiplex 5	Lr.P2BH6, APM1, AB06	0.14 - 0.08 - 0.08	PCR 2
Multiplex 6	D13S160, LEON21	0.10 - 0.10	PCR 2

B. Detailed thermal cycling profiles used for multiplex PCR.

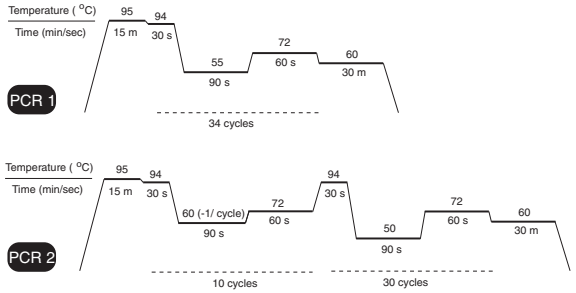

Fig. S2. Multiplex PCR combinations and PCR conditions used for genotyping. (*A*) Overview of the marker loci, primer concentrations, and thermal cycling profile used in each multiplex reaction. (*B*) Detailed thermal cycling profiles used for multiplex PCR.

Table S1. Reproductive and residency histories of offsprings' mothers

Adult female ID	No. of offspring in sample	Reproductive history	Residency history	No. of sons among the set of potential sires
BR	1	Multiparous	Natal	0
DB	1	Nulliparous	Natal	0
FE	2	Multiparous	Immigrant	0
GA	1	Multiparous	Immigrant	1
HE	1	Multiparous	Immigrant	2
IZ	1	Multiparous	Immigrant	2
JU	1	Multiparous	Immigrant	1
KA	1	Multiparous	Immigrant	0
KI-M2	1	Nulliparous	Immigrant	0
MD-J	1	Nulliparous	Immigrant	0
MY-M2	1	Nulliparous	Immigrant	0
NY	1	Multiparous	Present as adult since 1982	4
PL	1	Multiparous	Immigrant	2
SA	1	Primiparous	Immigrant	0
TN-M2	1	Nulliparous	Immigrant	0
TZ	1	Multiparous	Immigrant	3
UR	1	Primiparous	Immigrant	0
VD	1	Multiparous	Immigrant	0
XI	1	Nulliparous	Immigrant	0
YA	1	Primiparous	Immigrant	0
ZU	1	Nulliparous	Immigrant	0

Table S2. Potential sires' histories

Adult male ID	No. of offspring sired	Maximum no. of fertilizations	Maximum no. of fertilizations, excluding maternally related partners	Age (y) at first fertilization in this sample	Age (y) at last fertilization in this sample	No. of adult maternal brothers living	Male's mother living?	No. of adult maternal sisters resident
AG	0	22	22	12.90	15.36	1	Yes	0
AM	1	22	22	19.57	22.04	1	Yes	0
BE	4	22	21	15.37	17.84	0	Yes	2
BLK	0	22	22	15.34	17.81	0	No	0
CO	2	22	22	13.14	15.61	0	No	0
DA	3	22	21	18.79	21.25	1	Yes	1
DI	1	22	21	22.53	25.00	1	Yes	1
GU	0	22	21	7.14	9.61	0	Yes	0
HO	1	22	21	9.16	11.62	1	Yes	0
HR	0	10	10	6.25*	8.72	1	Yes	0
IJ	0	3	3	4.09*	6.56	1	Yes	0
IN	0	22	21	10.03	12.50	1	Yes	0
IV	1	11	?	32.23†	Deceased	?	?	?
JR	0	22	21	12.96	15.43	0	Yes	0
NE	1	22	21	17.12	19.59	3	Yes	0
NI	0	22	21	22.54	25.00	3	Yes	0
NO	1	22	21	11.25	13.72	3	Yes	0
NR	2	22	21	8.18	10.64	3	Yes	0
PB	0	11	10	5.19*	7.65	1	Yes	0
PE	1	22	21	8.28	10.74	1	Yes	0
RB	0	22	22	16.25	18.72	0	No	0
TH	3	22	21	9.18	11.65	2	Yes	0
TL	1	22	21	11.87	14.34	2	Yes	0
TU	0	12	11	6.31*	8.78	2	Yes	0

*Had not yet completed a copulation (see text) and were not included as possible sires in the paternity analysis until they were observed to do so.
†Present as an adult since 1982, thus age is estimated and maternal kin are unknown.

