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

Karen B. Strier[a,1], Paulo B. Chaves[b], Sérgio L. Mendes[c], Valéria Fagundes[c], and Anthony Di Fiore[b,d]

[a]Department of Anthropology, University of Wisconsin, Madison, WI 53706; [b]Department of Anthropology and Center for the Study of Human Origins, New York University, New York, NY 10003; [c]Departamento de Ciências Biológicas, Centro de Ciências Humanas e Naturais, Universidade Federal do Espírito Santo, Maruipe, Vitória, ES 29043-900, Brazil; and [d]Department of Anthropology, University of Texas at Austin, Austin, TX 78712

Contributed by Karen B. Strier, October 12, 2011 (sent for review September 11, 2011)

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

Author contributions: K.B.S., P.B.C., S.L.M., V.F., and A.D. designed research; K.B.S. and P.B.C. performed research; V.F. and A.D. contributed new reagents/analytic tools; K.B.S., P.B.C., and A.D. analyzed data; and K.B.S., P.B.C., S.L.M., and A.D. wrote the paper.

The authors declare no conflict of interest.

[1]To whom correspondence should be addressed. E-mail: kbstrier@wisc.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1116737108/-/DCSupplemental.

ANTHROPOLOGY

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

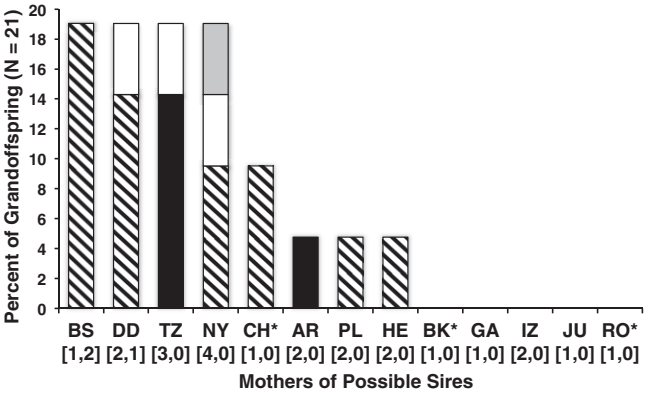

Fig. 1. Females' "grandmaternal" success through sons, based on the percentage of 21 infants sired. Excludes one infant sired by an old male (IV, >30 y) whose mother was unlikely to be alive and therefore not among the females sampled. Bars are the mothers of potential sires in this study; asterisks 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.

ACKNOWLEDGMENTS. We thank S. Lóss for assistance with labwork; all contributors to the long-term demographic records; A. Coli, M. Kaizer, C. Possamai, and F. Tabacow for help with sample collections; and Sarah Hrdy and Brenda Bradley for helpful comments on an earlier version of this manuscript. Fieldwork from 2004–present was supported by the National Science Foundation (BCS 0921013), National Geographic Society, Liz Claiborne and Art Ortenberg Foundation, Margot Marsh Biodiversity Foundation, Conservation International, Conservação Internacional-Brasil, and the University of Wisconsin-Madison (to K.B.S.); Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Proc. 484389/2006-8, 305462/2007-5, and 479054/2008-8) (to S.L.M.); sample collection was supported by CNPq (Proc. 620064/2006-4 and 620068/2008-6), The Critical Ecosystem Partnership Fund, Fundo de Apoio à Ciência e Tecnologia (FACITEC), and Fundação de Amparo à Pesquisa do Espírito Santo (FAPES) (to V.F.); travel, fellowship, and additional sample collection were supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Fulbright, New York University (NYU), and the New York Consortium in Evolutionary Primatology (NYCEP; National Science Foundation DGE 0333415) (to P.B.C.); and labwork was supported by NYU and NYCEP (to A.D.).

1. Port M, Kappeler PM (2010) The utility of reproductive skew models in the study of male primates, a critical evaluation. *Evol Anthropol* 19:46–56.
2. Altmann J, et al. (1996) Behavior predicts genes structure in a wild primate group. *Proc Natl Acad Sci USA* 93:5797–5801.
3. Surbeck M, Mundry R, Hohmann G (2011) Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proc Biol Sci* 278: 590–598.
4. Pope T (1990) The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. *Behav Ecol Sociobiol* 27:439–446.
5. Gerloff U, Hartung B, Fruth B, Hohmann G, Tautz D (1999) Intracommunity relationships, dispersal pattern and paternity success in a wild living community of Bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proc Biol Sci* 266:1189–1195.
6. Vigilant L, Hofreiter M, Siedel H, Boesch C (2001) Paternity and relatedness in wild chimpanzee communities. *Proc Natl Acad Sci USA* 98:12890–12895.
7. Bradley BJ, et al. (2005) Mountain gorilla tug-of-war: Silverbacks have limited control over reproduction in multimale groups. *Proc Natl Acad Sci USA* 102:9418–9423.
8. Muniz L, et al. (2010) Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. *Am J Primatol* 72:1118–1130.

