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Social Behavior, Reproductive Strategies, and Population Genetic Structure of *Lagothrix poeppigii*

Anthony Di Fiore[1,3] **and Robert C. Fleischer**[2]

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*For species of primates in which females emigrate, we would expect males within groups to be related to one another. Kin selection theory suggests that these males should associate preferentially with one another, be more affiliative and cooperative with one another than females are, and compete less overtly with one another over reproductive opportunities than males in female philopatric taxa do. Precisely these patterns of social behavior characterize well-studied populations of 2 of the 3 atelin primate genera: spider monkeys (*Ateles*) and muriquis (*Brachyteles*). For the third atelin genus,* Lagothrix*, patterns of intragroup social behavior have been less well-documented. We studied the social and reproductive behavior of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Ecuador during a one-year observational study and subsequently used molecular techniques to investigate population genetic structure and dispersal patterns for this taxon.*

Among adult male woolly monkeys, both affiliative and agonistic interactions were rare, and males were seldom in close proximity to one another. Relationships among male woolly monkeys are best characterized as tolerant, especially in the context of mating wherein direct competition among males was minimal despite the fact that females mated with multiple males. Relationships among females were likewise generally tolerant but nonaffiliative, though females often directed harassment towards copulating pairs.

[1] Department of Anthropology and Center for the Study of Human Origins, New York University and NYCEP (New York Consortium in Evolutionary Primatology).

[2] Genetics Program, Department of Systematic Biology, National Museum of Natural History Smithsonian Institution.

[3] To whom correspondence should be addressed at Department of Anthropology, New York University, Rufus Smith Hall, Room 802/803, 25 Waverly Place, New York, NY 10003; e-mail: anthony.difiore@nyu.edu.

Affiliative interactions that did occur among woolly monkeys tended to be directed either between the sexes—primarily from female to male—or from younger towards older males, and the proximity partners of females tended to be members of the opposite sex. These results suggest that bonds between the sexes may be more important than same-sex social relationships and that direct female-female competition is an important feature of woolly monkey reproductive biology. Our genetic results indicate that, as in other atelins, dispersal by females is common, but some male dispersal likely occurs as well. In some but not all groups we studied, nonjuvenile males within social groups were more closely related to one another on average than females were, which is consistent with greater male than female philopatry. However, differences in these patterns among our study groups may reflect local variation in dispersal behavior.

KEY WORDS: atelins; woolly monkeys; *Lagothrix*; social behavior; mating strategies; female competition; PCR; microsatellite; population structure; intragroup relatedness.

INTRODUCTION

Many species of primates are characterized by female philopatry and male-biased dispersal, resulting in social groups organized around a core of related females (Gouzoules and Gouzoules, 1987; Pusey and Packer, 1987). However, the Atelinae—woolly monkeys (*Lagothrix*), spider monkeys (*Ateles*), and muriquis (*Brachyteles*)—are unusual in that dispersal is female-biased and males are believed to be the more philopatric sex (Di Fiore and Campbell, in press). Among muriquis and spider monkeys, dispersal by females has been well-documented in observational studies and appears to be obligate. For example, in a long-term field study of muriqui population dynamics, Strier (1991) noted 5 confirmed or suspected cases of emigration by parous adult females as well as 8 cases of immigration by nulliparous females but saw no cases of transfer by males. Similarly, although information on dispersal in wild spider monkeys is scarce, all observations to date suggest that females leave their natal communities before first reproduction, while males become sexually active in their natal groups (Symington, 1987b, 1988a, 1990; S. Suarez, personal communication). For woolly monkeys, too, the available observational and molecular data suggest substantial female dispersal (Nishimura, 1990b, 2003; Stevenson *et al.*, 1994; Stevenson, 2002; Di Fiore, 2002), though the degree to which males remain as adults in their natal groups is unknown. During 12 years of observation, Nishimura (2003) observed multiple cases of female transfer, including secondary dispersal, and no case of male dispersal in a population of Colombian woolly monkeys (*Lagothrix lugens*), but multiple solitary adult and subadult males and a bachelor group of 5 males of various age have been noted in populations of *Lagothrix poeppigii* (Di Fiore, personal observation), suggesting possible intrageneric variation in dispersal patterns.

In their apparent expression of female-biased dispersal and greater male than female philopatry, atelin primates converge with African hominoids, the only other major clade of primates in which these features of social organization are common. Kin selection theory suggests that when males within social groups or within local populations are closely-related, such as is presumably the case in male-philopatric species (Vigilant *et al.*, 2001), there may be important implications for the patterning of intra-group social behavior and for the expression of various forms of reproductive competition (Wrangham, 1980; Silk, 1987, 2002; Chapais, 2001). In particular, we might expect males in these species to associate preferentially with one another, to be more affiliative and cooperative with one another than females are with each other, particularly in the context of competitive intergroup encounters, and perhaps to compete less overtly with one another over reproductive opportunities. In fact, the close bonds among some pairs of male chimpanzees and their close cooperation during hunting and boundary patrolling, which are both conspicuous features of chimpanzee behavior, have been interpreted in terms of kin selection among closely related males (Goodall, 1986; Morin *et al.*, 1994), though recent genetic data on male relatedness is forcing a reevaluation of some of these conclusions (Gagneux *et al.*, 1999; Mitani *et al.*, 2000; Vigilant *et al.*, 2001).

For 2 atelin genera—the spider monkeys and muriquis—patterns of male behavior predicted by kin selection theory are generally substantiated. In both taxa, males spend more time in proximity to other males than to females (Ahumada, 1989; Strier, 1990, 1997b). Moreover, male spider monkeys are far more affiliative with one another than females are, and they cooperate to defend a community home range against males from adjacent communities (Cant, 1977; Fedigan and Baxter, 1984; Symington, 1987a, 1990; van Roosmalen and Klein, 1988). Male muriquis show similar male-bonded behavior (Strier, 1994a, 1997b). Less is known about the patterning of social relationships within and between the sexes in woolly monkeys, which live in large social groups typically containing 20–40 members with multiple reproductive age individuals of each sex. Although several populations of woolly monkeys have been the foci of long-term field research (Soini, 1986; Nishimura, 1990, 1994; Stevenson *et al.*, 1994; Defler, 1995; Defler and Defler, 1996; Di Fiore, 1997, 2003, 2004; Stevenson, 2002), little has been published specifically on their social behavior (but see Nishimura, 1994; Stevenson, 1999). Nonetheless, the few reports available hint that there might be important differences between woolly monkeys and the other atelins. For example, in contrast to the affiliative relationships seen among male spider monkeys and muriquis, Stevenson (1999) found that adult male woolly monkeys tended to have fewer individuals around them than members of other age-sex classes did, and Nishimura (1994) found that almost all affiliative interactions—e.g., close proximity, grooming—occurred between individuals of the opposite rather than the same sex. Interestingly, to date no genetic study has assessed patterns of kinship or average male and female relatedness within groups in any atelin taxon, though such data would clearly be useful to evaluate the extent to which kin selection might be invoked to explain patterns of social behavior in these primates.

We present the results of 2 complementary studies that together provide insights into the social behavior and population genetic structure of lowland woolly monkeys (*Lagothrix poeppigii*). We first summarize data on intragroup spatial relations, grooming patterns, agonism, and reproductive behavior for a population in the Upper Amazon of Ecuador, based on a year-long field study of several habituated social groups. We then describe the results of a molecular study of genetic variation and relatedness at several hierarchical levels of woolly monkey population organization. In presenting our genetic results, we first characterize the genetic variation within a regional woolly monkey population, including the study site at which the behavioral data were collected. We then look in detail at likely kin relationships between individuals within and between 2 local populations, both to explore this aspect of population structure and to test the following specific predictions derived from the hypothesis that dispersal is female-biased in woolly monkeys:

1. If there is greater male than female philopatry then
    - A. average pairwise relatedness among nonjuvenile males within social groups should be greater than among nonjuvenile females, and
    - B. nonjuvenile males should have more nonjuvenile same-sex kin in their social groups than nonjuvenile females do.
2. If both sexes disperse but females tend to disperse farther distances than males then
    - A. average relatedness between pairs of males from different social groups within a local population should be greater than that among females,
    - B. males should have more same-sex kin in their local population than females do, and
    - C. any evidence of genetic substructuring to the regional population or of an association between genetic distance and geographic distance between pairs of individuals sampled from

different groups should be more apparent among males than among females.

Finally, we discuss the implications of our genetic results for explaining some of the patterns of social behavior revealed in our observational study, and we compare the social and reproductive strategies of woolly monkeys to those of other atelin primates.