Table S3. Genotypes and DNA template concentrations for each individual

ID | *LOCI*	*LL113*	*LL1110*	*LL1115*	*LL1118*	*LL157*	*SB30*	*SB38*	*LEON15*	*LEON21*	*APM01*	*AB06*	*Lr.P2BH6*	*D5S111*	*D8S165*	*D8S260*	*D13S160*	*D17S804*	DNA (ng/μL)
Mothers																		
NY	183/183	220/223	200/200	138/160	224/232	97/103	126/128	263/263	367/379	200/204	271/273	102/112	164/168	137/137	205/205	243/243	154/160	0.96
BR	179/180	212/221	200/200	142/145	224/224	97/97	128/132	263/265	367/379	204/210	267/271	98/112	174/174	141/141	201/211	239/245	154/162	0.36
ZU	180/185	212/212	196/200	147/147	226/226	103/103	132/138	265/267	379/379	200/210	267/271	112/114	164/170	139/141	205/211	239/243	152/154	1.40
YA	180/183	212/220	194/194	138/147	224/230	83/87	132/138	259/267	379/379	202/202	261/271	108/112	164/168	143/146	211/211	243/243	156/160	2.16
KI	180/185	212/220	194/206	140/160	224/224	87/103	138/140	267/267	379/379	204/206	261/261	92/92	164/164	137/146	201/211	239/243	152/160	4.95
MD	180/183	220/220	200/200	142/147	224/232	87/97	126/132	265/265	379/379	200/204	271/273	98/114	168/174	137/141	211/211	239/243	160/160	2.25
MY	180/183	212/220	200/206	142/147	224/230	101/103	132/144	265/267	367/379	202/206	271/273	98/108	164/168	137/137	205/205	243/243	152/154	2.43
SA	179/185	212/212	200/200	142/147	226/226	87/87	126/132	259/267	379/379	200/210	271/273	112/112	162/170	139/141	205/211	243/243	160/160	1.92
TN	183/185	220/221	200/200	140/142	224/230	83/103	132/136	263/269	379/379	200/210	267/271	106/112	164/164	137/143	205/211	243/243	160/160	2.25
UR	180/185	212/212	194/200	142/147	226/226	97/103	126/132	265/265	379/379	200/200	271/273	112/112	162/174	141/141	211/211	239/243	154/156	1.37
VD	179/183	218/221	194/200	138/147	226/232	87/103	126/132	259/263	375/379	206/210	271/273	110/112	164/170	141/143	211/211	243/247	154/160	2.21
XI	179/185	220/221	206/206	158/160	224/224	83/103	132/144	263/269	379/379	200/202	271/273	98/112	164/164	146/146	211/211	239/243	152/156	1.23
DB	180/183	220/221	200/206	142/160	224/230	97/101	136/140	263/263	375/379	200/210	261/267	108/112	164/164	139/143	205/211	229/243	156/160	2.10
FE	180/183	212/212	194/200	138/142	224/230	103/103	132/132	259/265	375/379	200/204	261/271	102/112	164/168	137/139	211/211	243/247	154/154	1.56
GA	183/183	220/220	200/200	147/147	224/232	97/103	128/144	259/263	367/375	200/202	271/273	112/114	162/170	139/143	205/205	243/243	156/160	2.14
IZ	183/185	212/218	200/200	142/158	226/232	87/97	138/144	263/265	379/379	200/204	267/273	98/112	162/162	137/141	201/211	243/245	154/162	1.17
JU	180/183	212/220	194/200	142/147	226/230	83/97	132/132	259/263	375/379	200/210	271/271	112/112	162/170	137/139	211/211	247/247	154/160	0.74
HE	183/185	218/220	200/200	142/142	224/226	97/101	132/144	263/265	367/379	200/200	271/273	112/112	162/174	137/139	205/211	239/243	154/160	0.93
TZ	183/183	212/218	196/200	142/147	224/226	97/103	126/136	259/265	375/379	200/210	267/273	92/112	162/170	141/146	211/211	239/243	154/160	0.85
KA	180/180	212/212	194/200	142/142	226/226	87/87	132/144	265/267	379/379	200/200	271/273	108/112	164/170	137/137	211/211	243/243	154/160	1.30
PL	180/185	218/220	194/200	142/147	224/226	103/103	132/132	259/265	367/379	200/202	271/271	112/112	162/170	137/137	205/211	239/247	154/156	0.46
