Chapter 9
Genetic Approaches to the Study of Dispersal and Kinship in New World Primates

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9.1 Introduction

Among social animals such as primates, "kinship" or genetic relatedness is commonly invoked as a key factor underlying and organizing the expression of within-group social behavior (Alexander 1974; Wilson 1975; Gouzoules 1984; Bernstein 1991; Silk 2001, 2002). Indeed, kin-correlated behavior – particularly kin-directed beneficent behavior or "nepotism" – is often considered a hallmark feature of the social lives of group-living primates (Gouzoules 1984; Gouzoules and Gouzoules 1987).

Within primate social groups, the patterns of genetic relatedness among group members are influenced principally by the dispersal and mating behaviors of those individuals. Dispersal directly shuffles genes across the physical and social landscapes, reassorting how the genetic variation present in a population is partitioned geographically and both within and among the various demographic units (e.g., social groups) into which the population is divided. Individuals' social and reproductive behaviors (e.g., mating frequency, choice of partners) likewise can influence the structuring of genetic variation within and among social groups across time. For example, high reproductive skew among males within a social group can lead to cohorts of similarly aged individuals being more closely related to one other through common paternity than are animals of different ages. Similarly, extra-group mating by either males or females can act to reduce the extent of genetic differentiation between groups.

These two key behavioral factors influencing the kinship structure of primate groups – the dispersal and reproductive tactics of individual animals – are some of the most intractable features of primate social systems for researchers to study in the field. For long-lived species such as primates, dispersal events tend to be rare – i.e., individual animals typically disperse only once or a small number of times during their lives. Even in the most detailed, long-term field studies, it is often difficult

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to accurately discern the fates of individuals who disappear from the social groups under investigation. For many primate species, sexual behavior is also not always easily observed. Moreover, sexual behavior in primates can serve many different social functions, and it is often largely decoupled from reproduction. Thus, even for those taxa in which matings are relatively conspicuous, the actual pattern of reproductive success may not be well predicted from behavioral observations.

Fortunately, molecular genetic data (e.g., multilocus genotypes, DNA sequence data, various kinds of DNA "fingerprints") provide a powerful, indirect means of studying the dispersal and reproductive behavior of individuals and for examining patterns of relatedness among animals both within and among primate social groups (Di Fiore 2003). With the development of high-throughput hardware for DNA sequencing and genotyping and with the optimization of methods for storing and extracting DNA suitable for molecular analysis from noninvasively collected samples such as feces or hair (Morin et al. 2001; Nsubuga et al. 2004; Roeder et al. 2004), such data are becoming ever easier and more cost-effective to collect. Interestingly, however, to date relatively few studies of wild nonhuman primates – and fewer still of New World monkeys – have used molecular data either to investigate dispersal patterns or to examine genetic relatedness among the animals within social groups.

In this chapter, I outline some of the ways in which genetic data can be applied to the study of dispersal patterns and kinship, and I review a range of case studies drawn from South American primates to illustrate some of these methods. The New World monkeys are a particularly interesting taxonomic group within which to consider these issues because dispersal patterns and social systems within this clade are so varied. For example, based on observational studies, some taxa of New World monkeys are characterized by predominantly female dispersal (e.g., *Ateles*: Symington 1987; *Brachyteles*: Strier 1990, 1994a, b; *Lagothrix*: Nishimura 2003; Central American squirrel monkeys, *Saimiri oerstedii*: Mitchell et al. 1991), some by predominantly male dispersal (e.g., *Cebus*: Jack and Fedigan 2004a, 2004b; western Amazonian squirrel monkeys, *Saimiri boliviensis*: Mitchell et al. 1991), and some by routine dispersal of individuals of both sexes (e.g., callitrichines: Baker and Dietz 1996; Savage et al. 1996; *Aotus*: Fernandez-Duque and Huntington 2002; *Callicebus*: Kinzey 1981; *Alouatta*: Clarke and Glander 1984; Rumiz 1990; Glander 1992; Crockett and Pope 1993). In still other genera (e.g., *Cacajao*, *Chiropotes*), dispersal patterns are either completely unknown or poorly understood. Genetic data have been collected on only a handful of these taxa, but in some cases reveal interesting dispersal patterns not anticipated from observational work.

The few studies of New World monkeys that have looked at within-group kinship have provided insight into the mating systems of several platyrrhine species, and these studies hint at an impressive and underappreciated diversity in reproductive patterns and behavior within the platyrrhine clade. But much additional work remains to be done. Given the widespread acceptance of kinship as a key explanatory principle underlying and structuring much of primate social lives, it is imperative that future primate studies pay more attention to exploring the link between relatedness and individual behavior using molecular data.

9.2 A Brief Review of Theory and Methods

A range of analytical methods have been developed for **evaluating dispersal patterns** using molecular data (e.g., Paetkau et al. 1995; Rannala and Mountain 1997; Goudet et al. 2002), for **estimating the degree of relatedness** between pairs of individuals using various kinds of marker data (e.g., Queller and Goodnight 1989; Lynch 1990; Li et al. 1993; Lynch and Ritland 1999; Wang 2002), and for **inferring the likely pedigree relationship** among those individuals (e.g., Goodnight and Queller 1999; Epstein et al. 2000; Milligan 2003). In recent years, a number of excellent review papers have been published that discuss in detail many of these methods and their important assumptions and limitations (e.g., van de Casteele et al. 2001; Prugnolle and de Meeus 2002; Blouin 2003; Piry et al. 2004; Manel et al. 2005; Csilléry et al. 2006; Weir et al. 2006; Lawson Handley and Perrin 2007), and thus only a brief introduction to some of these methods is given here.

9.2.1 Evaluating Gene Flow

At its most fundamental level, dispersal reflects a process by which genes are shuffled among populations or social groups that exist in a spatial landscape. If the dispersal rate is high enough, then the genetic variation present is effectively homogenized. By contrast, if the dispersal rate is low or if significant physical or social barriers to dispersal exist – i.e., in a geographically or socially subdivided population – then, as random mutation and genetic drift alter local gene frequencies, different portions of the landscape should come to be characterized by different local gene pools. One way, then, to evaluate the extent of gene flow among different local gene pools is to infer backwards from some measure of population subdivision.

Traditionally, population geneticists take a hierarchical view of population subdivision based on Wright's (1931) simple island model, which imagines that local populations are semi-isolated demes connected to one another via the movement of dispersers (Fig. 9.1). In the general n-island model, dispersers can move between any subpopulation, although other migration models (e.g., "stepping stone" island models or isolation by distance models) may better approximate animals' true dispersal options. Under the basic island model, Wright's (1965) fixation index F_{ST}, which summarizes the proportion of the total genetic variation found in a population that is explained by subpopulation or group membership, is inversely related to subpopulation size (N_e) and the proportion of individuals that migrate among subpopulations per generation (m). Thus, a crude estimate of the total number of migrants per generation ($N_e m$) among subpopulations can be estimated from empirical measures of F_{ST}, which can be derived from a variety of molecular marker data. Obviously, a number of crucial assumptions made under the island model are unlikely to be met in natural populations (e.g., that subpopulations are of equal and constant size, that there is a symmetric rate of migration among subpopulations), which makes the interpretation of estimated rates of gene flow among subpopulations based on F_{ST} problematic. Nonetheless, estimates of relative $N_e m$ for species with similar
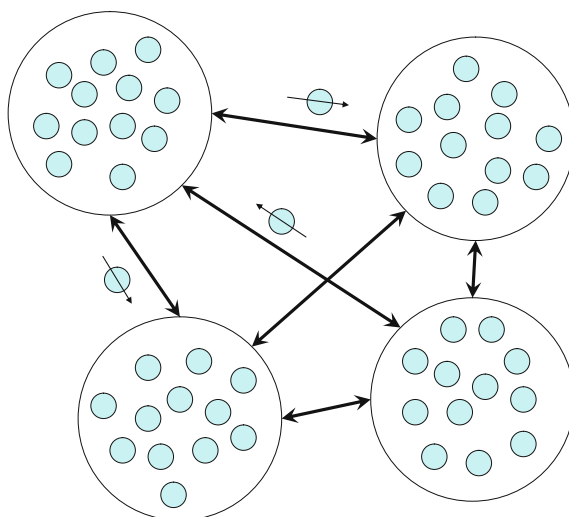
Fig. 9.1 Sewall Wright's (1931) island model of population structure and migration. Local populations are denoted by *large circles* and individuals within these populations are denoted by smaller, *filled circles*. Under the model, mating is random within each of several equal-sized local populations. Local populations are connected to one another via the movement of dispersers, with dispersal possible between any pair of populations

grouping patterns or for different demographic subgroups within populations of the same species (e.g., males versus females) can be very informative.

9.2.2 Identifying Dispersing Individuals

When an individual changes social groups or changes the area in space it normally occupies, it often becomes a member of a different deme from the one in which it was born. Because dispersing individuals carry with them genetic material characteristic of their natal group and local population, genetic data provide an indirect way to identify dispersing animals – one that does not rely on observations of animals immigrating into or transferring between social groups. Specifically, if the genetic variation characterizing the population or social group that an animal joins is sufficiently distinct from that of its deme of origin, then it should be possible to identify which individuals in a population are immigrants and, potentially, the source populations from which those immigrants came.

A variety of analytical methods have been proposed in recent years that use genotype data (e.g., multilocus microsatellite or SNP genotypes) for identifying immigrants and for assigning individuals to a likely population of origin (Paetkau et al. 1995; Favre et al. 1997; Rannala and Mountain 1997; Cornuet et al. 1999; Banks and Eichert 2000; Pritchard et al. 2000; Piry et al. 2004; Manel et al. 2005). Many of these

methods are based on calculating, for each individual of interest, a so-called **assign-
ment index** (AI), which is a measure of the likelihood that their genotype originated in
the population in which they were sampled versus other sampled populations for which
genotype data are available. When assignment indices are standardized such that the
mean index within a population equals 0 – i.e., by subtracting the mean assignment
index (mAI) for the sampled population from each individual's AI (Favre et al. 1997) –
animals with positive corrected assignment index (AIc) values are those more likely
than average to have been born in the sampled population, while those with negative
AIc values are more likely to be immigrants.

9.2.3 Sex-Biases in Dispersal Behavior

As in most vertebrates (Greenwood 1980; Waser and Jones 1983; Johnson and
Gaines 1990), dispersal in most primate species tends to be heavily sex-biased
(Melnick and Pearl 1987; Pusey and Packer 1987) – i.e., individuals of predomi-
nantly one sex leave their natal range and social group and join another prior to
beginning reproduction. Sex-biased dispersal generates clear predictions for sex
differences in structuring of genetic variation within and between social groups in a
population (Melnick and Hoelzer 1992; Avise 1994; Melnick and Hoelzer 1996; Di
Fiore 2003; Avise 2004; Hoelzer et al. 2004; Lawson Handley and Perrin 2007), and
a number of analytical approaches can be used to evaluate sex-biases in dispersal
patterns using molecular data.