METHODS

Study Area and Subjects

We conducted the field study within Yasuní National Park and the adjacent Huaorani Ethnic Reserve in Amazonian Ecuador (Fig. 1A). Together, they constitute a roughly 1600-km^2 area of largely pristine tropical rain forest. The primate community of the region comprises 10–12 species

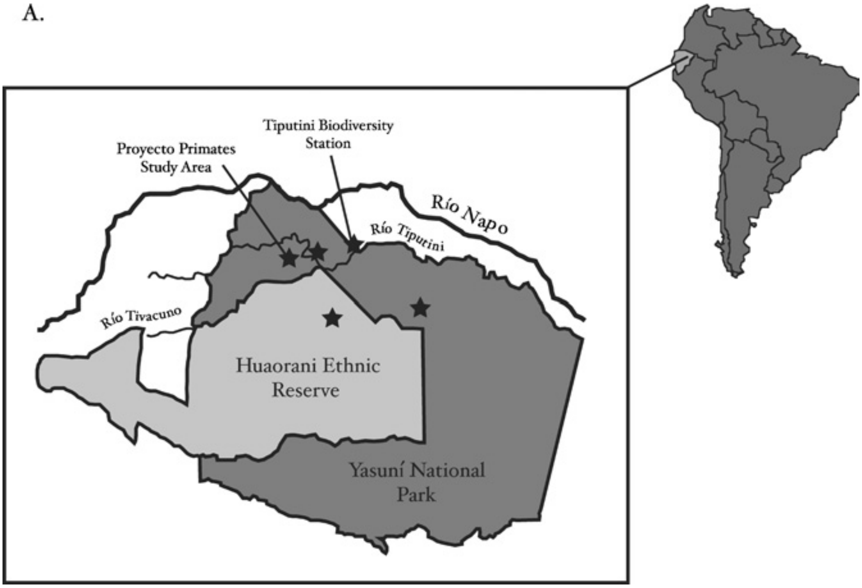


Fig. 1. [A] Yasuní National Park and the Huaorani Ethnic Reserve in eastern Ecuador. Locations of the Proyecto Primates Study Area, the Tiputini Biodiversity Station, and other genetic sampling sites are indicated by stars. [B] Home ranges of the 2 primary study groups (1 and 2), for which we collected behavioral data in 1995–1996. [C] Home ranges of 5 study groups for which were collected tissue and fecal samples in 1998–1999. Groups 4 and 5 were sampled intensively.

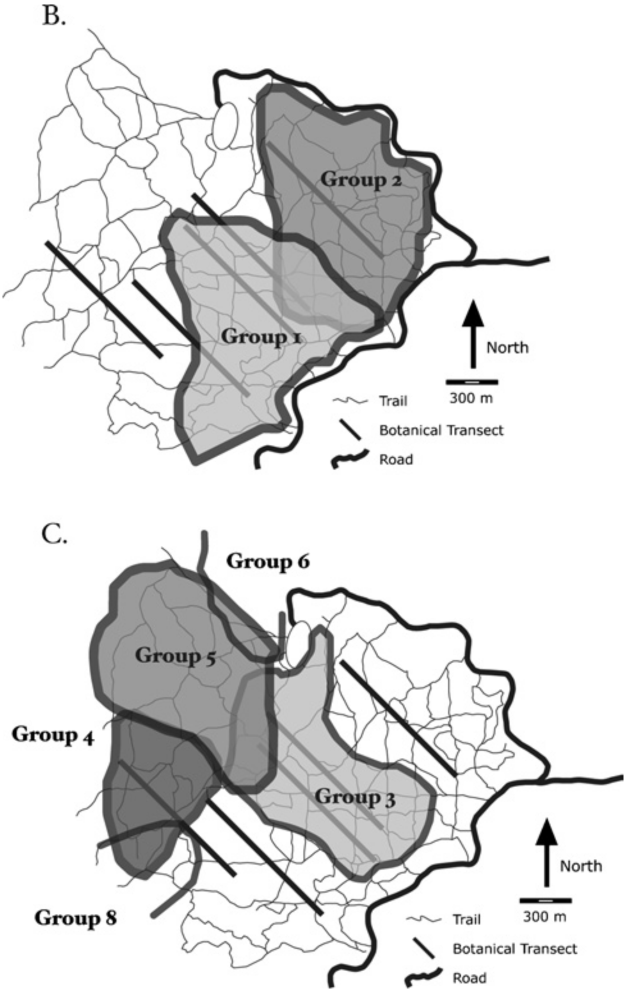


Fig. 1. Continued.

from 10 genera, including 2 atelins (spider monkeys and woolly monkeys), and the region boasts one of the highest diversities of woody plant species in the neotropics (Romoleroux *et al.*, 1997; Pitman *et al.*, 1999). Yasuní woolly monkeys live in large social groups of 20–40 individuals containing multipleadult males and reproductive-age females, and the population density of *Lagothrix* in this region is higher than reported elsewhere (Di Fiore, 2001,2003).

Behavioral Sampling Methods

Di Fiore studied several habituated social groups of woolly monkeys between April 1995 and March 1996 in the Proyecto Primates Study Area in the northwest corner of Yasuní National Park (Fig. 1B). All groups were of typical composition containing between 2 and 5 adult males, several subadult males, 9–11 reproductive-age females, and 4–6 juveniles. The 2 groups that ranged nearest to an access road (Groups 1 and 2) were the principal ones sampled during the behavioral study (Di Fiore, 1997, 2001; Di Fiore and Rodman, 2001).

Behavioral data were collected during 2-5-day follows of each group each month, with each follow comprising 2 days of instantaneous scan sampling and 3 days of focal sampling (Altmann, 1974). Scans were performed at 10-min intervals between 0630 and 1730 h and lasted 5 min. During a scan, a variety of data on each individual that came into view over the course of the scan were recorded, most importantly, its identity (or age-sex class, if individual identity could not be determined), its behavior, and the identity of and distance to its nearest conspecific neighbors. Four nonjuvenile age-sex classes were recognized: adult males; subadult males; adult females with dependent offspring (either being carried or traveling in clear association with the female); and nonjuvenile females, which could be either adults or subadults, unburdened by dependent offspring. Omitting 42 scans taken during aggressive encounters between groups and 27 taken on rarely-encountered solitary animals, a total of 4227 scans comprising 19,656 individual behavioral records and representing roughly 705 h of observation was collected, including 2242 scans (373.7 h) on Group 1 and 1602 scans (267 h) on Group 2. The remaining scans were collected either on other groups in the area or on occasional peaceful multigroup associations involving one of the principal study groups (Di Fiore and Rodman, 2001; Di Fiore, 1997, 2003).

During focal sampling, observations we alternated between nonjuvenile males and nonjuvenile females roughly every hour according to a regular schedule. The first individual of the target age-sex class to come into view we selected as a focal subject, and a continuous record of its activity was dictated onto microcassette tapes, paying particular attention to social behaviors such as aggression, mating, grooming, and time spent in proximity (≤ 2 m) or in physical contact with other animals. When a focal subject went out of view, observations were switched to the next-encountered individual of the same age-sex class, and a new sample was started. If a focal subject disappeared within 30 sec of starting a sample, the sample was discarded, and sampling was always terminated once 30 min of data on an individual was obtained. We analyzed *ca.* 160 h of focal data collected during the last 6 mo of the behavioral study for the results that we discuss here.

Molecular Methods

We collected tissue and fecal samples of woolly monkeys primarily during 1998 and 1999 from multiple study groups in 2 local populations: the Proyecto Primates Study Area and the area surrounding the Tiputini Biodiversity Station (TBS) *ca.* 36 km away. Within the Proyecto Primates Study Area, it was unfortunately impossible to sample the same individuals or the same study groups for which behavioral data had been collected because some of them had been taken by local hunters. Instead, we targeted 2 newly habituated groups (Groups 4 and 5) that were similar in composition and also collected additional samples from several adjacent groups (Fig. 1C). For the TBS site, samples are principally from a single social group, group T, which ranged close to the research station and contained *ca.* 30 independently-locomoting individuals; we also collected a few samples from each of 3 adjacent social groups. We collected 2 additional tissue samples from a social group near the Estación Científica Yasuní, between the 2 primary sampling sites, and salvaged several others tissue samples opportunistically, during 1998–1999 and subsequently, from woolly monkeys killed by indigenous hunters at several other locations in Yasuní National Park and the Huaorani Ethnic Reserve (Fig. 1A). Finally, during fieldwork in the summers of 2000, 2001, and 2002, we collected samples within the Proyecto Primates Study Area from Group 3 and a small "bachelor" band comprising 5 males various ages. We used only the 56 samples from 1998–1999 in calculating background population allele frequencies.

Tissue samples, except those from hunted monkeys, were collected remotely using biopsy darts (Karesh *et al.*, 1987) constructed in the field. We stored samples from 1998–1999 in NaCl-saturated DMSO preservation buffer (20% DMSO, 5 M NaCl, 0.25 M EDTA) and more recent samples in 90–100% ethanol. The few fecal samples analyzed in the data set were collected fresh and stored either in lysis buffer (1% SDS, 100 mM Tris-HCl, 100 mM NaCl, 10 mM EDTA) or 90–100% ethanol or were desiccated and stored in silica gel (Sigma$^{\text{TM}}$ Type II Silica Beads, 1/8th.)" We maintained both tissue and fecal samples in the field at room temperature for up to 6 mo before transport to the laboratory, and in the laboratory at –20°C for up to several years before DNA extraction.

We performed extractions via commercial nucleic acid extraction kits for tissue (QIAgen$^{\text{TM}}$ DNeasy Tissue Kit) and feces (QIAmp$^{\text{TM}}$ DNA Stool Mini Kit). We genotyped each extracted sample at 6–7 dinucleotide-repeat microsatellite loci that were identified in woolly monkeys via a subtractive enrichment protocol (Hamilton *et al.*, 1999). Microsatellite primer sequences, PCR mixes, and thermal-cycling profiles for each of the loci were summarized by Di Fiore and Fleisher (2004). We fluorescently-labeled the 5' end of either the forward or reverse amplification primer at each locus. We combined 1–4 microliters of PCR product dilated up to 1:20 in water, with a fluorescent size standard (ABI^{TM} GeneScan-350[Tamra] or GeneScan-500[Tamra]) and electrophoresed it on either an ABI^{TM} 373XL Automated DNA Sequencer or an ABI Prism$^{®}$ 310 Genetic Analyzer for genotyping. We repeated genotypes 2–8 times for most individuals at most loci. The one exception was for locus 113, the last to be optimized, for which several individuals could be genotyped only once due to sample volume limitations. However, all individuals for which only a single genotype could be made at the locus ($N = 18$) possessed clean, heterozygous genotypes, thus allelic dropout is unlikely be a problem for allele frequency and relatedness estimates.