Infants																		
BM	179/180	218/221	200/200	142/142	224/224	87/97	132/138	263/267	367/379	204/210	267/271	112/112	162/174	137/141	211/211	239/245	152/162	2.53
HG	183/183	218/220	200/200	142/158	226/232	97/101	128/132	263/265	379/379	200/200	271/271	92/112	168/174	137/139	205/211	243/243	154/160	2.76
JB	180/183	212/221	200/200	142/147	226/230	83/103	132/132	259/265	375/375	200/210	271/271	112/112	162/164	137/141	211/211	247/247	156/160	1.40
KPA	180/180	212/220	194/194	142/142	224/226	87/97	132/132	265/267	379/379	200/210	271/271	112/112	164/164	137/141	211/211	229/243	156/160	1.62
NV	183/183	212/220	200/200	142/160	224/232	103/103	126/126	259/263	379/379	200/200	273/273	106/112	164/170	137/137	205/205	243/243	154/160	2.33
PTN	183/185	218/220	194/200	142/142	226/230	97/103	132/136	259/267	379/379	200/202	267/271	112/112	162/164	137/139	211/211	239/243	154/156	2.85
TCA	180/183	218/221	196/200	142/147	224/224	103/103	132/136	265/265	379/379	204/210	267/271	112/112	170/170	141/146	211/211	229/239	154/160	1.77
FRD	179/180	212/220	194/200	138/142	224/226	87/103	132/144	259/267	367/375	200/204	271/273	102/112	168/168	139/146	211/211	243/247	154/160	1.15
IC	183/185	218/221	200/200	142/142	226/232	87/87	128/144	265/267	367/379	204/204	267/273	112/112	162/164	137/141	211/211	245/245	154/160	3.99
KNA	183/185	220/221	194/200	140/142	224/224	87/103	132/138	263/267	379/379	206/206	261/271	92/106	164/170	141/146	211/211	239/243	152/154	2.84
MEL	180/183	212/220	200/200	138/147	232/232	97/101	132/136	265/265	375/379	200/204	267/271	98/112	168/174	137/141	205/211	243/243	154/160	2.83
MTR	180/183	220/221	200/200	138/142	224/224	97/101	144/144	259/267	379/379	200/202	273/273	98/112	164/164	131/137	205/205	243/247	152/160	3.02
XHI	180/185	212/220	194/206	158/160	224/226	83/103	132/132	259/263	379/379	200/202	267/273	98/112	164/170	137/146	211/211	239/243	152/160	4.12
YY	180/183	220/220	194/206	138/142	224/230	83/97	138/140	259/259	379/379	202/210	261/261	108/112	164/168	143/143	211/211	243/243	156/160	1.71
DN	183/183	220/221	200/200	142/160	224/224	101/103	126/136	263/263	379/379	206/210	267/273	106/112	164/170	141/143	211/211	243/243	154/160	3.03
FELC	179/180	212/221	194/200	138/142	224/230	87/103	132/144	259/265	375/379	200/204	271/273	102/112	164/164	137/141	205/211	243/243	154/154	1.31
GH	183/183	212/220	200/200	142/147	230/232	103/103	136/144	263/267	375/379	202/202	271/273	112/114	164/170	139/139	205/211	243/243	154/160	2.85
SF	179/183	212/223	200/200	147/160	226/230	87/101	132/136	263/267	367/379	204/210	267/271	112/112	168/170	137/139	205/205	243/243	154/160	4.12
US	180/180	212/212	200/200	142/158	226/232	97/103	132/132	265/265	379/379	200/210	271/271	102/112	162/164	139/141	205/211	243/247	156/160	3.96
VG	179/183	212/221	200/200	147/160	226/226	97/103	126/132	263/265	367/375	210/210	271/273	110/112	162/164	137/141	211/211	243/243	154/154	1.84
TRN	183/185	220/221	200/200	140/142	230/230	97/103	132/136	263/267	379/379	202/210	267/271	112/112	164/164	131/137	205/211	243/243	154/160	3.90
ZMA	183/185	212/220	196/200	142/147	226/226	103/103	132/136	259/267	379/379	200/200	267/271	112/112	164/164	139/141	205/211	243/243	152/160	0.36