   One set of approaches looks for genetic signatures of **sex-biased gene flow** over
the population's past history (Prugnolle and de Meeus 2002; Lawson Handley and
Perrin 2007), either by examining the diversity, phylogeny, and geographic distri-
bution of non-recombining, uniparentally inherited markers (e.g., Y chromosome
microsatellite haplotypes, mitochondrial DNA sequence haplotypes) or by taking a
classical population genetics approach (Wright 1943, 1965) and examining, for the
set of post-dispersal age individuals, how genetic variation is partitioned hierarchi-
cally among and within various demographic units from the sampled population.
Briefly, if sex-biased gene flow has characterized a population's past demographic
history, we would expect to see differences between post-dispersal males and post-
dispersal females in how genetic variation is partitioned, with the more philopatric
sex showing greater evidence of genetic substructuring because of its more restricted
gene flow.

   A second set of approaches focuses on **sex differences in individual or instanta-
neous dispersal** rather than on population-level assessments of historical gene flow.
These approaches take advantage of the assignment techniques discussed above
(Prugnolle and de Meeus 2002; Lawson Handley and Perrin 2007), evaluating for
each post-dispersal age individual the likelihood of its genotype having originated
in the population in which it was sampled. In this case, under sex-biased dispersal,
we would expect aspects of the assignment indices of post-dispersal age males and
post-dispersal age females to differ in predictable ways. Below are summarized a
number of the key predictions of various molecular tests of sex- biased dispersal.

9.2.3.1 Genetic Relatedness Among Nonjuvenile Animals

Where dispersal is predominantly by individuals of one sex, nonjuvenile, post-dispersal aged group members of the more philopatric sex are expected, on average, to be more closely related to one another than are group members of the dispersing sex (Morin et al. 1994b; Goudet et al. 2002; Di Fiore 2003; Hammond et al. 2006). Thus, if dispersal is predominantly by males and females are the philopatric sex – as is common in most cercopithecine and many cercopithecoid primates – then measures of average relatedness among dispersal-aged females within groups are predicted to be greater than measures of average relatedness among males. The opposite pattern is expected for taxa in which males are philopatric and where dispersal is argued to be primarily by females, such as chimpanzees, bonobos, red colobus monkeys, and some atelin primates of the New World (Morin et al. 1994b; Di Fiore 2003; Hammond et al. 2006). Additionally, if individuals of both sexes disperse but members of one sex travel farther, on average, than those of the opposite sex, then we would expect to see higher average relatedness among same-sexed members of different social groups within the same local population for the more philopatric sex (Di Fiore and Fleischer 2005). Some recent theoretical work suggests that the expected pattern of greater average relatedness among individuals of the philopatric sex should hold true mainly in small social groups and in groups where the reproductive skew among males is high (Lukas et al. 2005).

9.2.3.2 Diversity and Structuring of Genetic Variation Among Nonjuveniles

For portions of the genome that are transmitted to offspring through only one parent (e.g., mitochondrial DNA from the mother, Y chromosomal DNA from the father) the structuring of genetic variation is also expected to covary with sex differences in dispersal behavior. Thus, within social groups of species where females are philopatric, much lower diversity is expected in the mitochondrial DNA of post-dispersal age females compared to males, because of the dual processes of restricted female-mediated gene flow (as females are recruited into the adult, breeding population primarily from within their natal social group) and stochastic lineage sorting (Melnick and Hoelzer 1996; Wallman et al. 1996). Under female philopatry, too, greater genetic substructuring is expected for the mitochondrial versus the nuclear genome among nonjuvenile females. This is because mitochondrial genes would not be shuffled among social groups to the extent that nuclear genes are by the process of male dispersal (Avise 1995; Melnick and Hoelzer 1996; Avise 2000; Di Fiore 2003). For evaluating these predictions, the extent of population substructuring – i.e., the amount of genetic differentiation seen between different subpopulations or social groups – is typically characterized using F_{ST}, one of Wright's (1965) fixation indices or F-statistics, or an analogous summary statistic (e.g., R_{ST}, G_{ST}, δ_{ST}, θ_{ST}: Weir and Cockerham 1984; Nei 1987; Michalakis and Excoffier 1996; Goodman 1997), which summarizes the proportion of the total genetic variation in the population that is explained by subpopulation or group membership. Fixation indices are commonly calculated within the general framework of analysis of molecular variance (AMOVA: Excoffier et al. 1992, 2005).

For male philopatric taxa, by contrast, there is no expectation of much lower mitochondrial DNA diversity within groups for post-dispersal age males versus females, because dispersing females carry their mitochondrial haplotypes with them when they move. Similarly, little or no difference in the extent of population sub-structuring is expected for the mitochondrial versus nuclear genomes of either males or females (Hapke et al. 2001; Di Fiore 2003). In male philopatric taxa, however, Y chromosomal diversity among males is expected to be low (and lower than mitochondrial DNA diversity among the same males), while F_{ST} values between groups for Y chromosomal markers should be high – the opposite pattern to that expected for mitochondrial DNA in female-philopatric taxa (Eriksson et al. 2006). In fact, comparison of the degree of structuring seen in maternally inherited mitochondrial DNA versus paternally inherited Y chromosomes for the same individuals from the same populations can also provide strong insight into the direction and degree of sex-biased dispersal (Hammond et al. 2006). For female-philopatric taxa, then, the ratio of $F_{ST \bullet mtDNA}$ to $F_{ST \bullet Y}$ found in the population is expected to be much greater than one – that is, mitochondrial DNA is expected to be more divergent among groups than is Y chromosomal DNA (Laporte and Charlesworth 2002). Note that this assumes roughly equivalent effective population sizes (N_e) for males and females, given that F_{ST} is inversely proportional to the product of N_e and the mutation rate (Wright 1943, 1965). For male-philopatric taxa, by contrast, Y chromosomal DNA should be far more divergent between groups than mitochondrial DNA, and $F_{ST \bullet Y}$ is expected to be much greater than $F_{ST \bullet mtDNA}$ (Laporte and Charlesworth 2002; Eriksson et al. 2006; Hammond et al. 2006).

Another of Wright's (1965) F-statistics – the inbreeding coefficient F_{IS} – can also be used to evaluate sex biased gene flow. F_{IS} measures the extent of excess homozygosity in a sample. Because within any social group, nonjuvenile members of the dispersing sex will consist of a mix of immigrants coming from different social groups plus some nondispersing residents, homozygosity among these individuals (and thus F_{IS}) is expected to be increased (i.e., be less negative or more positive) relative to that found within nonjuvenile members of the more philopatric sex (Goudet et al. 2002).

9.2.3.3 Intraspecific Phylogeny of Uniparentally Inherited Markers Among Nonjuveniles

An additional way to investigate sex-biased dispersal is to apply phylogenetic methods haplotype data derived from non-recombining portions of the genome (e.g., mitochondrial and Y chromosomal DNA) to infer the evolutionary relationships among the various haplotypes segregating in the population. For example, where females are philopatric and female-mediated gene flow is thus restricted, we would expect to see a strong association between the inferred intraspecific phylogeny for female mitochondrial DNA and the geographic location or group of origin from which the sample was collected. That is, under female philopatry, females from the same social group are expected have closely related or identical mitochondrial DNA haplotypes, and female mitochondrial DNA haplotypes are expected to show evidence of isolation by distance, i.e., greater divergence between

geographically distant samples than among less-separated samples (Wright 1943). No such strong geographic clustering of closely related mitochondrial DNA types or evidence of isolation by distance is expected for males (Melnick 1987; Melnick and Hoelzer 1992, 1996; Di Fiore 2003). By contrast, when males are philopatric and females regularly disperse from their social groups, we do not expect to see a strong geographic structuring to mitochondrial DNA variation among females. Rather, females from the same social group are likely to possess widely divergent mitochondrial DNA types (Morin et al. 1994b; Di Fiore 2003) and female mitochondrial DNA types should not show evidence of significant isolation by distance (Hapke et al. 2001; Douadi et al. 2007).

9.2.3.4 Mean and Variance in Assignment Indices Among Nonjuveniles

As noted above, individuals with negative corrected assignment indices possess genotypes that are more likely than average to have originated outside of the social group in which they were sampled and are likely to have been immigrants. Animals with positive AIc values, by contrast, are more likely than average to be natal, philopatric individuals. Thus, if dispersal is sex-biased, then the mean corrected assignment index is expected to differ significantly between the sexes: under female philopatry, the mean AIc of females is expected to be greater than that of males, while the reverse should be true if males are the more philopatric sex (Goudet et al. 2002; Lawson Handley and Perrin 2007).

   If dispersal is sex-biased, then the variance in assignment index scores of males and females is also expected to differ significantly. Members of the dispersing sex are expected to show greater variance in assignment index scores (vAIc) because any set of sampled group members will theoretically contain a mix of resident and immigrant individuals, the latter of whom will have presumably originated in multiple other social groups. By contrast, the variance in assignment index scores is expected to be less for the more philopatric sex. Simulation experiments have demonstrated that these various molecular tests for sex-biased dispersal are sensitive to not only the extent of the bias in dispersal seen between males and females but also on the sampling strategy – e.g., the number of populations and individuals per population sampled as well as the variation present at the loci used to genotype sampled animals (Goudet et al. 2002).

9.2.3.5 Comparing Pre-dispersal and Post-dispersal Age Individuals

Yet another approach to evaluating sex differences in dispersal patterns using molecular data is to compare aspects of classical population genetic structure and assignment indices for pre-dispersal and post-dispersal age individuals. The expectation is that there will be no difference between the sexes in average relatedness (mean r), F_{ST} (for either mitochondrial, Y chromosomal, or autosomal loci), F_{IS}, mAIc, vAIc, or evidence of isolation by distance in uniparentally inherited markers among same-sexed individuals at the pre-dispersal (i.e., juvenile) stage. Amongst post-dispersal individuals, however, the various patterns outlined above

with respect to these parameters should obtain. More importantly, comparison of some of these parameter values between pre-dispersal and post-dispersal individuals can yield quantitative estimates of sex-specific dispersal rates (Vitalis 2002; Fontanillas et al. 2004).