Although it was possible to determine the sex of most individuals in the field, for undetermined individuals and for all but 2 of the field-sexed monkeys, i.e., for 97% of all individuals sampled, We verified sex genetically either by amplifying homologous regions of the zinc finger protein gene on the X and Y chromosomes via published PCR primers and protocols (Wilson and Erlandsson, 1998) or by multiplex amplification of shorter, nonhomologous regions of the X (amelogenin) and Y (SRY) chromosomes (Di Fiore, in press). In anthropoid primates, the X and Y amplicons produced by either method show fixed differences in size (~1100 vs. ~700 bp for the ZFX/ZFY assay, ~200 vs. ~165 bp for the amelogenin X/SRY assay), thus males should display 2 product fragments, while females should display only the larger one. We used benchtop electrophoresis in either 1.5–2.0% agarose minigels (for ZFX/ZFY) or 8–10% polyacrylamide minigels (for amelogenin X/SRY) to separate PCR product fragments and to assign sex. For the 7 cases in which an assigned field sex did not match the genetic sex of a sample, we used the genetic sex.

We considered any sample that had the same microsatellite genotypes at all screened loci and that were assigned the same genetic sex, regardless of the group or sex assigned tentatively in the field, to be multiple samples of the same individual. Given population allele frequencies based on all individuals sampled in 1998–1999, the probability that any 2 individuals drawn at random from the population would share the same multilocus genotype by chance, i.e., the total probability of identity, $P_{(ID)}$ (Paetkau and Strobeck, 1994) was <1 in 68 million, and the chance probability of identity among full siblings ($P_{(ID)SIB:}$ Evett and Weir, 1998) was < 1 in 540. The final data set, derived from 101 genotyped samples, comprised 56 individuals

Table I. Individuals and samples used in molecular analyses

Population	Sex			# Individuals	# Samples
	Males	Females	Undetermined		
Proyecto Primates	19	20	2	41	71
Group 4	3	8	0		
Group 5	9	8	0		
Additional[a]	7	4	2		
Tiputini Biodiversity Station	10	10	0	20	25
Group T	4	6	0		
Additional[b]	6	4	0		
Other Sites	1	4	0	5	5
Estación Científica Yasuní	0	2	0		
Kilometer 77	1	1	0		
Unknown	0	1	0		
Total	30	34	2	66	101

[a] (Groups 3, 6, and 8, undetermined groups and bachelor group)
[b] (Groups R, G, H and a solitary adult male)

sampled in 1998–1999 plus 10 additional monkeys sampled in 2000–2002 (Table I).

We used several population genetics software packages to analyze the extent and patterning of molecular diversity in the Yasuní woolly monkey population. We used CERVUS 2.0 (Marshall *et al.*, 1998) and FSTAT 2.9.3 (Goudet, 2001) to calculate allele frequencies and to test for deviation from Hardy-Weinberg equilibrium genotype frequency expectations for each microsatellite locus. For these analyses, we used FSTAT 2.9.3 (Goudet, 2001) to estimate θ_{ST} values to examine population subdivision. We calculated pairwise relatedness among individuals within and between groups in the regional population from genotype data via RELATEDNESS 5.0.8 and explored it further via KINSHIP 1.3 (Queller and Goodnight, 1989; Goodnight and Queller, 1999). We derived background population allele frequencies from the total set of monkeys in the 1998–1999 sample, with individuals weighted equally and allele frequency bias corrected by group. We programmed permutation tests of average male versus average female relatedness in Visual Basic for Applications within Microsoft Excel (code available from Di Fiore). We used KINSHIP 1.3 to screen the regional population for pairs of close relatives and to examine the distribution of likely pedigree relationships within and between social groups in the 2 main study populations. Finally, we used Mantel matrix correlation tests, implemented in GENETIX 4.04 (Belkhir *et al.*, 2003), to evaluate the association between pairwise genetic distance and geographic distance for males versus females.

RESULTS

Proximity and Association Patterns

On average, woolly monkeys had ≥1 individual ≤10 m from them during 70% of individual behavioral records and ≤5 m from them during 48% of records; however, they spent relatively little time (*ca.* 5%) in physical contact with other individuals. These averages differed depending on the age-sex class of the animal. Subadult and adult males had neighbors around them less often than females did if juveniles are included in the data set (54.3% and 59.6% of records for adult and subadult males versus 62.4% and 83.7% for unburdened females and females with dependents. This pattern changes somewhat if juveniles are excluded; then adult males and females with dependent offspring had nonjuvenile neighbors less often (35.0% and 33.0%) than subadult males or unburdened females did (41.9% and 41.4%). Focusing on nonjuveniles and dividing the data set into males versus females, it is apparent that males tended to associate with nonjuvenile members of each sex roughly in proportion to their representation in the population, i.e., the number of times that a male had a male versus a female proximity partner does not differ significantly from expectation based on the nonjuvenile sex ratio of the population (Chi Square test: $\chi^2 = 1.6$, $df = 1$, NS; Fig. 2A). However, most male-male neighbor dyads involved either subadult-subadult or subadult-adult pairs; far fewer than expected by chance involved 2 adult males, suggesting that adult males avoid one another (Chi Square test: $\chi^2 = 25.8$, $df = 2$, $P < 0.001$). For females, nonjuvenile nearest neighbors are significantly more likely than expected to be males and less likely to be other females (Chi Square test: $\chi^2 = 48.7$, $df = 1$, $P < 0.001$, Fig. 2B). Moreover, most female-female dyads involved either 2 unburdened females or, less commonly, one female with a dependent and one without; far fewer female-female dyads consisted of 2 females with dependents than expected by chance (Chi Square test, $\chi^2 = 285.7$, $df = 2$, $P < 0.001$).

Grooming

We observed 57 bouts of grooming during scan samples over the course of the year-long behavioral study and recorded an additional 44 bouts during focal sampling in the last 6 mo of that study (Table II). The few grooming bouts recorded in their entirety were generally short and typically lasted <5 min. Adult males were the recipients of most bouts of grooming (55%) and were the age-sex class least likely to groom others. In fact, males as a whole were significantly more often the recipients of grooming and

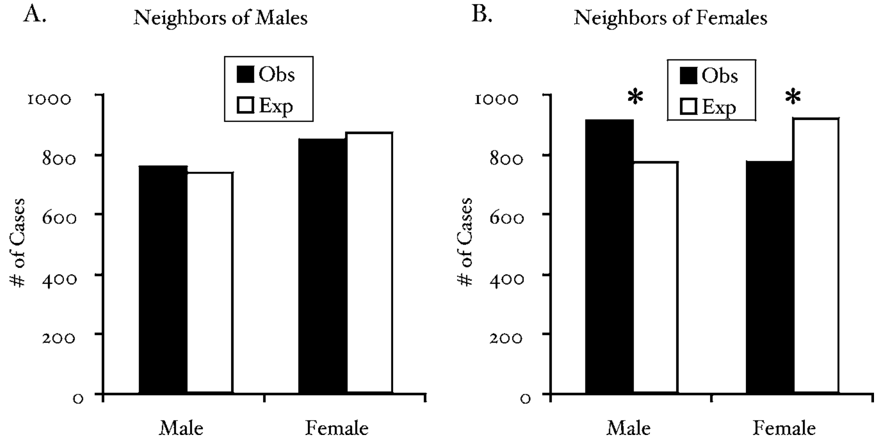


Fig. 2. Nearest neighbors of nonjuvenile woolly monkey males [A] versus females [B]. Males had males versus females as their nearest neighbors roughly as often expected by chance, given the nonjuvenile sex ratio, while females had males as neighbors more often and females as neighbors less often than expected by chance. Asterisk (*) indicates a statistically-significant difference (Chi Square tests, $P < 0.05$).

Table II. Percent distribution of 101 grooming bouts noted during scan and focal samples according to the age-sex class of the groomer and recipient

	Recipient						
Groomer	AM	SM	AFD	AFU	JUV	Unknown	Total
AM	2.0	0.0	2.0	1.0	0.0	0.0	5.0
SM	27.7	2.0	3.0	4.0	1.0	0.0	37.6
AFD	6.9	1.0	0.0	0.0	4.0	0.0	11.9
AFU	10.9	6.9	0.0	1.0	1.0	1.0	20.8
JUV	5.9	1.0	4.0	2.0	2.0	1.0	15.8
Unknown	2.0	0.0	0.0	3.0	0.0	4.0	8.9
Total	55.4	10.9	8.9	10.9	7.9	5.9	100.0

Note. AM: adult male, SM: subadult male, AFD: adult female with a dependent, AFU: adult female unburdened by a dependent, JUV: juvenile.

females the recipients less often than expected by chance, given their respective proportional representation in the study population (Chi Square test: $\chi^2 = 8.8$, $df = 1$, $P < 0.01$). Subadult males groomed adult males during 74% of their 38 bouts, and subadult male-adult male dyads were, by far, the dyad with the highest grooming rate. As a result, male-male grooming dyads were more common than expected by chance, and female-female dyads less common (Chi Square test: $\chi^2 = 21.9$, $df = 2$, $P < 0.01$), the latter contributing to only 1% of all grooming interactions.