Table S3. Cont.

ID | *LOCI*	*LL113*	*LL1110*	*LL1115*	*LL1118*	*LL157*	*SB30*	*SB38*	*LEON15*	*LEON21*	*APM01*	*AB06*	*Lr.P2BH6*	*D5S111*	*D8S165*	*D8S260*	*D13S160*	*D17S804*	DNA (ng/μL)
Possible sires																		
JR	180/180	212/220	200/200	142/142	224/230	87/97	132/140	263/263	375/375	200/210	261/271	112/112	164/170	139/143	211/211	243/247	154/156	1.75
RB	180/185	221/223	200/200	142/142	224/226	87/103	132/132	259/263	379/379	202/204	271/271	112/112	162/164	137/141	205/211	239/243	154/160	0.62
PE	180/185	212/220	194/200	142/160	224/226	103/103	132/138	259/259	379/379	200/202	267/271	112/114	170/174	137/146	211/211	239/243	156/160	1.95
TU	180/183	212/212	200/200	142/147	224/226	87/97	132/136	259/259	379/379	200/204	267/271	112/112	164/170	131/141	205/211	239/243	160/160	0.97
HO	179/185	212/218	200/200	142/142	224/224	87/101	132/138	265/267	367/379	200/204	267/271	112/112	162/174	123/137	211/211	239/243	152/154	1.45
NI	179/183	220/221	200/206	138/160	224/224	103/103	126/138	259/263	367/379	204/206	267/273	112/112	162/168	137/141	201/205	243/243	154/160	0.96
GU	183/185	220/220	200/200	142/147	224/224	97/103	128/128	259/263	367/367	202/206	261/273	92/112	162/164	139/146	205/211	229/243	156/160	1.51
AG	179/183	213/220	200/200	142/160	224/232	97/103	136/144	263/265	375/379	200/204	267/273	112/114	164/164	137/146	201/211	239/243	154/160	1.13
CO	179/183	220/221	200/200	142/142	226/226	87/103	128/144	259/267	367/379	204/204	267/273	112/112	164/168	141/146	211/211	245/247	160/160	0.51
IN	180/185	212/218	200/200	142/142	226/230	87/97	144/144	265/265	379/379	200/200	273/273	98/112	162/164	137/141	211/211	245/247	154/154	3.16
BE	179/183	212/220	200/200	142/142	226/230	97/103	132/136	259/267	367/379	200/202	267/271	112/112	164/164	131/139	205/211	243/243	154/160	0.77
NE	179/183	221/223	200/200	138/142	224/230	87/97	126/144	259/263	379/379	200/204	273/273	112/112	164/164	131/137	205/205	243/247	160/160	2.01
DA	180/180	220/221	200/200	142/142	224/226	97/103	132/144	259/265	375/379	204/210	271/273	112/112	164/170	141/141	211/211	229/247	156/160	0.95
TH	183/183	212/221	196/200	142/142	224/224	103/103	126/132	259/263	379/379	200/206	271/273	92/106	164/170	137/141	205/211	243/243	154/160	2.68
PB	183/185	220/221	200/206	147/158	224/226	103/103	132/136	259/259	379/379	202/206	267/271	98/112	162/170	137/141	201/211	243/247	156/160	2.20
NR	183/183	212/223	200/200	138/160	230/232	97/101	128/136	263/265	367/375	204/206	267/271	108/112	168/168	137/137	205/205	243/243	154/154	4.33
IJ	179/185	212/212	200/200	142/142	226/226	87/97	144/144	265/265	379/379	204/204	273/273	98/112	164/164	141/141	201/205	243/245	154/154	0.79
HR	179/185	218/221	200/200	138/142	224/226	97/101	126/144	263/265	379/379	200/204	273/273	112/112	164/174	131/139	205/205	243/247	154/160	0.86
TL	183/183	212/220	200/206	147/160	224/226	97/103	126/126	263/265	367/379	204/210	273/273	92/112	162/168	137/146	205/211	243/243	154/154	0.77
AM	179/180	212/213	200/200	147/158	224/232	103/103	132/136	259/265	379/379	204/210	271/273	92/102	164/164	137/139	205/211	243/247	160/160	0.83
BLK	180/183	212/212	194/200	142/145	224/230	83/103	132/136	263/265	379/379	202/210	267/271	112/112	168/174	139/139	205/211	243/247	154/156	0.34
DI	180/180	220/220	200/206	142/142	224/224	87/97	132/140	259/263	375/379	206/210	261/271	112/112	164/164	141/143	205/211	229/243	156/160	0.13
IV	179/180	212/221	200/200	142/142	226/230	87/103	132/144	259/265	379/379	200/204	271/273	112/112	164/164	131/141	205/211	243/247	154/160	0.03
NO	180/183	212/220	200/200	138/158	224/232	87/97	128/132	263/267	367/379	200/204	267/271	92/112	168/174	137/139	205/211	243/243	152/160	1.09
JR	180/180	212/220	200/200	142/142	224/230	87/97	132/140	263/263	375/375	200/210	261/271	112/112	164/170	139/143	211/211	243/247	154/156	1.75