9.2.4 Within-Group Kinship and Behavior

The association patterns and social behaviors of group-living primates have long been argued to be shaped heavily by patterns of kinship among group mates (Wrangham 1980; Gouzoules 1984; Gouzoules and Gouzoules 1987; van Schaik 1989; Silk 2001, 2002, 2006). The theoretical case for the importance of kinship's influence on behavior was articulated formally by W.D. Hamilton (1964a, 1964b) in his discussion of the concept of "inclusive fitness". Hamilton (1964a, 1964b) noted that because animals share genes with relatives, natural selection should favor those individuals who behave in ways that maximize their "inclusive fitness" – defined as personal or direct fitness augmented or decremented by the effects of their behavior on the reproductive success of relatives. Even behaviors that are costly to an animal's personal fitness can nonetheless be favored by natural selection, provided that the benefits (**b**) to the recipient, discounted by the degree of genetic relatedness (**r**) between the recipient and the actor, exceed the net cost (**c**) to the actor of performing the behavior (Hamilton 1964a), i.e., if **br – c > 0**. This condition, often referred to as "Hamilton's Rule", forms the basis of "kin selection theory" in behavioral ecology, which generates simple predictions about how actors should interact socially with conspecifics of different degrees of relatedness. All else being equal, given a choice of behaviors and related recipients toward whom those behaviors might be directed, actors are expected to choose that combination which maximizes the value of **br –c**.

Molecular marker data can be used to generate quantitative estimates of **r** among pairs of individuals, and a variety of relatedness estimators (and softwares for calculating these estimators) have been proposed for both codominant (e.g., microsatellites, SNPs) and dominant markers (e.g., AFLP, RAPD, and minisatellite DNA "fingerprints") (Queller and Goodnight 1989; Li et al. 1993; Goodnight and Queller 1999; Lynch and Ritland 1999; Wang 2002, 2004; Ritland 2005; Kalinowski et al. 2006; *see also* reviews by Milligan 2003; van de Casteele et al. 2001; Blouin 2003; Weir et al. 2006). If kinship is an important predictor of affiliative and agonistic social behavior in primates, as primatologists have long assumed, then patterns of within-group relatedness revealed by genetic data are expected to correlate positively with patterns of spatial and affiliative social associations (e.g., grooming, support in coalitions) and negatively with agonistic social interactions. Additionally, given the clear significance that social dominance has within groups of many primate taxa, genetic estimates of reproductive success are expected to correlate positively with dominance status, although until recently it has proved difficult to test this assumption. Finally, assuming that there is a risk of inbreeding depression associated with mating with close relatives, then animals of both sexes are expected to avoid mating and breeding with close kin.

9.3 Genetic Studies of Dispersal and Kinship in Primates

9.3.1 A Brief Review of Results for Non-Platyrrhines

To date, very few primate studies – and fewer still of platyrrhines – have actually used genetic data to examine dispersal patterns or to investigate directly the relationship between genetic relatedness and social behavior. With respect to predictions based on sex-biased dispersal, Melnick (1987, 1988) and Melnick and Hoelzer (1992, 1996) have documented greater mitochondrial diversity in males versus females within groups of several species of macaques, as would be expected for female philopatric taxa. More recently, Altmann et al. (1996) and de Ruiter and Geffen (1998) examined average female and average male pairwise relatedness in groups of baboons (*Papio hamadryas cynocephalus*) and long-tailed macaques (*Macaca fascicularis*), respectively, using genotype data. As expected, given observations of predominantly male exogamy and female philopatry in these taxa, they found that females within social groups were more closely related to one another, on average, than were males. Similar results have been reported for several group-living strepsirrhines (e.g., Verreaux's sifaka: Lawler et al. 1995; Alaotran gentle lemurs: Nievergelt et al. 2002; red fronted lemurs: Wimmer and Kappeler 2002). For chimpanzees and bonobos – where observational studies suggest that female exogamy and male philopatry are the rule – males do not generally appear to be more closely related to one another than females, contrary to expectation (Gerloff et al. 1999; Vigilant et al. 2001; Lukas et al. 2005). Nonetheless, among bonobos paternally inherited Y chromosomal markers do show much greater geographic differentiation than maternally inherited mtDNA (Eriksson et al. 2006), which is a strong signature that dispersal is female-biased, and a similar pattern has been found in Arabian hamadryas baboons (Hammond et al. 2006). Among Eritrean hamadryas baboons, too, the lack of population structure in mitochondrial DNA variation seen in a country-wide sample likewise strongly implicates female-biased dispersal (Hapke et al. 2001).

With respect to associations between genetic relatedness and affiliative within-group social behavior, results from Old World primates have been mixed. For example, two seminal studies of chimpanzees that examined the association between within-group social behavior and (matrilineal) kinship found that, contrary to expectation, males who were matrilineal kin (e.g., shared a mtDNA haplotype) were not more cooperative or affiliative with one another than males from different matrilines (Goldberg and Wrangham 1997; Mitani et al. 2000). More recently, Langergraber et al. (2007) used a large suite of autosomal, X, and Y chromosomal microsatellite markers to identify pairs of maternal and paternal half-siblings in one large community of chimpanzees and indeed found evidence that males preferentially affiliated and cooperated with their maternal half-brothers, though not their paternal ones. Nonetheless, most pairs of males that were highly affiliative and cooperative were not closely related, suggesting that male chimpanzees' decisions about their social interactions have more to do with direct rather than indirect fitness benefits. Thus, it is unclear the extent to which affiliative social behavior among male chimpanzees is,

in fact, generally kin-based, although this has long been assumed (Goodall 1986). By contrast, several recent studies of female rhesus macaques and baboons have found that both maternally and paternally related half-siblings do behave more affiliatively with one another than nonkin, as is predicted by kin selection theory, although maternal half-siblings tend to be more affiliative than paternal ones (Widdig et al. 2001, 2002; Smith et al. 2003).

With respect to reproductive behavior, molecular data provide the only tractable means for assessing parentage in wild populations where it is often impossible to observe matings. In several studies of wild and free-ranging cercopithecines, researchers have found support for a positive relationship between male dominance rank and paternity success (Melnick 1987; de Ruiter et al. 1992; de Ruiter and Inoue 1993; Paul et al. 1993; Altmann et al. 1996; Alberts et al. 2003; Widdig et al. 2004). However, for other species, including male-philopatric chimpanzees (Morin et al. 1994a; Constable et al. 2001) and bonobos (Gerloff et al. 1999), reproductive skew toward dominant males is less pronounced, and multiple males sire offspring within the same groups.

None of these aspects of primate behavioral ecology have been well explored in very many platyrrhine taxa using molecular data. In the remainder of this chapter, I review those few studies that have used molecular data to address the issues of dispersal, within-group kinship, and social behavior among platyrrhines. I then conclude with a discussion of the implications of these studies for our appreciation of platyrrhine social organization and dispersal patterns.

9.3.2 Cebids: Callitrichines

Two studies of callitrichines living in multimale groups – one of common marmosets (*Callithrix jacchus*: Nievergelt et al. 2000) and one of moustached tamarins (*Saguinus mystax*: Huck et al. 2005) – have used molecular data to investigate issues of kinship, dispersal, and mating patterns. Using genotype data from nine variable microsatellite marker loci, Nievergelt et al. (2000) evaluated patterns of genetic relatedness among a set of 40 individual marmosets that comprised most of the individuals in three wild social groups plus a portion of the animals resident in two adjacent groups. Within two of the well-sampled groups, adult females were closely related to one another – on the order of mother–daughter or full sibling pairs – and in all groups, all reproductively inactive adults and immatures were closely related to either the dominant female or a second, breeding female. Resident adult males were not closely related either to the adult females in their social groups or to one another, though several showed a high average relatedness to the members of another well-sampled group. A single, solitary male was also more closely related to the members of a different social group from the one he was commonly seen following. The limited paternity analyses afforded by the dataset found that the dominant males within each study group were the likeliest sires of most infants born during the study, although for more than half of offspring one or more extragroup males

also could not be excluded as possible sires. Together, these genetic results are consistent with the idea that common marmosets live in polygynous, extended family groups. The results are also suggestive of male transfer among groups (Nievergelt et al. 2000), although observational data confirm that females also emigrate from their natal groups (Digby and Barreto 1993).

In a similar study, Huck et al. (2005) evaluated patterns of kinship and paternity among 62 moustached tamarins from eight social groups using a set of 12 microsatellite marker loci. As in common marmosets, a single male in each group was identified as the most likely sire for almost all of the offspring born within each group, indicative of strong reproductive skew among males, although behavioral data indicated that more than one resident male typically mated with a group's sole breeding female. Interestingly, the study also found one case where a breeding female's twin offspring were apparently sired by different males. Among the tamarins, the average degree of relatedness among individuals from the same group was much greater than the average relatedness of members of different groups (mean R = 0.31 versus −0.03), and mating partners tended to be unrelated to one another (mean R = −0.06), two patterns also seen in *Callithrix jacchus* (Nievergelt et al. 2000). However, where the mean relatedness among resident adult males in common marmoset groups was low, among moustached tamarins the mean relatedness among males (mean R = 0.34) was not significantly less than that among females (mean R = 0.38). This might suggest that dispersal patterns among the tamarins are less biased toward males or may simply reflect the fact that animals of both sexes more commonly remain in their natal groups past the juvenile stage. Finally, based on an allele-sharing analysis among adult group members, Huck et al. (2005) concluded that while some closely related adults were likely to be parent-offspring pairs, others are more likely to be siblings or half siblings. This observation suggests that pairs of animals may sometimes join a group or inherit a territory together, a phenomenon that has been seen in behavioral studies of other populations of moustached tamarins (Garber et al. 1993).

9.3.3 Cebids: Cebines

Among the cebines, few studies have used molecular data to examine patterns of kinship or dispersal or social behavior within social groups, which is interesting given the variation in dispersal patterns seen among species of squirrel monkeys (*Saimiri*) (Mitchell et al. 1991; Boinksi 1999; Boinski et al. 2002; Boinski et al. 2005a, 2005b) and the strong same-sex affiliative behavior that has been reported among males (Robinson 1988b; Perry 1998; Jack 2003) and among females (O'Brien and Robinson 1991; O'Brien 1993) in various species of capuchins (*Cebus*). Two notable exceptions include studies by Valderrama Aramayo (2002) examining male reproductive success and population genetic structure in wedge-capped capuchins (*Cebus olivaceus*) in Venezuela and by Muniz et al. (2006) examining patterns of paternity in white-faced capuchins (*Cebus capucinus*) in Costa Rica.

Valderrama Aramayo (2002) evaluated paternity for 22 offspring born in a multi-male group of wedge-capped capuchins over a ten-year period that encompassed the tenure of two closely related alpha males. She found that paternities were skewed in favor of the two alpha males, who together sired just over half of all the offspring born during this period, a proportion that conformed well with predictions based on a priority-of-access model of male breeding success (Altmann 1962). The remaining offspring were sired by a combination of eight other resident or extragroup males. Nonetheless, alpha males sired a smaller proportion of the offspring of females from high ranking matrilines than low ranking matrilines, possibly implicating some degree of female behavioral preference for particular non-alpha males (Valderrama Aramayo 2002).