Intragroup Agonism and Dominance Relations

During scan and focal sampling, we recorded 215 agonistic interactions, excluding incidents associated with harassed matings (Table III). About 41% ($N = 89$) of agonistic interactions involved passive supplants or displacements, wherein one monkey approached another to ≤10–15 m and the second monkey moved off without an overt interaction between them. However, this value is undoubtedly an underestimate, given the likelihood of missing such subtle behavior under the poor observation conditions of the rain forest. The remaining agonistic interactions involved threat displays, lunges, chases, or direct physical conflict. All but 3 agonistic interactions involved just 2 individuals. In one of the triadic interactions, an adult female intervened in a fight between 2 nonadult individuals (further determination of the age-sex class of the original participants was impossible); in the second, an adult male intervened in a fight between 2 adult females; and in the third, an adult male chased a subadult male and an unidentified animal simultaneously.

The contexts in which agonistic behavior occurred could usually not be determined, but ≥21% of the agonism recorded in scan samples took

Table III. Percent distribution of 215 agonistic interactions noted during scan and focal sample according to the age-sex class of the aggressor and recipient. Values in parentheses exclude 89 displacement interactions

	Recipient							
Aggressor	AM	SM	AFD	AFU	JUV	Unknown	Other Species	Total
AM	2.8 (0.0)	5.1 (2.4)	1.9 (1.6)	8.8 (5.6)	5.1 (4.8)	3.7 (2.4)	0.9 (0.8)	28.4 (17.5)
SM	0.0 (0.0)	2.3 (1.6)	2.3 (1.6)	5.6 (5.6)	2.3 (1.6)	1.4 (1.6)	0.0 (0.0)	14 (11.9)
AFD	0.0 (0.0)	1.4 (0.8)	1.9 (1.6)	2.3 (1.6)	1.9 (2.4)	0.5 (0.8)	0.0 (0.0)	7.9 (7.1)
AFU	0.0 (0.0)	4.2 (3.2)	1.4 (2.4)	9.3 (9.5)	0.9 (0.8)	0.9 (0.8)	0.0 (0.0)	16.7 (16.7)
JUV	0.0 (0.0)	0.0 (0.0)	0.5 (0.8)	0.5 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.9 (1.6)
Unknown	0.9 (0.0)	0.9 (0.8)	0.9 (1.6)	2.3 (2.4)	0.5 (0.8)	26.5 (39.7)	0.0 (0.0)	32.1 (45.2)
Total	3.7 (0.0)	14 (8.7)	8.8 (9.5)	28.8 (25.4)	10.7 (10.3)	33 (45.2)	0.9 (0.8)	100.0 (100.0)

Note. AM: adult male, SM: subadult male, AFD: adult female with a dependent, AFU: adult female unburdened by a dependent, JUV: juvenile.

place in feeding trees, suggesting that some direct intragroup competition over food resources occurs. Conversely, individuals were much more likely to be close to one another while feeding, which is likely to affect the frequency with which agonistic interactions occur. Only one case of agonism potentially occurred between males over access to estrous females, despite the fact that most copulations took place within view of other group members and were often conspicuous events attended to by other individuals. This event involved a small subadult male that began to wrestle—a behavior commonly associated with play—with a larger subadult male while the latter was engaged in a mount, leading to the breakup of the mount.

Considering only the agonistic interactions, including displacements, amongst nonjuveniles in the 2 main study groups and for which the sex class of both participants was known, agonism by males was more common than expected by chance and agonism by females was less common than expected (Chi Square test: $\chi^2 = 4.0$, $df = 1$, $P < 0.05$). However, the frequency with which males versus females were the victims of agonism was not statistically different ($\chi^2 = 2.5$, $df = 1$, NS), and the distribution of agonistic interactions across either same-sex or opposite-sex dyads did not deviate significantly from expected ($\chi^2 = 0.3$, $df = 2$, NS). However, when displacements are excluded, male-male agonism is rarer and female agonism is more common, suggesting that agonism between males is less overt than that between females.

Given that male philopatry is presumed to characterize all atelins, a further focus on patterns of agonism among males is in order. At Yasuní, adult male woolly monkeys interacted aggressively with one another only rarely; the 6 cases of intra-group agonism between adult males recorded during focal and scan samples consisted entirely of passive displacements. Adult males were never the targets of overt physical aggression, with the exception of 2 cases recorded *ad libitum* on focal sampling days that seemed to deal directly with male membership in a social group. The first involved 2 adult males in Group 1 that engaged in prolonged fights ($>$10 min) on $\geq$2 occasions separated by several days during August 1995. The victim disappeared from the group shortly thereafter and was not seen in the study area during the remainder of the study. The second exception involved $\geq$1 males from Group 2 and a solitary adult male that associated with the group for several days during November 1995. When we first saw him in the group, he had a large wound on the side of his mouth, and over the next day he fought repeatedly with $\geq$1 of the resident males several times before again disappearing. Several months later, another solitary adult male (perhaps the same one) used portions of Group 2's home range and once was noted to move off hurriedly when the group approached.

In general, dominance relations among males seemed to be related to age and body size: adult males could regularly supplant large subadult males that could supplant smaller subadult and juvenile males; however, too few interactions occurred between adult males to comment on the presence or absence of a formal dominance hierarchy with any certainty, though it is clear that adult males were dominant over all other age-sex classes, probably because of their larger size. The fact that the majority of adult females could not be distinguished individually in the field makes it difficult to comment on the nature of female dominance relations at Yasuní, though female-female aggression was fairly common. We never observed coalitionary behavior, though, animals of both sexes occasionally intervened in aggressive disputes between other monkeys.

Mating Behavior

We witnessed 44 copulatory bouts during scan sampling and another 15 during focal samples or *ad libitum* during the last 6 mo of the study. As described for other populations of both wild and captive woolly monkeys, mounts were often preceded by females actively soliciting the male. Solicitations most commonly consisted of an open-mouthed grin accompanied by head-shaking directed towards a single male $\leq$10 m from the female. On occasion, the male repeated the display back at the female. The same facial expression was also occasionally performed by both sexes during mounts. Solicitations did not always result in copulation; males sometimes ignored the solicitation completely or inspected the genital area of the female and then lost interest. Occasionally, females, pursued a seemingly uninterested male (typically a subadult), repeatedly approaching and soliciting him, sometimes to the apparent annoyance of the male who might threaten or chase her away.

Of the 59 mounts, 28 were performed by adult males, 29 were performed by subadult males, one involved a male of undetermined maturity, and one involved a small juvenile male. Average mating bout duration was 236 sec based on 25 mounts for which we recorded start and stop times. Mounts ranged from 12 sec to 25 min, though it is likely that the shortest of them did not involve intromission. During completed copulatory bouts, males generally appeared to remain intromitted for periods up to several min following ejaculation.

Mating occurred during all months of the study except May 1995. On 7 of 30 separate dates on which copulations were seen, multiple males (up to 3) were seen mating. On 2 days, the same male mated multiple times with the same female: for 1 of these days, the adult male that mated twice was the only male we observed to mate, and for the second, he and a large subadult male mated with the same female 2 and 3 times, respectively, and a different subadult male also mated that day.

Frequently, several other animals were spectators during copulations, resting within 2–5 m of the copulating pair and clearly watching the mating. Spectators most commonly were other adult females and juveniles and only rarely other mating-age males. Twelve copulations (20%), involving ≥3 females in 3 mo of the year, were harassed by other adult females, and another 2 copulations in 2 different mo were potentially broken up by harassment. Harassment typically involved the harassing female standing in front of the copulating pair, baring her teeth, and bouncing or branch-shaking at them. Harassment often led to the breakup of a mount, with the male aggressively threatening and chasing off the harasser. Once, a consort subgroup of a subadult male and receptive female was followed by another adult female and her juvenile as they ranged several hundred meters from the main body of the group. The female harassed each attempted copulation by the consorting pair until they rejoined the main group. At least one other case involved several females jointly harassing the mating couple. None of the females targeted for harassment had dependent juveniles obviously associated with them, and females with dependents were harassers in ≥3 cases. Overt harassment of matings by females was not limited to the two principal study groups observed in 1995–1996. During 1998–1999 and again between 2000 and 2003, we noted multiple additional cases of harassment by females in several different social groups of woolly monkeys. Other reproductive-age males did not harass matings; in fact, males were remarkably tolerant of matings by other males.

Nonharassed copulations generally ended with one or both participants moving several meters away from the spot at which mating occurred. Males frequently urinated immediately following copulation. It appeared that there may be some locking of the male and female genitalia during copulation because in at least one instance of harassed mating, the male tried unsuccessfully for several seconds to extricate himself from the female in order to chase off the harassing party, forcing the mating female to move along with him briefly.

Genetic Variation and Population Subdivision

Table IV is a summary of the variation in 7 microsatellite loci for 56 individual woolly monkeys sampled from various sites in Yasuní National Park during 1998 to 1999. We genotyped all individuals at all loci, except for locus 113 for which only 53 individuals could be genotyped. Allelic diversity ranged from 4 to 21 alleles per locus (mean = 10.4 ± 2.3 SE), and several additional alleles were found in the additional monkeys sampled between

Table IV. Characterization of variation at 7 microsatellite loci within 56 individuals woolly monkeys sampled in 1998–1999

Locus	# Alleles	Size range (in base pairs)	Expected heterozygosity (H_e)	Observed heterozygosity (H_o)
1110	11	202–222	0.857	0.857
1115	11	196–226	0.841	0.875
1118	14	128–165	0.894	0.911
157	5	215–223	0.721	0.768
311	5	191–203	0.303	0.321
312	4	186–195	0.584	0.714
113	21	177–225	0.896	0.925
Average	10.1 ± 2.3 S.E.		0.728 ± 0.083 S.E.	0.767 ± 0.080 S.E.