Table S4. Summary statistics for the 17 microsatellite marker loci used in this study

Locus	Alleles	HObs	HExp	PIC	F(Null)	H-W	Reference
LL113	4	0.76	0.72	0.66	−0.03	NS	(1)
LL1110	6	0.79	0.74	0.69	−0.04	NS	(1)
LL1115	4	0.39	0.43	0.40	0.05*	ND	(1)
LL1118	7	0.72	0.69	0.66	−0.01	NS	(1)
LL157	4	0.66	0.70	0.64	0.03*	NS	(1)
SB30	5	0.76	0.73	0.68	−0.02	NS	(2)
SB38	7	0.79	0.78	0.75	−0.02	NS	(2)
LEON15	5	0.76	0.75	0.70	−0.01	NS	(3)
LEON21	3	0.43	0.46	0.41	0.04*	NS	(3)
APM01	5	0.79	0.77	0.72	−0.02	NS	(4)
AB06	4	0.76	0.70	0.63	−0.06	NS	(5)
Lr.P2BH6	8	0.58	0.55	0.53	−0.04	NS	(6)
D5S111	5	0.69	0.73	0.69	0.04*	NS	(7)
D8S165	7	0.79	0.78	0.74	−0.01	NS	(8)
D8S260	3	0.46	0.51	0.42	0.05*	NS	(9)
D13S160	5	0.60	0.59	0.55	−0.01	NS	(9)
D17S804	5	0.79	0.69	0.63	−0.08	NS	(9)
Mean	5	0.68	0.67	0.62	−0.01	—	—

HExp, expected heterozygosity; Hobs, observed heterozygosity; H-W, Hardy–Weinberg equilibrium test (ND, not done; NS, not significant; some genotype frequencies are lower than 5%); F(Null): estimated frequency of null alleles (*indicates a positive and significant estimated frequency of null alleles); PIC, polymorphic information content.