Valderrama Aramayo (2002) also examined patterns of relatedness among the sampled individuals in the capuchin population. She found that among the set of immigrant males in her main study group, there existed many pairs who were esti-mated to be related to one another at the level of either half or full siblings, highlight-ing a potential role of kinship for influencing male dispersal decisions and possibly dispersal success. Mean female relatedness was higher within groups than between groups, and within groups the mean relatedness among females was somewhat greater than that seen among males, a pattern consistent with observation-based reports of male-biased dispersal (Robinson 1988a; Valderrama Aramayo 2002)

For white-faced capuchins, *Cebus capucinus*, a recent paternity analysis of 41 infants born over a 14-year period in three social groups revealed that the long-term alpha males resident in these groups sired from 38% to 80% of the offspring born in their respective social groups, indicative of a strong association between male rank and reproductive success (Muniz et al. 2006). More interestingly, however, is the fact that while long-term alpha males sired 79% of offspring born to adult females other than their daughters, only 1 of 17 infants (6%) born to daughters' resulted from father-daughter inbreeding. After discounting other explanations for these results, Muniz et al. (2006) conclude that behavioral avoidance of father-daughter mating is the most likely. If correct, this would be one of the very few documented cases among platyrrhines of individuals biasing their social interactions with conspecifics on the basis of relatedness.

9.3.4 Atelids: Howler Monkeys

The earliest molecular studies of kinship, dispersal patterns, and social behavior in New World primates focused on red howler monkeys (*Alouatta seniculus*) liv-ing in central Venezuelan llanos (Pope 1990, 1992, 1996, 1998, 2000). Howler monkeys belong to the platyrrhine family Atelidae, a monophyletic grouping that also includes woolly monkeys, spider monkeys, and muriquis. In Venezuela, red howler monkeys live in both single-male and age-graded multimale groups typi-cally containing two to three adult males (Crockett and Eisenberg 1987; Rudran and Fernandez-Duque 2003). Prior observational data concluded that both male and

female red howler monkeys often disperse from their natal social groups prior to breeding, although some individuals of either sex may remain as adults in their natal groups (Rudran 1979; Crockett 1984; Pope 1989; Crockett and Pope 1993). Dispersal was observed to be female-biased, in the sense that females appeared to disperse greater distances from their natal groups, on average, than males (six versus one home range diameters: Pope 1989).

Pope (1992) examined the genetic structure of the llanos population using genotype data for a suite of 9 variable allozyme markers scored in 137 animals from 18 social groups that were split into two local populations separated by over four kilometers of open savanna. Based on F_{ST} values, Pope (1992) found that groups within the same local population were highly differentiated from one another, a result of both the strong monopolization of reproduction within groups by a single male and the fact that groups often contained matrilines of closely related females.

With respect to the possible influence of within-group relatedness on social behavior, molecular studies of red howler monkeys provide perhaps the strongest evidence from any primate in support of positive fitness consequences of kin-directed nepotism. For example, in an early study, Pope (1990) found that multimale groups held together by coalitions of related males lasted longer and enjoyed greater overall fitness than did multimale groups where the resident males were unrelated. Later, Pope (1992) demonstrated that long-established groups of red howler monkeys also tend to be characterized by a greater average degree of relatedness among the resident females, who cooperate with one another to prevent unrelated females from joining the group. Importantly, females in these groups also enjoyed greater per capita reproductive output than females in groups with lower mean relatedness among the resident females. Finally, with respect to mating patterns, Pope (1990) also examined paternity in five single-male and four multimale red howler groups. In no case were offspring found to have been sired by extragroup males. Additionally, within each of the multimale groups, paternities appeared to be limited to solely the dominant male, highlighting a clear link between dominance rank and male fitness.

In contrast to red howler monkeys, mantled howler monkeys (*Alouatta palliata*) typically live in much larger social groups containing up to six adult males. Ellsworth (2000) investigated patterns of population genetic structure among Costa Rican mantled howler monkeys using genotype data from suite of eight microsatellite marker loci for 65 individual animals from nine social groups. In contrast to the results from red howler monkeys, groups within the same local population were not highly genetically differentiated from one another. The global F_{ST} calculated for these nine groups, while significantly differing from zero indicating some genetic structure to the population, was nonetheless very low (0.02), suggesting that the population is essentially panmictic.

This dramatic difference from red howler monkeys is likely due in part to differences in the dispersal patterns seen in the two species. While dispersal by both males and females is common in both species, in red howler monkeys, dispersing females are seldom able to integrate themselves into established social groups, and instead they must form new social groups with other dispersing animals before they begin breeding (Crockett 1984; Crockett and Pope 1988, 1993; Pope 2000).

The situation is somewhat different in mantled howler monkeys where female dispersers sometimes succeed in directly moving into established groups (Jones 1980; Glander 1992). Differences in mating system also probably play a role in explaining differences in population structure between red and mantled howler monkeys. While a single male tends to monopolize both mating opportunities and paternity in red howler monkeys, within mantled howler monkey groups multiple males may mate with females and, presumably, sire offspring. Indeed, in a very limited study of paternity, Ellsworth (2000) found that out of five cases where DNA samples were available for a mother, her offspring, and the alpha male resident at the time of conception, the alpha male could be excluded as a potential sire in three cases.

Ellsworth (2000) also examined patterns of relatedness within groups and found that, on average, males were slightly more closely related to one another than were females, though this pattern was not significant. More importantly, the mean relatedness among group members was low relative to that seen in red howler monkeys, most likely reflective of the fact that groups of mantled howler contain greater numbers of immigrant individuals of both sexes.

9.3.5 Atelids: Woolly and Spider Monkeys

Within the family Atelidae, woolly monkeys (genus *Lagothrix*), spider monkeys (genus *Ateles*), and muriquis (genus *Brachyteles*) form a monophyletic clade – the atelins – that is a sister group to the howler monkeys. Among atelins, dispersal has long been thought to be strongly female-biased (Di Fiore and Campbell 2007). Observational studies of spider monkeys (Symington 1987, 1988; Ahumada 1989) and muriquis (Strier 1987, 1990, 1991) suggest that dispersal is solely or largely by females. For woolly monkeys, too, females have been observed to transfer between groups, sometimes multiple times during their lifetimes (Nishimura 1990; Stevenson et al. 1994; Stevenson 2002; Nishimura 2003). However, at two different sites in Yasuní National Park, Ecuador, solitary adult and subadult males have been seen, as well as small bachelor groups of ~5 individuals of various ages (Di Fiore 2002, unpublished data). In La Macarena, Colombia, too, Nishimura (1990) has reported that animals of both sexes occasionally disappear from their social groups and even join other groups temporarily. Thus, whether strongly female-biased dispersal characterizes all atelins remains an important question.

As noted above, the patterns of relatedness seen among individuals within a population are expected to reflect dispersal patterns. In turn, kin selection theory predicts that the quality of social interactions among individuals should be sensitive to their genetic relatedness. However, apart from one published study on patterns of within-group relatedness in several social groups of woolly monkeys (*Lagothrix poeppigii*) in lowland Ecuador (Di Fiore and Fleischer 2005), molecular data have not been used to investigate the link between dispersal patterns, kinship, and social behavior in any atelin taxon. Here, I revisit the results of that study and present new, preliminary data on these subjects for both woolly and spider monkeys.

9.4 Methods

Between 1998 and 2007, tissue and fecal samples were collected from animals in multiple social groups of woolly and spider monkeys at two different sites in lowland Ecuador – the Proyecto Primates Research Area (PPRA) and the region around the Tiputini Biodiversity Station (TBS) – as well as opportunistically from several other sites within Yasuní National Park (Fig. 9.2). Sampling was done intensively at both sites in 1998 and at the TBS site between 2005 and 2007. Intermittent samples from the intervening years were also collected at one or the other site. The sampling procedures used follow those reported elsewhere (Di Fiore and Fleischer 2005). DNA was extracted from each sample using commercially available nucleic acid isolation kits for tissue (Qiagen DNeasy Blood and Tissue Kit) or feces (QIAmp DNA Stool Mini Kit). These samples were then genotyped via PCR for a suite of polymorphic microsatellite (SSR) markers – 8 and 16 loci, respectively, for woolly and spider monkeys (Di Fiore and Fleischer 2004) (*see also* Table 1A,B) – using a modification of the multiple tubes approached followed in other studies (Taberlet et al. 1996; Alberts et al. 2006). Finally, most samples were also sex-typed using PCR-based sexing assays (Wilson and Erlandsson 1998; Di Fiore 2005a, 2005b) to confirm or correct field assignments of sex.
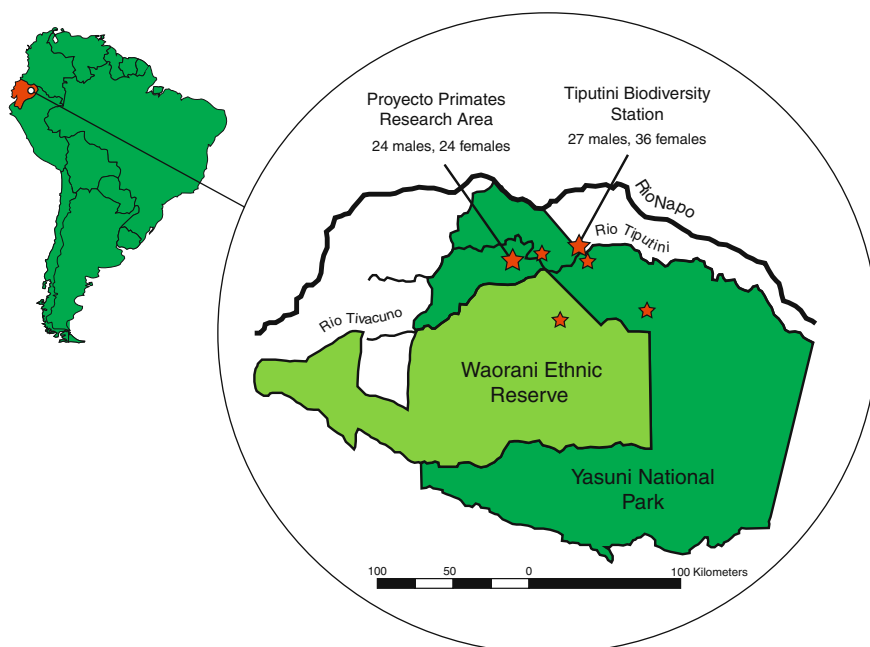
Fig. 9.2 Map of Yasuní National Park and the surrounding area in lowland Ecuador indicating the locations where samples were collected and the number of individuals of each sex sampled at the PPRA and TBS sites. Small stars indicate several other locales from which a handful of samples were collected

During the periods of intensive sampling many samples were collected without individual identification – particularly for woolly monkeys, which are difficult to distinguish individually – hence, two or more samples from the same species at the same site often yielded identical multilocus genotypes. In all such cases, the assigned genetic sexes also always matched. These samples were therefore assumed to be replicates from the same individual and were analyzed as such, which is a reasonable assumption given the low probability of identity (PI) afforded by both the woolly and spider monkey genotyping panels: the chance of even two full siblings sharing the same multilocus genotype was less than one in 2000 for woolly monkeys and less than one in 1,000,000 for spider monkeys.