2000 and 2002. Observed heterozygosities ranged from 0.321 to 0.925. For all loci but 1110, observed heterozygosities were slightly higher than expected, but in no case do they differ significantly from ones expected under Hardy-Weinberg equilibrium.

As an estimator of genetic differentiation and population subdivision between the 2 well-sampled local populations—the Proyecto Primates Study Area and TBS—we calculated θ_{ST} (Weir and Cockerham, 1984) based only on individuals sampled in 1998–1999 ($N_{PP} = 34$, $N_{TBS} = 20$) via the program FSTAT 2.9.3 (Goudet, 2001). There is only slight (albeit significant) genetic differentiation between the 2 local populations, with each local population containing *ca.* 98% of the total genetic variance present in the regional sample ($\theta_{ST} = 0.020$, $P < 0.01$), suggesting a very high rate of gene flow between sites.

Average Male and Female Relatedness Within and Between Groups

To test predictions 1A and 2A concerning the patterning of average male and average female relatedness within and between groups, we first used the programs RELATEDNESS 5.0.8 and KINSHIP 1.3 to calculate estimates of relatedness (Queller and Goodnight, 1989) between all pairs of individuals in the population in 1998–1999. We then calculated average coefficients of relatedness (R) among males and among females, first, among pairs within social groups (for the 3 best-sampled groups, Groups 4 and 5 in the Proyecto Primates Study Area and Group T at TBS, using only nonjuveniles) and, second, among all combinations of pairs from different social groups within the same local population (Proyecto Primates and TBS, using all specimens, regardless of age).

At the social group level, average relatedness among males is markedly greater than that among females for the 2 well-sampled social groups in the Proyecto Primates Study Area. For Group 5, the 7 nonjuvenile males were more closely related, on average, than 8 nonjuvenile females were (mean $R_{\mathrm{male}} = 0.197 \pm 0.04$ S.E. versus mean $R_{\mathrm{female}} = 0.054 \pm 0.04$ S.E.). We used a permutation procedure to evaluate the significance of the difference in mean pairwise relatedness among males versus females. We randomly assigned the 15 nonjuveniles from Group 5 to 2 classes, one comprising 7 "males" and the other 8 "females." We repeated the procedure 10,000 times, and for each replication, calculated the difference in mean R between the 2 classes. In 98% of the permutation runs, the difference between the mean R values of the simulated male and female classes was less than the observed difference, i.e., less than 0.143, the value for observed mean $\mathrm{R}_{\mathrm{male}}$−observed mean $\mathrm{R}_{\mathrm{female}}$, indicating significantly greater average male than average female relatedness within the group at $P < 0.05$.

Group 4 contained 3 nonjuvenile males: we collected tissue samples from 2 of them. The pairwise R for them is 0.771, indicating that they were much more closely related than even an average full sibling pair. A fecal sample tentatively attributed to the third nonjuvenile male yielded the same multilocus genotype as a tissue sample assigned in the field to an adult female but genetically sexed as a male. Assuming that the sample, in fact, came from the third male, then the average pairwise relatedness among males in Group 4 is 0.253 ± 0.26 S.E., and average relatedness among 7 nonjuvenile females is considerably lower: 0.089 ± 0.05 S.E. A similar permutation procedure showed that the observed difference in average relatedness among males is greater than that among females in 86% of permutation runs, again providing (albeit somewhat more equivocal) support for the hypothesis that males, on average, are more closely related than females in woolly monkey groups.

In contrast to the Proyecto Primates groups, and counter to our predictions, average male and average female relatedness showed the opposite pattern in Group T at TBS. Although females were not, on average, closely related to one another (mean female $R = 0.011 \pm 0.04$ S.E, $N = 6$ nonjuvenile females), male relatedness in Group T was considerably lower (mean male $R = -0.111 \pm 0.07$ S.E., $N = 4$ nonjuvenile males). In fact, the observed difference between average female pairwise R and average male pairwise R among the samples is greater than that in 90% of 10,000 permutation runs, indicating that the difference approached significance. The marked contrast between this group and those at the Proyecto Primates site is notable and could reflect local variation in dispersal patterns. However, Group T was much less thoroughly sampled than either Group 4 or Group 5 was in the Proyecto Primates Study Area. While we estimate that 50–60% of the total number of individuals in Groups 4 and 5 were sampled, importantly including most or all of the nonjuveniles, that was not the case for the much larger Group T. We suspect that we only managed to collect samples from 1/4–1/3 of T, and ≥2 non-juvenile males that we know of were not sampled, which may contribute, in part, to our not finding greater average male than female relatedness in T.

At the between social-group level, the average pairwise relatedness of males in different social groups within the Proyecto Primates population was greater than that among females (mean $R_{\text{male}} = 0.056$ versus mean $R_{\text{female}} = 0.005$). We tested the significance of the difference with a slightly different permutation test. In 10000 runs, we first randomly assigned the 31 samples from known social groups in the Proyecto Primates population to 2 simulated subpopulations, one comprising 14 individuals and the other 17, as per the sexual ratio in the real population. Then, we calculated the average R between each individual and all other same sex individuals in the population not from the same social group and averaged them across individuals within each subpopulation. The difference in these average "male" and average "female" between group relatedness values for each simulation was then compared to the observed difference. In >94% of runs, the observed difference is greater than the simulated difference, providing fairly strong support for the hypothesis that even if male woolly monkeys are dispersing they are not dispersing as far as females do. However, in the TBS population, the situation was again different: the average degree of relatedness among females in different social groups is higher than that among males (mean $R_{\text{female}} = 0.064$ versus mean $R_{\text{male}} = -0.016$). Based on a permutation test, the difference is significant at $P < 0.05$, which suggests that males may be dispersing farther than females there.

Kinship and Population Structure

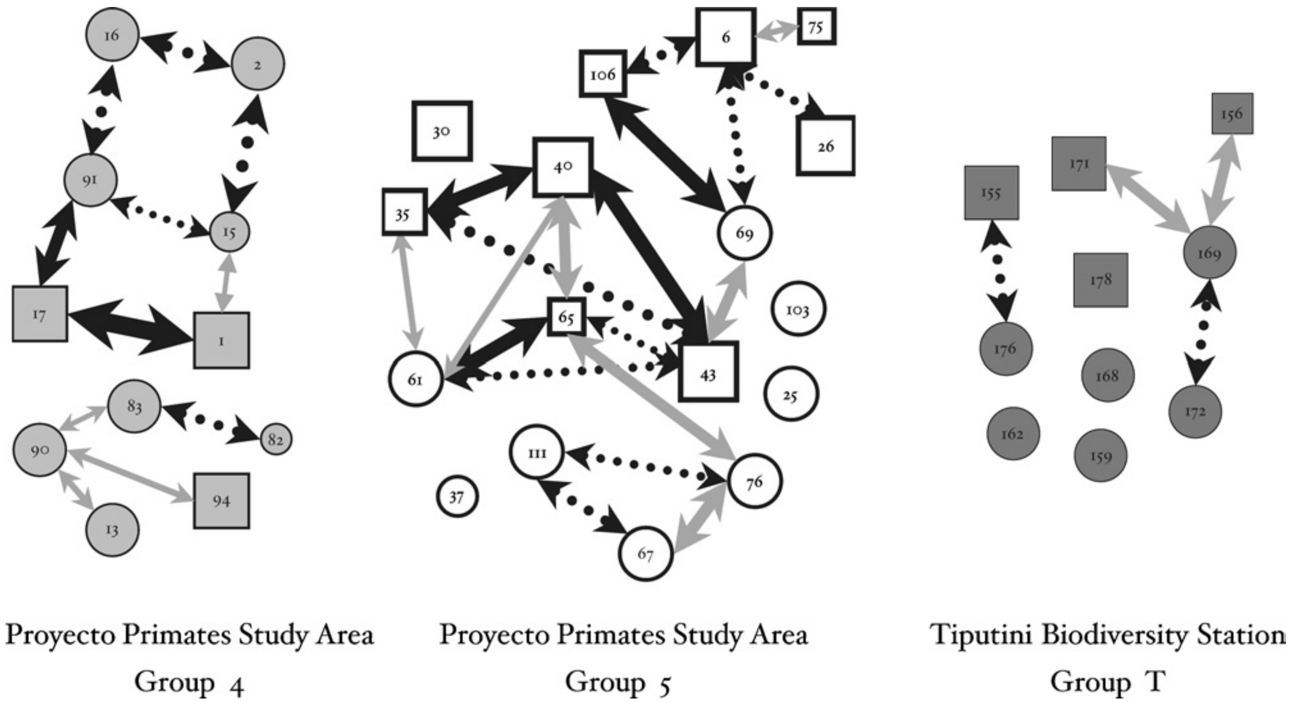
In order to further explore genetic relationships within and between Yasuní social groups and to test predictions 1B and 2B, we used likelihood methods along with pairwise R values to identify pairs of close relatives. Specifically, for every dyad in the population, we used KINSHIP 1.3 (Goodnight and Queller, 1999) to derive the likelihood ratios associated with each pairwise R value for several hypothesized pedigree relationships (primary versus null hypothesis): full sibling versus nonkin, half sibling versus nonkin, full sibling versus half sibling, and parent-offspring versus nonkin. We evaluated the significance of the likelihood ratios via a simulated sample of 10000 dyads each for the primary and null hypotheses. We conservatively considered related dyads to be ones with pairwise R value ≥0.200 and for which the likelihood ratio for full sibling or half sibling versus nonkin or parent-offspring versus nonkin was significant at $P < 0.05$.