9. Boesch C, Kohou G, Néné H, Vigilant L (2006) Male competition and paternity in wild chimpanzees of the Taï forest. *Am J Phys Anthropol* 130:103–115.
10. Wroblewski EE, et al. (2009) Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Anim Behav* 77:873–885.
11. Newton-Fisher NE, Thompson ME, Reynolds V, Boesch C, Vigilant L (2010) Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *Am J Phys Anthropol* 142:417–428.
12. Langergraber KE, Mitani JC, Vigilant L (2007) The limited impact of kinship on cooperation in wild chimpanzees. *Proc Natl Acad Sci USA* 104:7786–7790.
13. Strier KB (1997) Mate preferences of wild muriqui monkeys (*Brachyteles arachnoides*): Reproductive and social correlates. *Folia Primatol (Basel)* 68:120–133.
14. Strier KB, Dib LT, Figueira JEC (2002) Social dynamics of male muriquis (*Brachyteles arachnoides hypoxanthus*). *Behaviour* 139:315–342.
15. Strier KB, Boubli JP, Possamai CB, Mendes SL (2006) Population demography of Northern muriquis (*Brachyteles hypoxanthus*) at the Estação Biológica de Caratinga/ Reserva particular do Patrimônio Natural-Feliciano Miguel Abdala, Minas Gerais, Brazil. *Am J Phys Anthropol* 130:227–237.
16. Strier KB, Ziegler TE (1997) Behavioral and endocrine characteristics of the reproductive cycle in wild muriqui monkeys, *Brachyteles arachnoides*. *Am J Primatol* 42: 299–310.
17. Pissinatti A, Coimbra-Filho AF, Rylands AB (1998) Observations on reproduction and behavior of the muriqui, *Brachyteles arachnoides*, in captivity. *Neotrop Primates* 6: 40–45.
18. Strier KB, Mendes SL, The northern muriqui (*Brachyteles hypoxanthus*): Lessons on behavioral plasticity and population dynamics from a critically endangered primate. *Long-Term Studies of Primates*, eds Kappeler PM, Watts D (Springer-Verlag, Heidelberg).
19. Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol* 16:1099–1106.
20. Nonacs P (2000) Measuring and using skew in the study of social behavior and evolution. *Am Nat* 156:577–589.
21. Alberts SC, Watts HE, Altmann J (2003) Queuing and queue-jumping: Long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Anim Behav* 65:821–840.
22. Possamai CB, Young RJ, de Oliveira RC, Mendes SL, Strier KB (2005) Age-related variation in copulations of male northern muriquis (*Brachyteles hypoxanthus*). *Folia Primatol (Basel)* 76:33–36.
23. Strier KB (2008) The effects of kin on primate life histories. *Annu Rev Anthropol* 37: 21–36.
24. Hawkes K (2003) Grandmothers and the evolution of human longevity. *Am J Hum Biol* 15:380–400.
25. Furuichi T (2011) Female contributions to the peaceful nature of bonobo society. *Evol Anthropol* 20:131–142.
26. Tolentino K, Roper JJ, Passos FC, Strier KB (2008) Mother-offspring associations in northern muriquis, *Brachyteles hypoxanthus*. *Am J Primatol* 70:301–305.
27. Lukas D, Reynolds V, Boesch C, Vigilant L (2005) To what extent does living in a group mean living with kin? *Mol Ecol* 14:2181–2196.
28. Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. *Science* 302:1231–1234.
29. Silk JB, et al. (2009) The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proc Biol Sci* 276:3099–3104.
30. Stumpf RM (2011) Chimpanzees and bonobos. *Primates in Perspective*, eds Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (Oxford University Press, New York), 2nd Ed, pp 340–356.
31. Hrdy SB (2009) *Mothers and Others* (Harvard University Press, Cambridge, MA).
32. Mendes SL, et al. (2005) Directives for the conservation of the northern muriqui, *Brachyteles hypoxanthus* (Primates, Atelidae). *Neotrop Primates* 13(Supplement): 7–18.
33. Strier KB, Mendes SL, Santos RR (2001) Timing of births in sympatric brown howler monkeys (*Alouatta fusca clamitans*) and northern muriquis (*Brachyteles arachnoides hypoxanthus*). *Am J Primatol* 55:87–100.
34. Morin PA, Chambers KE, Boesch C, Vigilant L (2001) Quantitative polymerase chain reaction analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). *Mol Ecol* 10:1835–1844.
35. Taberlet P, et al. (1996) Reliable genotyping of samples with very low DNA quantities using PCR. *Nucleic Acids Res* 24:3189–3194.
36. Possamai CB, Young RJ, Mendes SL, Strier KB (2007) Socio-sexual behavior of female northern muriquis (*Brachyteles hypoxanthus*). *Am J Primatol* 69:766–776.
37. Muniz L, et al. (2006) Father-daughter inbreeding avoidance in a wild primate population. *Curr Biol* 16:R156–R157.