Genotypes were derived for a total of 35 individual woolly monkeys from at least four social groups at the PPRA site and 16 individuals from at least three social groups at the TBS site sampled in 1998. An additional nine individuals were sampled at the PPRA site between 2000 and 2002, and four more were sampled in 2006. At the TBS site, an additional 47 individuals from at least three social groups were sampled between 2005 and 2007. Finally, ten individuals from various other sites in the region were sampled at various times between 1998 and 2005. For spider monkeys, 24 individuals were sampled from one social group at the PPRA

Table 1A Locus characteristics for woolly monkeys by population and overall

Population	Locus	N	Na	Ho	He	
PPRA	**LL1-1#10**	48	11	0.85	0.85	ns
	LL1-1#18	48	14	0.92	0.88	ns
	Locus 5	48	8	0.73	0.78	ns
	LL1-1#15	48	11	0.83	0.80	ns
	LL1-1#3	48	20	0.92	0.85	ns
	LL1-5#7	47	6	0.79	0.73	ns
	Leon21	48	7	0.77	0.71	ns
	LL3-1#2	48	4	0.77	0.60	*
Average			**10.1**	**0.82**	**0.78**	
TBS	**LL1-1#10**	63	11	0.81	0.83	*
	LL1-1#18	63	11	0.86	0.88	ns
	Locus 5	62	8	0.74	0.70	ns
	LL1-1#15	63	10	0.84	0.81	ns
	LL1-1#3	62	19	0.92	0.92	ns
	LL1-5#7	63	5	0.75	0.68	ns
	Leon21	63	7	0.67	0.73	ns
	LL3-1#2	63	4	0.57	0.54	ns
Average			**9.4**	**0.77**	**0.76**	
Overall	**LL1-1#10**	111	13	0.83	0.85	ns
	LL1-1#18	111	15	0.88	0.89	ns
	Locus 5	110	10	0.74	0.74	ns
	LL1-1#15	111	13	0.84	0.83	ns
	LL1-1#3	110	24	0.92	0.91	ns
	LL1-5#7	110	6	0.76	0.71	ns
	Leon21	111	8	0.71	0.73	ns
	LL3-1#2	111	4	0.66	0.57	ns
Average			**11.6**	**0.79**	**0.78**	

Table 1B Locus characteristics for spider monkeys by population and overall

Population	Locus	N	Na	Ho	He	
PPRA	D17S804	24	5	0.71	0.72	ns
	D5S111	24	7	0.75	0.67	ns
	D8S165	24	7	0.83	0.74	ns
	D8S260	24	13	0.88	0.89	ns
	Leon 15	24	3	0.46	0.61	ns
	Leon 2	24	8	0.88	0.81	ns
	Leon 21	24	8	0.83	0.78	ns
	LL 1-1#10	24	10	0.83	0.87	ns
	LL 1-1#18	24	12	0.92	0.88	ns
	LL 1-5#7	24	9	0.83	0.87	ns
	LL 3-1#1	24	2	0.04	0.04	ns
	LL 3-1#2	21	5	0.76	0.71	ns
	Locus 5	24	8	0.83	0.80	ns
	SB 19	24	3	0.67	0.57	ns
	SB 30	24	3	0.63	0.63	ns
	SB 38	24	8	0.83	0.84	ns
Average			**6.9**	**0.73**	**0.71**	
TBS	D17S804	25	4	0.64	0.57	ns
	D5S111	25	8	0.64	0.67	ns
	D8S165	25	6	0.64	0.70	ns
	D8S260	25	10	0.84	0.83	ns
	Leon 15	25	4	0.48	0.61	ns
	Leon 2	25	7	0.92	0.82	ns
	Leon 21	25	9	0.92	0.84	ns
	LL 1-1#10	25	12	0.88	0.83	ns
	LL 1-1#18	25	8	0.84	0.83	ns
	LL 1-5#7	25	11	0.92	0.86	ns
	LL 3-1#1	25	2	0.08	0.08	ns
	LL 3-1#2	25	5	0.84	0.76	ns
	Locus 5	25	5	0.72	0.71	ns
	SB 19	25	3	0.56	0.61	ns
	SB 30	25	4	0.40	0.54	*
	SB 38	25	6	0.48	0.57	ns
Average			**6.5**	**0.68**	**0.68**	
Overall	D17S804	49	5	0.67	0.67	ns
	D5S111	49	8	0.69	0.71	ns
	D8S165	49	7	0.73	0.78	ns
	D8S260	49	13	0.86	0.87	ns
	Leon 15	49	4	0.47	0.61	ns
	Leon 2	49	8	0.90	0.85	ns
	Leon 21	49	10	0.88	0.82	ns
	LL 1-1#10	49	13	0.86	0.87	ns
	LL 1-1#18	49	13	0.88	0.87	ns
	LL 1-5#7	49	12	0.88	0.88	ns
	LL 3-1#1	49	2	0.06	0.06	ns
	LL 3-1#2	46	5	0.80	0.74	ns
	Locus 5	49	8	0.78	0.76	ns
	SB 19	49	3	0.61	0.60	ns
	SB 30	49	4	0.51	0.62	ns
	SB 38	49	8	0.65	0.75	ns
Average			**7.7**	**0.70**	**0.72**	

site in 1998 and subsequently 25 were sampled from one social group at the TBS site between 2005 and 2007. The total dataset then, comprised genotypes from 121 woolly monkeys and 49 spider monkeys.

For both woolly and spider monkeys, genotype data for each locus in each of the two best sampled populations (PPRA and TBS) were checked for deviation from Hardy-Weinberg expectations and for the likely presence of null alleles using the softwares GenAlEx version 6 (Peakall and Smouse 2006) and ML-Relate (Kalinowski et al. 2006). For this analysis, genotype data were combined across all sampling years, which is appropriate given the long lifespans of individual animals and the demographic continuity of populations at each site. Indeed, some of the same animals sampled in 1998 or 1999 were resampled in 2006 or 2007. For woolly monkeys, in each population genotype data for one locus deviated significantly from Hardy-Weinberg expectations (Table 1A). At the TBS site, this was due to the presence of a particular private allele seen only in this population and only one individual. In the PPRA population, an excess in the frequency of one particular heterozygous genotype at locus LL 3-1#2 is not easily explained, thus, this locus was both included and excluded from the calculation of F statistics and from the estimation of pairwise relatedness among individual animals in the sample. The results are qualitatively unchanged whether the locus is included or excluded, and the analyses presented below exclude data from this locus.

Looking at each population of spider monkeys separately, genotype frequencies showed significant deviation from Hardy-Weinberg expectations in only one population, the TBS site, and at only one of 16 loci, SB30 (Table 1B). The slight excess homozygosity at this locus in the PPRA population could be explained by the presence of a null allele. Looking at the complete set of spider monkey genotypes from both populations, at one locus, Leon 15, the observed heterozygosity was both low (less than 0.50 in both populations and overall) and substantially lower than the expected heterozygosity (0.61). Analyses in ML-Relate (Kalinowski et al. 2006) suggested the possible presence of a null allele at this locus as well.

Genotype data for each taxon were used to derive two estimators of pairwise relatedness – the regression-based estimator of Queller and Goodnight (1989) and the maximum-likelihood-based estimator of Kalinowski et al. (2006) – for all individuals sampled in the PPRA and TBS populations, again using GenAlEx (Peakall and Smouse 2006) and ML-Relate (Kalinowski et al. 2006). Results are qualitatively unchanged when these different relatedness estimators are used, thus I present results on average relatedness based on the estimator of Queller and Goodnight (1989). Sex-biased dispersal was evaluated using assignment tests as implemented in the softwares FSTAT version 2.9.3 (Goudet 2001) and GenAlEx version 6 (Peakall and Smouse 2006).

Finally, for woolly monkeys sampled in 1998 at both sites, I sequenced up to 528 base pairs of hypervariable region I (HV1) of the mitochondrial control region. This region was amplified from tissue or fecal sample derived DNA extracts using ateline specific primers, either as one large fragment or as three smaller, overlapping fragments. Unincorporated bases and excess primers were removed from the amplified PCR products either via QiaQuick cleanup procedures or by subjecting the products

to ExoSap treatment. Cycle-sequencing of each strand of the amplified products was performed using either ABI Dye-Terminator or Big-Dye sequencing chemistries, and then fragments were separated and visualized on ABI 373XL and ABI 3730 automated DNA analyzers. Sequences were aligned using the software Sequencher (GeneCodes) and checked by eye. MEGA 3.1 (Kumar et al. 2004) was used to estimate haplotype sequence divergence. The phylogenetic relationships among haplotypes were inferred using Bayesian maximum-likelihood methods, as implemented in Mr. Bayes 3.1.2 (Huelsenbeck and Ronquist 2001). Additional control region sequences extracted from GenBank for the other atelids (*Alouatta*, *Brachyteles*, *Ateles*, and *Lagothrix*) were included in the phylogeny inference, with *Alouatta seniculus* specified as an outgroup. A reticulating network of relationships among the Yasuní woolly monkey control region haplotypes was also inferred using the softwares Network 4.2.0.1 (Fluxus Technology Ltd 2007) and TCS 1.2.1 (Clement et al. 2000).

With respect to these sequence data, it is important to note that no special procedures were undertaken to overcome the potential for preferentially amplifying nuclear copies of the mitochondrial genome (i.e., "numts": Lopez et al. 1994; Zhang and Hewitt 1996). However, several lines of evidence suggest that this was not a problem. First, for a subset of three individuals I subsequently amplified a much larger section of mtDNA (∼3000 base pairs) using long-range PCR and then sequenced the same HV1 fragment from within this larger amplicon, and for each sample the resultant HV1 sequences were identical, suggesting the same target was amplified using the ateline HV1 primer sequences as was recovered via long-range PCR. Second, even if numts were present among the set of recovered woolly monkey HV1 sequences, it should only serve to diminish any signal of sex-biased dispersal seen in the patterning of mtDNA variation among males and females. The fact that a definite pattern is still seen (*see below*) suggests that the pattern is robust. Finally, looking within each study site, the members of each of four likely mother-offspring pairs identified by ML-Relate shared the same mitochondrial DNA haplotype, again strongly suggesting that these were true maternally inherited mitochondrial sequences.