Figure 3 is a diagram of the distribution of related pairs thus identified in our population within each of the 3 best-sampled groups.

Clearly, hypothesis 1B is supported for group 5 in the Proyecto Primates Study Area: 6 of 7 nonjuvenile males versus 3 of 8 nonjuvenile females in group 5 had at least 1, and typically more than 1, same-sex nonjuvenile relative in the group. Additionally, for males, a greater proportion of all of the other same-sex nonjuvenile individuals sampled in the group were, on average, close relatives than was true for females. For Group 4, females again had proportionally fewer close relatives among the set of available females than males did, though with only 3 males in the group, 2 of which were closely related, this is not a very robust result. Finally, both groups appeared to contain ≥ 1 male full sibling pair but no full sibling female pair. For group T at TBS, very few close relatives were identified among the set of sampled individuals, which included no male-male pair, one female-female pair, and 2 male-female pairs.

Within each of the 2 well-sampled local populations, many close pairwise relationships existed between groups and several clear clusters or networks of closely-related individuals are apparent (Fig. 4). In many cases, the networks comprise both same and opposite sex individuals from 2 or more social groups. However, contrary to prediction 2B, males did not tend to have more close relatives in the local population, i.e., their own social group plus other local groups, than females did in either the Proyecto Primates Study Area or TBS populations (Mann-Whitney test comparing the number of close relatives identified among sampled individuals for males versus females: Proyecto Primates, $U = 151$, $P = 0.79$; TBS, $U = 105.0$, $P > 0.99$).

Finally, considering the entire set of samples in 1998–1999, we identified several closely related dyads that spanned different local populations. Roughly 3.7% of possible pairs of monkeys from different local sites manifest a pairwise $R \geq 0.20$ and a significant likelihood ratio for the primary/null hypothesis of full sibling/unrelated individuals. Accordingly, in combination with the low overall θ_{ST} value between the Proyecto Primates Study Area and TBS, it appears that nuclear gene flow across the region is extensive. To test prediction 2C, i.e., that if dispersal is female biased then the regional population should show more evidence of substructuring for males versus females, we recalculated θ_{ST} between the Proyecto Primates Study Area and TBS separately for males and females via FSTAT 2.9.3 (Goudet, 2001). We also used Mantel matrix correlation tests, implemented in GENETIX 4.04 (Belkhir, 2003), to evaluate the correlation between pairwise relatedness and geographic distance—measured as the distance between the estimated centers of the home ranges of the groups from which the samples were collected—separately for each sex. The expectation was that θ_{ST} should be higher and the matrix correlation coefficient



Proyecto Primates Study Area
Group 4

Proyecto Primates Study Area
Group 5

Tiputini Biodiversity Station
Group T

Fig. 3. Pairs of close relatives identified within social groups in the Proyecto Primates Study Area and at the Tiputini Biodiversity Station. Squares represent males and circles females; large shapes are adults, medium-sized shapes are subadults, and small shapes are juveniles; and, the number identifies the subject. All pairwise relatedness values >0.20 and associated with a significant likelihood score for the primary versus null hypothesis of full sibling versus unrelated, half-sibling versus unrelated, or parent-offspring versus unrelated are shown, and the width of the arrow is proportional to the pairwise R value of the dyad. Solid black arrows indicate pairs that are more likely to be full rather than half siblings. Dotted black arrows represent pairs that are not excluded from being parent and offspring and for which a parent-offspring relationship is significantly more likely than a full or half sibling relationship. Solid gray arrows represent other close relationships.

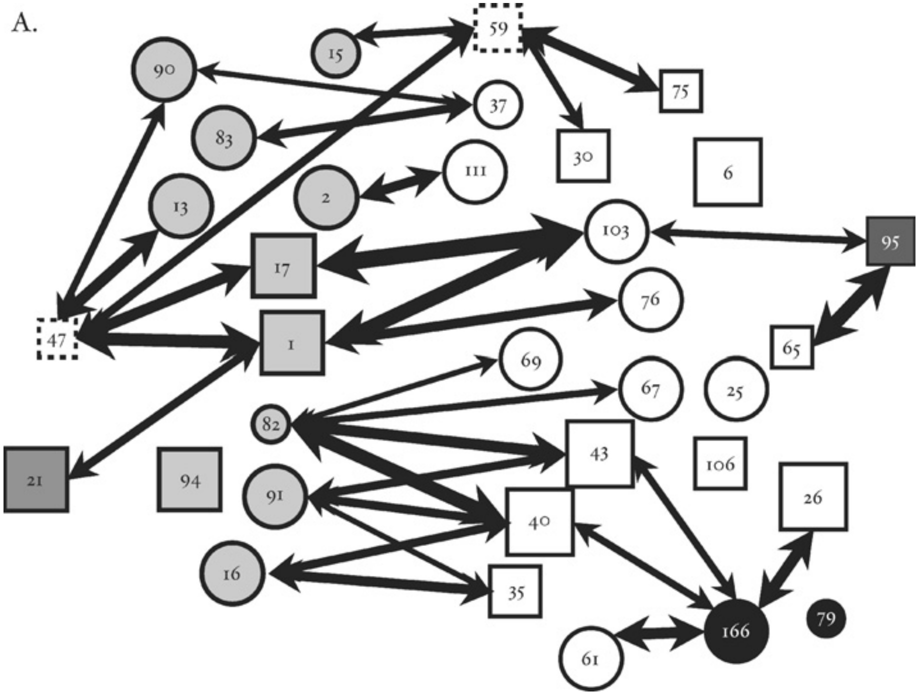


Fig. 4. Networks of “close relatives” between groups at (A) the Proyecto Primates Study Area and (B) the Tiputini Biodiversity Station. Icons indicate sex, age, and individual identification number as in Fig. 3. Individuals from the same social group, share the same shading, while individuals bordered by dashes either could not be assigned to a particular social group, e.g., individual 59 came from either Group 3 or 5, individual 47 from either Group 5 or 6) or were solitary when sampled, e.g., individual 185. All pairwise relatedness values >0.20 and associated with a significant likelihood score for the primary versus null hypothesis of full sibling versus unrelated are shown, and the width of the arrow is proportional to the pairwise R value of the dyad. Within group relationships, indicated in Fig. 3, are not shown. Where possible, the orientation of groups with respect to one another corresponds with their position in the landscape, (top is North) but for the sake of clarity in the figure, this was not always possible.

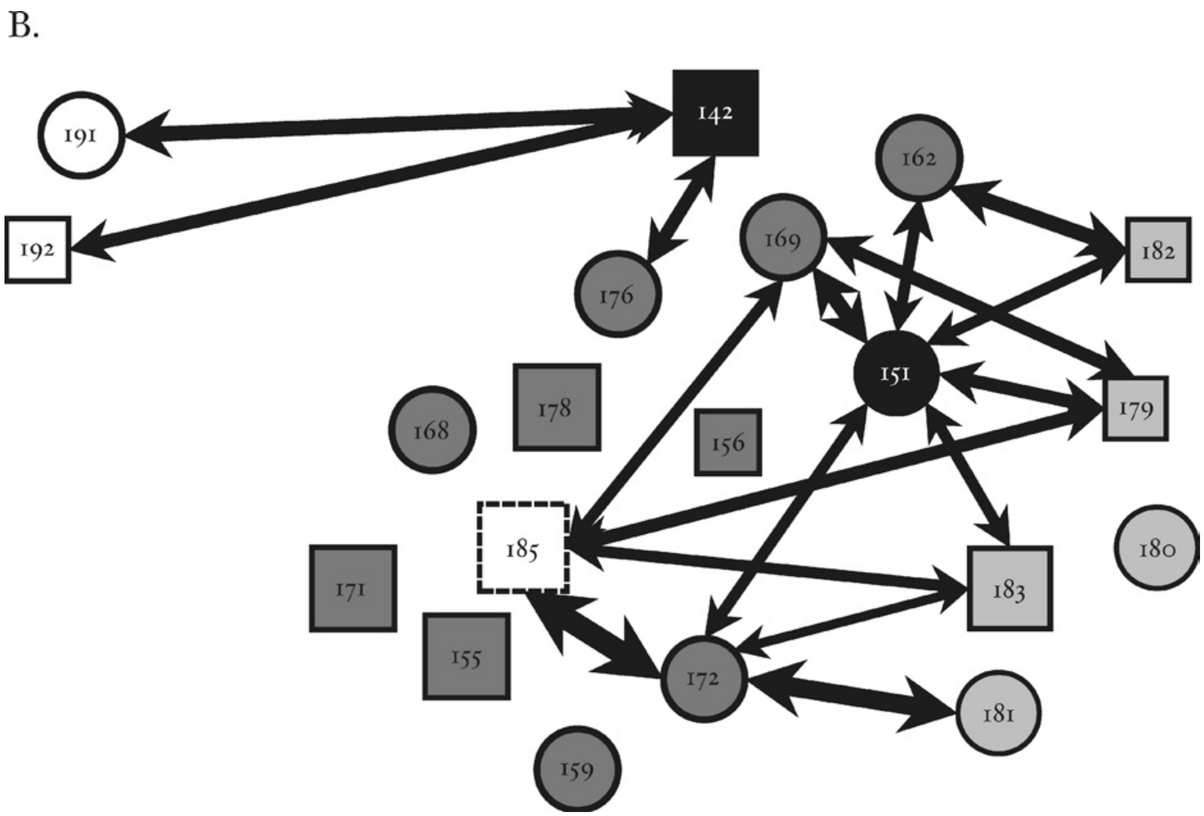


Fig. 4. Continued.

more negative for males than females if dispersal is heavily biased towards females. However, contrary to this expectation, θ_{ST} was very small (though significant) and essentially equivalent for both males and females (males: $\theta_{ST} = 0.020$, $P < 0.01$; females: $\theta_{ST} = 0.030$, $P < 0.01$); the correlation coefficients for the male and female Mantel tests were also similar and significant, but, counter to prediction, that for males was slightly less rather than more negative than that for females ($r_{\text{males}} = -0.157$, $P < 0.02$; $r_{\text{females}} = -0.201$, $P < 0.01$).