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4. Cortés-Ortiz L, Mondragón E, Cabotage J (2010) Isolation and characterization of microsatellite loci for the study of Mexican howler monkeys, their natural hybrids, and other Neotropical primates. *Conserv Genetics Resources* 2:21–26.
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6. Grativol AD, Ballou JD, Fleischer RC (2001) Microsatellite variation within and among recently fragmented populations of the golden lion tamarin (*Leontopithecus rosalia*). *Conserv Genet* 2:1–9.
7. Weber JL, Kwitek AE, May PE (1990) Dinucleotide repeat polymorphisms at the D5S107, D5S108, D5S111, D5S117 and D5S118 loci. *Nucleic Acids Res* 18:4035.
8. Weber JL, May PE (1989) Abundant class of human DNA polymorphisms which can be typed using the polymerase chain reaction. *Am J Hum Genet* 44:388–396.
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Table S5. Paternities assigned at ≥99% confidence based on 17- and 12-locus genotype datasets

Offspring ID (from oldest to youngest)	Most likely sire	17 loci: No. of mismatches with next most likely sire	12 loci*: No. of mismatches with next most likely sire
DN	TH	3	1
FELC	IV	2	1[†]
GH	BE	2	1
HG	NO	5	3
IC	CO	4	3
NV	TH	4	3
SF	NR	4	2
US	AM	5	3
VG	TL	4	2
BM	HO	4	4
JB	DA	2	1
MEL	NR	5	3
XHI	PE	3	2[‡]
YY	DI	3	1
FRD	CO	5	2
KNA	TH	4	3
KPA	DA	2	1
MTR	NE	2	2
PTN	BE	3	2
TCA	DA	3	1
TRN	BE	4	2
ZMA	BE	2	2

*Excludes the five loci with a positive estimated frequency of null alleles (Table S4): *LL1115*, *LL157*, *LEON21*, *D5S111*, and *D8S260*.

[†]In the analysis excluding two additional loci, *LL1110* and *1113*, a different male (IJ) was assigned paternity at the ≥95% confidence level, with male IV identified as the second most-likely sire. The genotypes of both IV and IJ were perfectly compatible with that of FELC, and the change in assignment in the 10-locus analysis is almost certainly because of discarding valuable information from seven variable loci. In all of the larger datasets, male IJ mismatches from that of FELC at ≥1 locus. Additionally, the young age of male IJ at the time of FELC's conception (which occurred before the onset of IJ's sexual activity) also argues strongly against the possibility that he could have been the sire.

[‡]In the analysis excluding two additional loci, *LL1110* and *LL113*, confidence in this assignment dropped to the ≥95% level.

Table S6. Results of the DADSHARE analysis examining which potential sires could have shared a father

Male IDs*	Possible paternal sibling set[†]	Maternal genotype included?[‡]	Age difference from closest younger potential male paternal sibling[§]
IJ	A	Yes	NA
PB	B	Yes	NA
HR	A	Yes	2.16
TU	C	Yes	NA
GU	D	Yes	NA
NR	E	Yes	NA
PE	F	Yes	NA
HO	G	Yes	NA
TH	C	Yes	2.87
IN	A	Yes	3.78
NO	G	Yes	2.09
TL	E	Yes	3.69
AG	E	No	**1.03**
JR	D	Yes	5.82
CO	A	No	3.11
BLK	H	No	NA
BE	H	No	**0.03**
RB	C	No	7.07
NE	A	Yes	3.98
DA	A	No	**1.67**
AM	I	No	NA
DI	D	No	9.57
NI	B	Yes	17.35
IV	A	No	13.44

*Adult males, listed from youngest to oldest, taken from the list of potential sires for the present study (Table S2).
[†]The potential paternal sibling set indicates those groups of males, indicated by the same letters, that DADSHARE identified as having the possibility of having been sired by the same father, given the potential sires' genotypes and the genotype of their mothers.
[‡]Maternal genotypes were included only if the males' mothers were among the set of females whose genotypes were known from the paternity study (i.e., those females who contributed offspring to the 2005–2007 infant cohorts).
[§]Closest difference in age (older minus younger) between adult males that DADSHARE identified as possibly sharing a father. NA indicates that no younger male with the same potential father exists in the dataset. There were only three cases (boldfaced and underlined) where the age difference between males who could have had the same father is <2 y, as described in the text. Male relative ages are as shown in Table S2.