9.5 Results

9.5.1 Average Relatedness Within and Gene Flow Among Populations

For woolly monkeys, the mean relatedness, r_{xy}, among all individuals sampled at the PPRA site was 0.008 and at the TBS site was 0.012. For both sites, mean r_{xy} within the population is significantly greater than the average relatedness among all individuals sampled, regardless of population of origin (overall mean $r_{xy} = -0.009$, $p \leq 0.05$ for both populations, tested by permutation). F_{IS} for both populations was close to, and did not differ significantly from zero, (PPRA $F_{IS} = -0.026$, TBS $F_{IS} = 0.004$), suggesting that the overall level of inbreeding within each population was minimal.

Woolly monkeys at the PPRA and TBS sites were slightly but significantly differentiated genetically from one another, regardless of whether the complete dataset, including juveniles, is used (overall $F_{ST} = 0.019$, 99% C.I. $= 0.009$ to 0.028, $p \leq 0.001$), or whether the data is limited to only adult individuals – i.e., those past the expected age of natal dispersal ($F_{ST} = 0.014$, 99% C.I. $= 0.005$ to 0.025, $p \leq 0.001$). The significant F_{ST} value suggests some restriction to gene flow between the two sites. Focusing on adults only, the degree of genetic differentiation seen between the sites was somewhat higher for males than for adult females ($F_{ST} = 0.023$ versus 0.014, $p \leq 0.005$ for both sexes), consistent with the idea that gene flow between the sites for males has been somewhat more restricted than it has for females.

For spider monkeys, the mean relatedness among animals sampled at the PPRA site was -0.005, while at the TBS site the mean relatedness was 0.049. The latter value is significantly greater than the average relatedness among all the individuals sampled across sites (mean $r_{xy} = -0.021$, $p \leq 0.001$ tested by permutation). The inbreeding coefficient for spider monkeys at the TBS site was higher than that for the PPRA population, indicating more local inbreeding, although neither inbreeding coefficient differed significantly from zero (PPRA: $F_{IS} = -0.002$, TBS: $F_{IS} = 0.023$).

As for woolly monkeys, the PPRA and TBS populations of spider monkey were significantly differentiated from one another genetically, both when juveniles are included in the dataset ($F_{ST} = 0.042$, 99% C.I. $= 0.015$ to 0.073, $p \leq 0.001$) and when only adults are considered ($F_{ST} = 0.031$, 99% C.I. $= 0.006$ to 0.060, $p \leq 0.001$). Among adults, the degree of genetic differentiation seen between the sites was much higher for males ($F_{ST} = 0.091$, $p \leq 0.005$) than for females, for whom differentiation between the sites was not significant at an alpha level of 0.05 ($F_{ST} = 0.017$, $p = 0.094$). This suggests that, historically, gene flow between the sites has been much more restricted for males than for females.

9.5.2 Genetic Relatedness Among Nonjuvenile Animals in Each Site

Woolly monkeys were sampled from a minimum of five different social groups at the PPRA site, although only two were sampled thoroughly. When genotype data for all of these groups are considered together, the average relatedness among 11 sampled adult males was 0.008 while that among 15 adult females was 0.024. While the mean relatedness among adult females at the PPRA site was slightly higher than that among males, a permutation test revealed that the difference was not significant ($p = 0.45$). At the TBS site, samples were also collected from woolly monkeys in a minimum of five social groups, each sampled only sparsely. The average relatedness among 19 sampled adult males was 0.017, while that among 23 adult females was 0.005. Here, the mean relatedness among adult males was slightly greater than that among adult females, but again difference was not significant ($p = 0.42$), suggesting comparable levels of dispersal by both males and females.

Di Fiore and Fleischer (2005) previously examined the mean pairwise relatedness among males versus females within groups in two well-sampled social groups

at the PPRA site, but they included subadults in their male and female datasets (presuming these to be post-dispersal individuals) and used a slightly different set of loci. Repeating their analysis with the current, more conservative dataset focusing only on adults, the mean pairwise relatedness among the three adult males in PPRA Group 4 was 0.347 and among the six adult females was 0.078. For this group, adult males, on average, were more closely related than adult females, but this result is driven by the fact that two of the three resident males were more closely related to one another than is expected even for full siblings (r = 0.834 versus r = 0.50). For PPRA Group 5, the mean relatedness among five adult males in PPRA Group 5 was 0.058, while the mean relatedness among seven adult females was only slightly less at 0.032, a difference that is not significant (p = 0.49). Note that this result differs from the earlier report of greater mean r_{xy} among males than among females for this same group when subadults were included in the dataset (Di Fiore and Fleischer 2005).

For spider monkeys, the average relatedness among six adult males from one completely sampled social group at the TBS site was 0.220, corresponding roughly to the degree of relatedness expected among half siblings (r = 0.25), which was significantly higher than the average relatedness among nine adult females sampled from the same group (mean $r_{xy} = 0.004$, p < 0.01). At the PPRA site, by contrast, the average relatedness among five resident adult males in one completely sampled social group was not significantly different from that among the 14 adult females sampled in the group (mean $r_{xy\ male} = -0.027$, mean $r_{xy\ female} = -0.012$, p = 0.40).

9.5.3 Presence of Close Kin Within Groups

The software ML-Relate (Kalinowski et al. 2006) was used to evaluate the likely kinship relationships among all pairs of woolly and spider monkeys within both well-sampled woolly monkey groups at the PPRA site and in each of the completely sampled groups of spider monkeys at the PPRA and TBS sites. The software estimates the likelihood that a particular pair of individuals falls into one of the four kinship classes "unrelated", "half siblings" (HS), "full siblings" (FS), or "parent-offspring" (PO), taking into account the allele frequencies found in the population and the possible presence of null alleles. In each of these groups, most adult individuals of both sexes had at least one other adult individual resident in their social group who was a likely close relative (i.e., an individual whose most likely category of relatedness was HS, FS, or PO rather than unrelated), and often more than one.

In one woolly monkey group at the PPRA site, Group 4, two of the three males were very closely related (HS or closer), as noted above, and five of six females had at least one same-sexed adult kin resident in the group (Fig. 9.3A). For these females, an average of 20%, of same-sexed group members were likely to be close kin. For Group 5 at the PPRA site, all five adult males had at least one same-sex close kin in the group, as did five of seven adult females (Fig. 9.3B). An average of

31% of same sexed adults were identified as likely close relatives for males, while for females an average of only 14% of same-sexed adults were likely to be close kin.

For the spider monkey group at the TBS site, all but one adult male could be linked to one another in a patriline comprising likely PO, FS, and HS relationships. Only three of nine females in this group showed likely close-kin relationships with same-sexed adults, and all of these were more likely to be HS than FS or PO relationships (Fig. 9.3C). For males, an average of 40% of the same-sexed individuals in this group were close kin, while an average of only 8% of same-sexed adults were close kin for females. The situation was somewhat different in the PPRA spider monkey group, where three of five males were linked to other males by likely HS relationships and nine of 13 females could be linked to other females by at least one likely HS relationship (Fig. 9.3D). Still, 20% of same-sexed adults were close kin for males versus only 13% for females. Thus, in all groups, a greater proportion of same-sexed pairs residing in the same group were likely to be HS, FS, or PO dyads for males than for females.
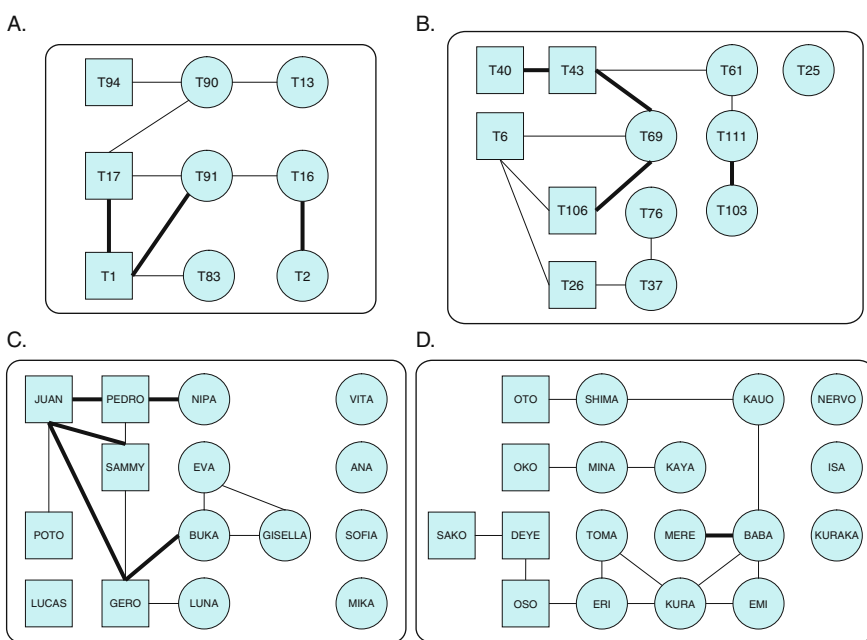
Fig. 9.3 Likely close-kin relationships among adults in two groups of woolly monkeys and two groups of spider monkeys, identified using ML-Relate (Kalinowski et al. 2006). Darker lines indicate a likely PO or FS relationship and thinner lines indicate a likely HS relationship. Males are squares, females are circles. (**A**) Woolly monkey Group 4 in the PPRA site. (**B**) Woolly monkey Group 5 in the PPRA site. (**C**) Spider monkey Group MQ-1 at the PPRA site. (**D**) Spider monkey group MQ-1 at the TBS site

Table 2 Mean and variance in assignment indices for males and females

		Male mAIc	Female mAIc	Male vAIc	Female vAIc
Spider	**PPRA**	0.074	−0.027	1.653	1.283
	TBS	1.438	−0.959	4.955	1.315
Woolly	**PPRA**	−0.035	0.026	0.754	1.666
	TBS	0.000	0.000	1.088	1.409

9.5.4 Assignment Tests for Nonjuvenile Animals

Assignment indices were calculated for all sampled adult woolly and spider monkeys at both the PPRA and TBS sites (Table 2). For woolly monkeys at both sites, the mean corrected assignment index (mAIc) of both males and females was close to zero and the distribution of assignment indices for the two sexes was similar, suggesting little bias in dispersal among the sexes (Fig. 9.4). For spider monkeys at the PPRA site, the mean corrected assignment index (mAIc) for males was slightly positive while that for females was slightly negative, and the variance in the corrected assignment index (vAIc) for males was greater than that for females. Overall, in the PPRA site assignment indices for male versus female spider monkeys were not significantly different (Mann-Whitney Test: $U_{(5, 14)} = 33$, $p = 0.891$). By contrast, at the TBS site, assignment indices for males were significantly higher than those of females (Mann-Whitney Test: $U_{(6, 9)} = 8$, $p < 0.05$), clearly implicating female-biased dispersal. Unexpectedly, the variance in assignment index scores was much higher for males, but this was due to the very low assignment index of one adult male, who was thus a likely immigrant into the community.