Direct Evidence of Dispersal by Both Sexes

Although the number of cases is small, our molecular results also document intergroup transfer—or at least temporary visitations—by animals of both sexes in $\geq$1 local population over a relatively short period of time, providing direct confirmation for the suggestion that members of both sexes disperse. During our study, $\geq$3 different individuals in the Proyecto Primates population were, unwittingly, sampled in multiple social groups. One is a female that we first sampled in Group 6 and then several months later in Group 5. The second is a male that we sampled 3 times, once early in the study in a small subgroup of *ca.* 10 monkeys that either was part of Group 5 or fused with them *ca.*, 2 mo into the study and remained part of that group until the end, a second time as a member of Group 5, and a third time in Group 3. The third case is another male that we sampled as a juvenile in Group 5 in 1998–1999 then resampled in Group 3 two year later.

DISCUSSION

Dispersal and Philopatry in Woolly Monkeys and other Atelins

Our molecular results paint a complex picture of woolly monkey social organization and dispersal patterns. In general, the results support the notion that, as in other atelin primates, dispersal by females is a common element in woolly monkey societies: average pairwise relatedness among females within groups is low in the 3 best-sampled social groups and is substantially lower than average male pairwise relatedness in 2 of them. Moreover, our results clearly demonstrate that at least for some groups, males reside as nonjuveniles in social groups with same-sex close kin: in the 2 best-sampled Yasuní social groups in the Proyecto Primates Study Area, the set of nonjuvenile males contained at least some close-kin dyads, including likely full or half siblings or both. While we also noted a few close kin relationships among pairs of females within social groups, several of these were more likely to represent parent-offspring pairs than pairs of full or half siblings. Overall, the pattern at the Proyecto Primates site seems to suggest female-biased dispersal and male-biased philopatry, wherein both sexes may disperse but males are more likely than females to continue to reside in their natal groups as adults; it might also arise if dispersing males are more likely than females to join groups already containing same-sex kin. Moreover, the fact that the average pairwise relatedness between males in different social groups within the same local population was also greater than the comparable value for females suggests that even though both sexes may be dispersing, females tend to move farther than males, a pattern reminiscent of that in red howlers (Pope, 1992).

Results are different for the TBS population where, average pairwise relatedness among females in the best-sampled social group is low, but average male relatedness is even lower, and the mean R between females from different social groups is much greater than that of males. Thus, while like spider monkeys and muriquis, some groups of woolly monkeys appear to be organized around a core of related males, clear patrilines may not be obvious in other groups. Although we suspect that the contrasting pattern at the 2 sites might be a result of our much more limited sampling of the TBS population, alternatively it might be taken as evidence for substantial male-mediated gene flow in addition to that of females, and perhaps thus reflect local geographic variation in woolly monkey dispersal behavior. Sampling of additional local populations is clearly needed in order to properly evaluate this possibility. Regardless, our finding of very little genetic differentiation between the Proyecto Primates Study Area and TBS sites, either for the population as a whole or for one or the other sex, indicates that nuclear gene flow across the region must be extensive.

Woolly monkeys have long been assumed to live in patrifocal societies where dispersal is strongly female-biased (Rosenberger and Strier, 1989; Nishimura, 1990b, 2003; Strier, 1994b), as is the case for spider monkeys and muriquis, but our findings suggest that such a simple characterization of woolly monkey dispersal patterns may need revision. The molecular results suggest not only substantial female dispersal but also dispersal by males. The pattern is, in fact, consistent with some previous field observations. For example, Nishimura (1990b) noted that subadult woolly monkeys of both sexes sometimes disappeared from his main study group for hours or days and occasionally joined other groups in the area temporarily. He likewise noted a known resident male from one group traveling alone for a period of several hours. At Yasuní, multiple observations of solitary adult and subadult males and of a temporary "bachelor" group comprising 5 males of various age suggest that male woolly monkeys may indeed transfer or visit other groups on occasion, raising the possibility that dispersal may be much less strongly biased towards females for *Lagothrix* than for either *Ateles* or *Brachyteles* (Di Fiore, unpublished data).

Finally, our molecular results also highlight an unanticipated but important feature of woolly monkey social systems—the existence of close kin relationships between individuals in adjacent social groups and perhaps between widely dispersed groups as well. This result is reminiscent of the "dispersed male network social structure" recently documented in western lowland gorillas (Bradley *et al.*, 2004, p. 511), a taxon in which both male and female dispersal occurs and where closely-related males are resident silverbacks in different social groups within the same local population.

Social Relationships in Woolly Monkeys and Other Atelins

If male atelins were more closely related to one another within their social groups than were females as a result of male philopatry, then this should, theoretically, have dramatic implications for the patterning of intragroup spatial associations and affiliative interactions (Strier *et al.*, 2002). In particular, we would predict male atelins to associate with one another more and to be more affiliative and cooperative with one another, than females are. This prediction is certainly substantiated in spider monkeys and muriquis, but, given our behavioral data, is clearly less true for woolly monkeys. For example, Strier (1990) noted that other males constituted close to 80% of the contact partners and >50% of the neighbors within 5 m of muriqui males, and, when adults only were considered, male muriquis had other adult males as their nearest neighbors 69% of the time (Strier, 1997b; Strier *et al.*, 2002). The pattern for female muriquis was similar: adult females had other adult females as their nearest neighbors 70% of the time when dependent offspring were not included in the data set (Strier, 1997b), and the contact partners of female muriquis were other females close to 65% of the time (Strier, 1990). Comparable data on spatial associations are not really available for spider monkeys; however, using an index of association based on membership in the same feeding party, Symington (1987a) found that the average male-male association index is greater than either the average female-female or male-female indices for *Ateles chamek*.

The situation is clearly quite different for *Lagothrix*. First, adult male woolly monkeys are not often in close proximity to other males: excluding juvenile neighbors, only 36% of the close proximity partners ($\leq$2 m) of Yasuní adult male woolly monkeys were either subadult or adult males, and only 4% were other adult males. Both values are much lower than expected given the number of adult and subadult males in the population. Second, adult female woolly monkeys, particularly ones with dependent offspring, appeared to avoid close proximity to one another: for females with dependents, 34% of close proximity partners were other females, and for unburdened females, 48% of partners were same-sex animals, versus the expected 51% based on the population sex ratio. Nishimura (1994) also documented the rarity of same-sex associations in woolly monkeys: in his study, <5% of observations of nonjuvenile animals in contact or close proximity (≤1 m) involved same-sex dyads. While it is possible that some of the differences among atelins in association patterns within and between the sexes may be due to methodological differences among studies, the pattern of clear same sex associations in spider monkeys and muriquis, and the relative lack thereof in woolly monkeys, seems quite robust.

Differences in spatial associations are but one manifestation of how the quality of intragroup affiliative relationships varies across atelin genera. Nonetheless, the expression of overtly affiliative behavior in atelins, e.g., grooming, embraces and participation in coalitions, generally mirrors the pattern of spatial association. For example, intermale affiliation in *Lagothrix* was largely nonexistent at Yasuní and at Nishimura's (1990b, 1994) site, with the notable exception of grooming bouts directed by younger males to older males and of cooperation in the context of agonistic intergroup encounters. In contrast, Strier (1986, 1992, 1994b, 1997b) has demonstrated close bonds among muriqui males, not only in terms of their spatial proximity to one another but also in their common expression of affiliative embraces and their lack of intrasexual aggression. In *Ateles*, males often travel together, cooperate in coalitionary attacks against females, and cooperatively patrol and defend a community range (Cant, 1977; Fedigan and Baxter, 1984; Symington, 1987a, 1990; van Roosmalen and Klein, 1988). Moreover, Fedigan and Baxter (1984) noted that male red spider monkeys (*Ateles geoffroyi*) showed higher rates of affiliative interactions, e.g., sitting together and grooming than females did, and directed 85% of their affiliative behavior towards other males. As in woolly monkeys, grooming between subadult and adult male spider monkeys is more common than between pairs of adult males (Symington, 1987a). Similarly, subadult male muriquis tended to be responsible for initiating and maintaining associations with adult males, rather than the reverse (Strier, 1997b; Strier *et al.*, 2002).