### 9.5.5 Mitochondrial DNA Diversity and Intraspecific Phylogeny

Mitochondrial sequence data was only collected for woolly monkeys. A total of 23 mitochondrial haplotypes were found among individuals sampled in the PPRA population and 13 were found among individuals in the TBS population. Three additional unique haplotypes were found in other populations within the Yasuní region that were sampled much less intensively. Of the 36 total unique mitochondrial DNA haplotypes recovered, only five were shared by individuals at more than one sampling site. Assuming a Tamura-Nei model of nucleotide substitution, the mean haplotype divergence across the whole set of unique haplotypes was 3.4 ± 1.5%. Within the set of females sampled, the mean haplotype divergence was 2.9 ± 1.6%, while among males, the mean divergence was 3.2 ± 1.7%.

At both the PPRA and TBS sites, the haplotype diversity seen among both females and males was high, suggesting high levels of transfer by females. Thirteen different haplotypes were seen among the 14 adult females sampled at the PPRA site, and a total of nine haplotypes were found among the 11 adult females sampled at the TBS site. For males, seven haplotypes were found in the set of eleven adult
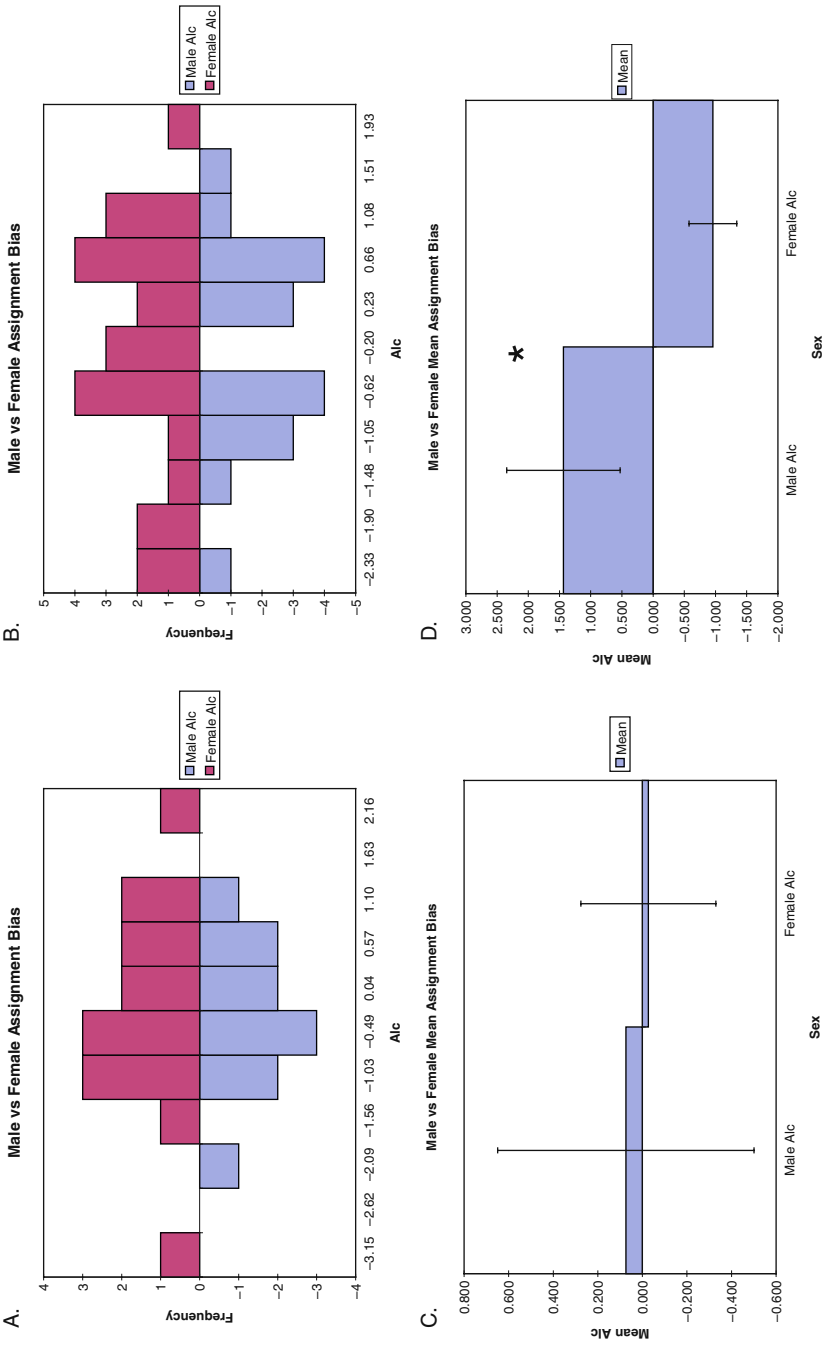
Fig. 9.4 (**A**) Distribution of assignment scores for male and female woolly monkey at the TBS sites. (**B**) Distribution of assignment scores for male and female woolly monkey at the PPRA site. (**C**) Average assignment indices for males versus females at the TBS sites. (**D**) Average assignment indices for males versus females in spider monkey Group MQ-1 at the PPRA site. Average assignment indices for males versus females in spider monkey Group MQ-1 at the TBS site. Assignment indices were calculated using GenAlEx (Peakall and Smouse 2006)