Compared to male-male interactions, affiliative associations between female woolly monkeys were even less common. We recorded only one grooming bout between Yasuní adult females and only 7% of grooming bouts among adults and subadults recorded by Nishimura (1990b) involved 2 females (versus the 21% expected by chance based on the sex ratio in that population). Affiliative associations among female *Ateles* are also uncommon. For example, Symington (1987a) found that the only strong grooming relationships that exist amongst female *Ateles chamek* are those between mothers and their young daughters, and she further noted that these relationships become weaker as daughters near the age of emigration. While it is difficult to gauge the relative strength of female-female versus male-male bonds in spider monkeys quantitatively, it nevertheless seems clear that male-male affiliative relationships are stronger, given their cooperative behavior in the contexts described above. In contrast, muriqui female-female relations are far more affiliative than those of either woolly monkeys or spider monkeys. Females are not only are each other's most common nearest neighbors (Strier, 1986, 1990, 1997b) but are also the most frequent embrace partners (Strier, 1992), and they assist one another in both intragroup and intergroup agonistic encounters and in aggression against immigrating females (Strier, 1986).

A clear result from our study is that, in contrast to *Ateles* and *Brachyteles*, the most salient affiliative social relationships in *Lagothrix* are the ones between, rather than within, the sexes, with females being the sex largely responsible for establishing and maintaining these relationships. Females actively solicit mating, initiate grooming bouts with adult males, and generally appear to associate preferentially with males rather than with other females. Although the data are not available to test this, it seems reasonable to suggest that female woolly monkeys may cultivate friendships (*sensu* Smuts, 1985) with particular males, considering how important direct female-female mate competition may be in determining a female's reproductive success. Alternatively, given the genetic relatedness results, it is possible that some intersexual associations reflect bonds between opposite-sexed full or half siblings.

Mating Behavior

The picture of woolly monkey mating behavior that emerges from our study is very similar to that reported by Nishimura (1988, 1990a, 1990b, 1994; Nishimura *et al.*, 1992) based on long-term studies in Colombia. First, as in Yasuní, female *Lagothrix* often mated with multiple males during the course of a single copulatory period (Nishimura, 1990a, 1994). Second, female woolly monkeys in both Colombia and Ecuador actively signaled their receptivity by means of facial expression and solicited copulations from males—even to the point of pursuing particular males for extended periods of time, which suggests that female choice of mates may be a very important element in the sexual behavior of *Lagothrix*. Finally, in both the Yasuní and Colombian populations, copulations were not limited to fully adult males, and males were very tolerant of one another and never interfered with the mating attempts of other males (Nishimura, 1990a, 1994), suggesting that aggressive contests over mating access must be costly to males. There are several possible reasons why this might be the case. The most obvious is that males can only provide effective defense of a group of females from extragroup males through cooperative defense and that the price for securing such cooperation is to relinquish some degree of mating access; such a hypothesis has been proposed for chimpanzees, spider monkeys, and muriquis. Indeed, the hypothesis may apply to woolly monkeys, too, given that intergroup interactions are generally hostile and result in the displacement of one group from the area of the encounter (Di Fiore, 1997). Alternatively, male-male contest competition for mates would be minimal if they are unable to override the mate choices of females, as might be the case for species in which males and females are codominant or where there is little sexual dimorphism in body size, e.g., spider monkeys and muriquis (Strier, 1994a, 1994b). This alternative hypothesis is less likely to apply to woolly monkeys given the more dramatic difference in size between males and females.

The most striking difference between our results and those on other populations of woolly monkeys is the prevalence of mating harassment by other females, a behavior not commented upon in earlier reports. The high frequency with which mating attempts were harassed indicates the importance of direct female-female mate competition in *Lagothrix*: at Yasuní, roughly one-fifth of all observed copulations were harassed, often to the point that the mating bout was terminated by the male chasing away the harassing female. Until recently, the role of female-female competition over mates (along with male mate choice) has seldom been considered as an important form of sexual selection influencing the evolution of social behaviors in nonhuman primates (Smuts, 1987; Altmann, 1997). Nonetheless, direct female-female competition over access to breeding males is a relatively common feature of some primates living in unimale groups and within one-male units of gelada baboons (Smuts, 1987) and has been reported for a few other species living in multimale-multifemale groups (savanna baboons: Seyfarth, 1976; rhesus macaques: Lindburg, 1971; and howlers: Young, 1981; Sekulic, 1983).

Turining to a comparison with other atelins, little is known about the mating behavior of *Ateles* despite the fact that several species have been the subjects of long-term field studies (*Ateles belzebuth*: Klein, 1972; *Ateles geoffroyi*: Cant, 1977; Chapman, 1988, 1990a, 1990b; Campbell, 2000; *Ateles paniscus*: van Roosmalen, 1985; *Ateles chamek*: Symington, 1987a). Mating appears to take place predominantly during consortships that may last from several hours to several days (van Roosmalen, 1985; Symington, 1987a; Campbell, 2000). Spider monkey females may mate with different males in subsequent estrous periods, though whether polyandrous mating occurrs within a single estrous period is uncertain (Symington, 1987a). As in woolly monkeys, spider monkey copulations are often preceded by solicitation from the female. For example, in all of the copulations ($N = 27$) of *Ateles paniscus*, observed by van Roosmalen (1985), the female advertised her receptive condition and initiated sexual activity with the male. This, coupled with the observation of a receptive female altering her ranging behavior to join up and to copulate with a vocalizing male, led van Roosmalen (1985) and van Roosmalen and Klein (1988) to suggest that female choice plays an important role in the reproductive behavior of *Ateles* as we suggest for *Lagothrix*.

The mating system of *Brachyteles* has been categorized as promiscuous, where in receptive females mate with multiple males during a single estrous period (Milton, 1985; Nishimura *et al.*, 1988). Although, typically, only 1 or 2 males associate and mate with a receptive female on any given day during her receptive period, it is not uncommon for multiple males to mate with her (Milton, 1985; Strier, 1985, 1986, 1992, 1997a; Strier *et al.*, 2002). For example, Milton (1985) noted that occasionally mating aggregations consisting of as 7–9 adult and subadult males form around a receptive female. During these aggregations, up to 4 or 5 males each copulated with the female several times over a period of 36–48 h, and, often, the copulations occurred sequentially, with one male replacing another as soon as the previous male finished mating. Strier (1992, 1997a) also observed sequential copulations in the context of mating aggregations. At Yasuní we observed neither large mating aggregations nor sequential copulations in *Lagothrix*. Even when females mated with several males on the same day, copulations typically occurred several hours apart. As with both *Lagothrix* and *Ateles*, intermale aggression in the context of reproduction was infrequent among *Brachyteles* (Strier *et al.*, 2000, 2002).

Several commonalties and contrasts emerge from this comparison of atelin mating patterns. First, it seems that minimization of overt male-male mating competition characterizes all 3 genera. Second, female choice appears to be an important form of sexual selection for all of them. The underlying ultimate explanation behind low male-male competition among the 3 atelins is likely to be the tendency for males within a group to be closely related. In this respect, our genetic results demonstrating a relatively higher degree of relatedness among males versus among females in at least some groups of woolly monkeys is significant and may help to explain the relative lack of competitive interactions among males over mating. To date, there has been no comparable study of average genetic relatedness among male and female have spider monkeys or muriquis; however, given the clearly affiliative nature of male relationships in those two taxa, we predict such results would reveal a higher level of average male relatedness than that in woolly monkeys.

CONCLUSIONS

Woolly monkeys appear similar to their closest relatives, the spider monkeys and muriquis, in showing substantial female dispersal, but based on our genetic results it seems likely that at least some males also disperse and that the frequency of male dispersal may vary considerably among populations.

Further, male woolly are not actively affiliative with one another, and this conspicuous lack of male bonding contrasts sharply not only with other atelins living in male-philopatric communities (Strier, 1997b; Strier *et al.*, 2002) but also with the only other 2 male-philopatric primates that typically live in multimale groups: chimpanzees (Goodall, 1986; Nishida and Hiraiwa-Hasegawa, 1987; Watts and Mitani, 2001) and red colobus monkeys (*Procolobus badius*: Struhsaker, 1975, 1980; Struhsaker and Leland 1987; *cf.* Starin, 1994). Strier (1994a, 1994b) attributes the lack of affiliation among presumably-related male woolly monkeys to a lack of competition between groups of males for access to mates, reasoning that the greater cohesion of females in woolly monkey groups (relative to female spider monkeys and female muriquis in some populations) allows males to more easily keep track of the reproductive status of female group members individually, without having to cooperate with other males to do so. This is a reasonable suggestion, though other explanations are possible. For instance, if some male woolly monkeys disperse or periodically visit other social groups (and perhaps sire offspring in them), then the average relatedness among males within groups of *Lagothrix* — even if greater than among females — may nonetheless be considerably lower than among males in muriqui or spider monkey communities.

Woolly monkey females are even less affiliative among themselves than males are: our nearest neighbor and grooming data suggest that adult females, particularly ones with dependent juveniles, may actively avoid same-sex conspecifics and preferentially associate with males. However, it is unclear whether association with males reflects a female strategy to gain protection, cultivate reproductive opportunities, solicit male investment in offspring, or something else (such as a close kin relationship between particular females and males). Clearly intersexual bonds appear to be more important to woolly monkeys than intrasexual ones are, with females being the sex largely responsible for establishing and maintaining these bonds.

Beyond their general lack of affiliation with one another, females also directly compete with other females by harassing their attempts to mate.

Our data on woolly monkey social behavior support the idea that direct male-male competition is a relatively less important force shaping the social interactions and mating patterns of many platyrrhine primates than it is for many catarrhine taxa (Strier, 1990). Instead, for woolly monkeys, intersexual mate choice and direct female-female mate competition seem to influence the nature of social relationships within and between the sexes. Until recently, the roles of direct female-female reproductive competition and of male mate choice have seldom been considered as important forms of sexual selection shaping the evolution of social behaviors in nonhuman primates (Altmann, 1997). Future research should be directed towards evaluating this possibility.

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