A
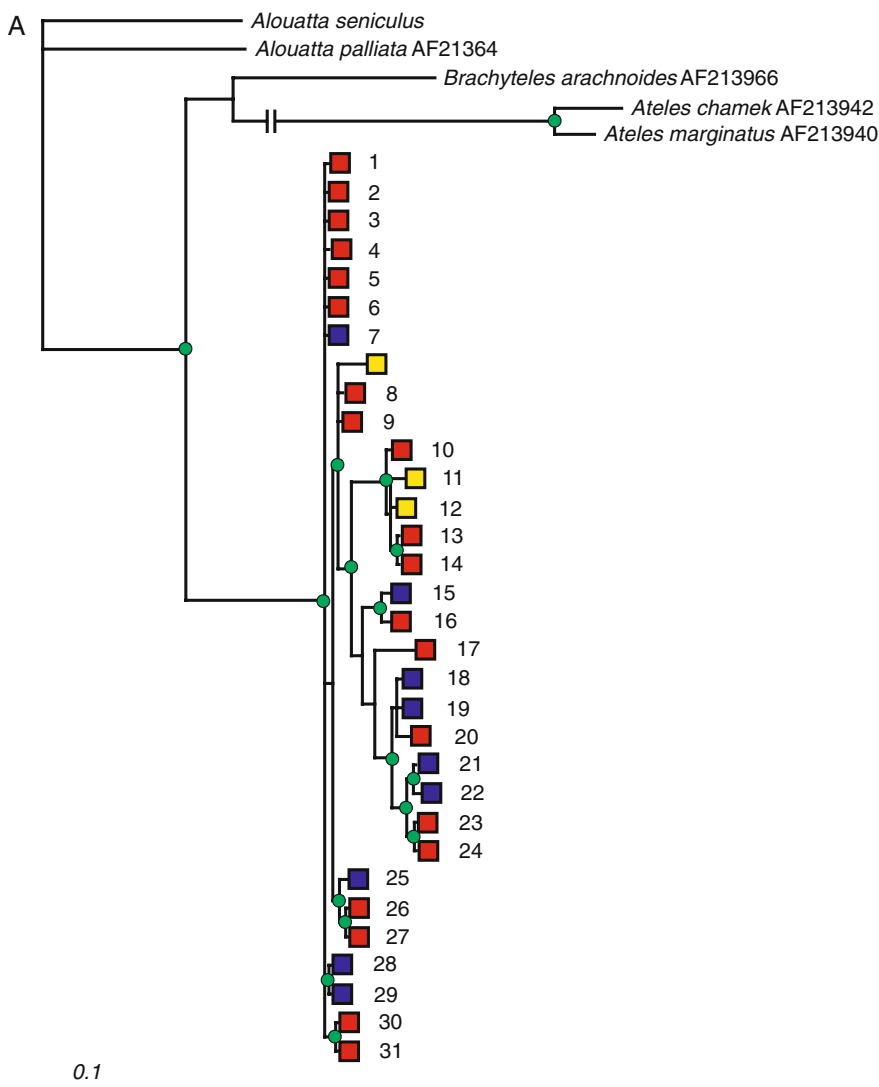
Fig. 9.5 (A and **B**) Phylogenies of male and female woolly monkey mitochondrial DNA haplotypes sampled at the PPRA and TBS sites and other locales within Yasuní National Park, as inferred by Bayesian maximum likelihood methods implemented in the software Mr. Bayes 3.1.2 (Huelsenbeck and Ronquist 2001). For the analysis, control region sequence from *Alouatta seniculus* (sampled in Yasuní) was used as an outgroup, and additional control region sequences extracted from GenBank for *Alouatta palliata*, *Brachyteles arachnoides*, *Ateles chamek*, and *Ateles marginatus* were also included (accession numbers indicated on figure). The analysis was run for 1×10^6 generations, with each of two simultaneous runs sampling four Markov chains every 100 generations under a GTR+I evolutionary model and using the software's default priors. The male and female trees shown are 50% majority rule consensus phylogenies derived from all alterantive topologies stored after a burnin period of 25000 generations. Darkest shaded samples come from the TBS site (in A: individuals 7, 15, 18-19, 21-22, 25, and 28-29; in B: individuals 5-6, 12, 17, 22, 24, 28, 31,
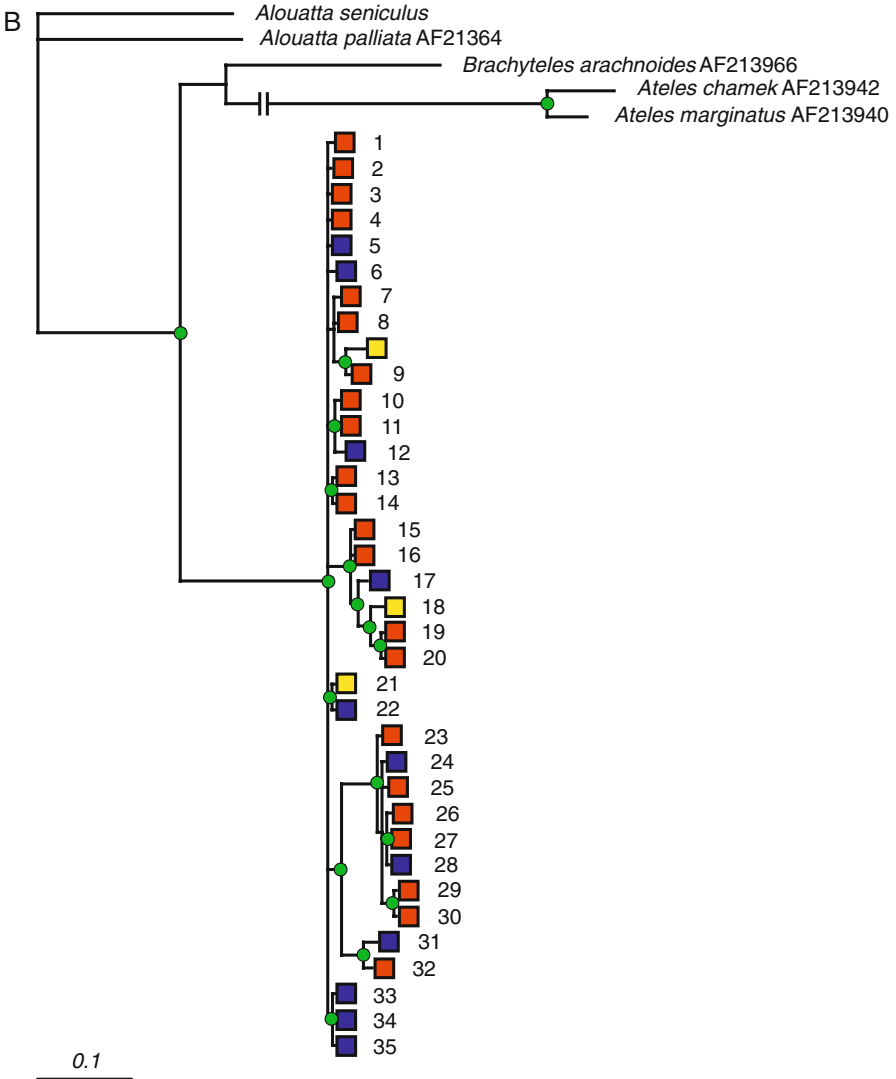
Fig. 9.5 (continued) and 33-35), those with medium gray shading come from the PPRA site (in A: individuals 1-6, 8-10, 13-14, 16-17, 20, 23-24, 26-27, and 30-31; in B: individuals 1-4, 7-8, 9-11, 13-16, 19-20, 23, 25-27, 29-30, and 32), and those with the lightest shading come from other locales. Nodes demarcated by filled circles reflect clades with >70% posterior probability on the consensus tree. (**C** and **D**) Networks of relationships among mitochondrial DNA haplotypes of males and females inferred using the Median-Joining algorithm (Bandelt et al. 1999) implemented in the software Network 4.2 (Fluxus Technology Ltd 2007). For the analysis, the value of epsilon was set at 0 for males and 10 for females, and all variable sites were weighted equally. Very similar networks are also recovered using TCS 1.2.1 (Clement et al. 2000) (data not shown). In each figure, on the terminal nodes the darkest shading refers to haplotypes sampled at the TBS site, medium gray shading refers to haplotypes sampled at the PPRA site, and the lightest shading to haplotypes sampled at one of the other locales indicated in Figure 9.2. Terminal node size reflects the relative
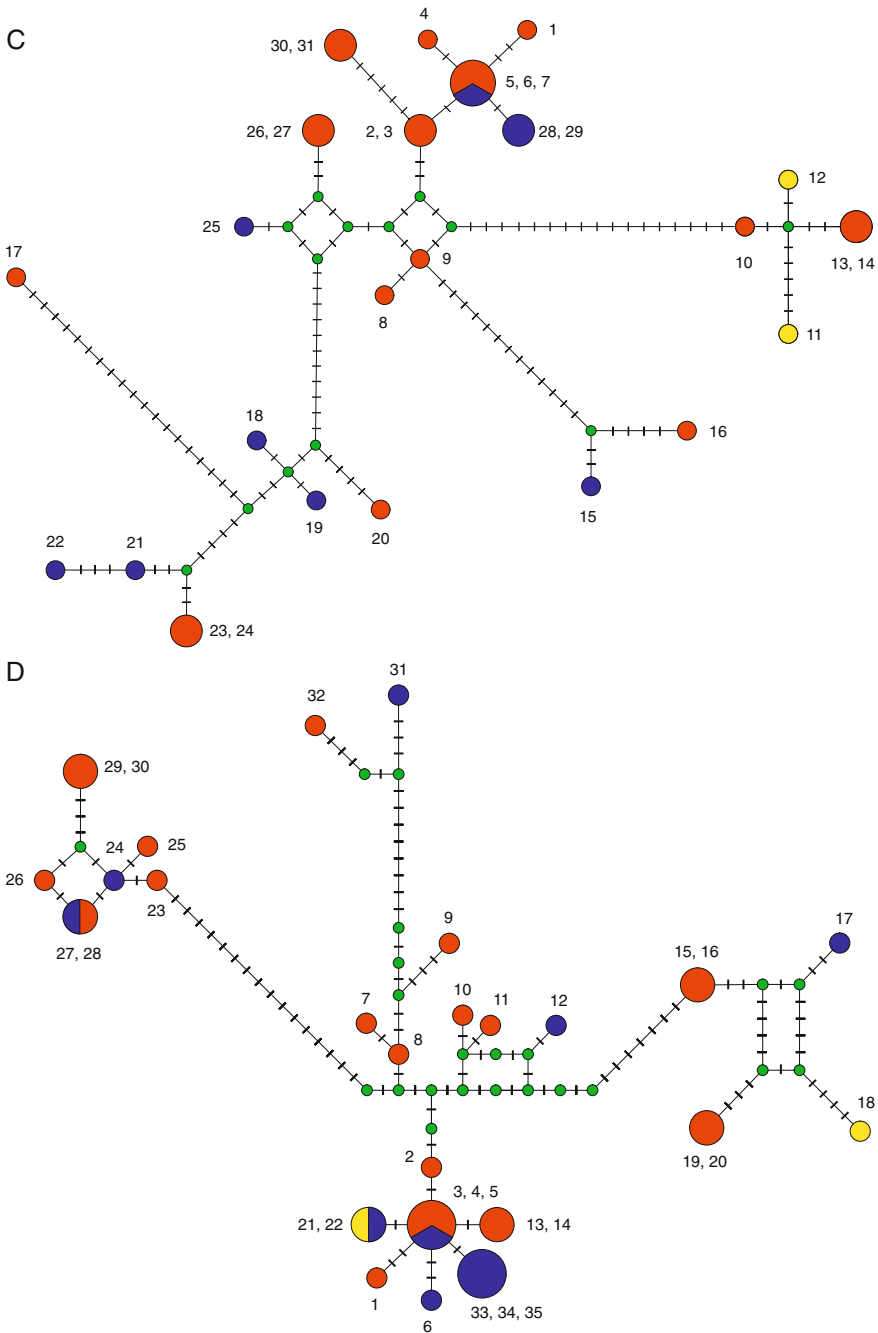
Fig. 9.5 (continued) frequency of that haplotype among the sampled individuals. Small, shaded internal nodes indicate reconstructed (unsampled) median haplotypes and black tick marks indicate the number of nucleotide differences between nodes. Numbers in each figure refer to unique individuals: males for Fig. 9.5A,C and females for Fig. 9.5B,D. *See* Color Insert.

individuals sampled at the PPRA site, and five of the six adult males sampled at the TBS site had different haplotypes.

The phylogenetic relationships and haplotype networks inferred for males and females are shown in Fig. 9.5A–D, along with an indication of the sampling locale (i.e., "PPRA", "TBS", or "other") where each haplotype was found. Importantly, for both sexes, closely related haplotypes (i.e., members of the same clade or haplotypes located close to one another in the network) were sampled at different sampling sites, while some haplotypes found at the same site were only distantly related (i.e., occurred in the same clade or portion of the network), suggesting a high level of female-mediated gene flow across the sampling sites.

Finally, pairs of adult males tended to share the same mitochondrial xDNA haplotype with one another more often than pairs of females. Four pairs of adult males – three pairs within one social group and one pair in a second group – shared mitochondrial DNA haplotypes at the PPRA site, and one pair of adult males, both in the same social group, shared haplotypes at the TBS site, implying they were close matrilineal kin. Among adult females, at the PPRA site only one pair (whose members resided in different groups) shared a haplotype, and at the TBS site one trio of females, two from the same group and one from a different group, shared the same haplotype.

9.6 Discussion

The studies reviewed above exemplify some of the utility of using molecular data to inform our understanding of primate dispersal patterns, even in the absence of long-term observational data and without directly observing dispersal events. These studies likewise highlight the variation in dispersal patterns seen among New World primates and reiterate the fact that, outside of the cercopithecoids, dispersal by females is fairly common among primates, a fact that several researchers have noted previously (Di Fiore and Rendall 1994; Strier 1994b). Additionally, the molecular data reviewed here provide several new insights into the dispersal behavior of woolly and spider monkeys and into patterns of kinship among group members.

First, for woolly monkeys, genetic analyses reveal that dispersal by females is indeed common. However, contrary to the traditional classification of *Lagothrix* as a male-philopatric taxon, a significant degree of dispersal by males appears to be occurring as well. Adult males, in general, are not more closely related to one another than are adult females within most woolly monkey groups or within two local populations, and assignment tests do not detect evidence of a strong female-bias to dispersal patterns. Some males do reside as adults in groups with close same-sexed kin but some adult females do as well, and members of both sexes often live in groups with close opposite-sexed kin as well. Still, based on mitochondrial DNA haplotype sharing, it may be more common for male matrilineal kin to co-reside in social groups than female matrilineal kin. Overall, these patterns might indicate that some individuals of both sexes remain philopatric while others disperse, or they

could reflect a tendency for animals of both sexes to disperse but settle in groups where close kin are already resident. Obviously, distinguishing among these possibilities will require significant longitudinal data on dispersal by known individuals, something that, at present, is lacking.

Second, with respect to spider monkeys, molecular data for one well-sampled social group at the TBS site conform to what has long been suspected about the social structure of *Ateles* – i.e., that females disperse while males remain philopatric, thus the adult members of groups comprise primarily close male relatives and unrelated females. Interestingly, however, this pattern was not seen in the well-studied group of spider monkeys at the PPRA site, where many adult females seemed to reside with likely close kin and where the mean degree of relatedness among both adult males and females was close to zero. It is worthwhile noting, however, that we suspect that several animals from this study group were lost to local hunters during the mid-1990s, prior to genetic sampling. It is thus possible that males related to the current residents were lost from the study population or that hunting opened up opportunities for unrelated males to immigrate into the community. Since 2003, however, the only animals known to have moved into this group have been females (Link and Di Fiore, unpublished data; Shimooka et al. in press), reinforcing the idea that dispersal in spider monkeys is, in general, strongly female-biased. The fact that one adult male in the TBS group was unrelated to the remaining adult males, however, suggests that male immigration into spider monkey groups can sometimes occur. Indeed, several cases of male immigration have been documented for *Ateles geoffroyi* in Costa Rica (Filippo Aureli, personal communication).

Differences between woolly monkeys and at least some groups of spider monkeys in the mean level of relatedness among males relative to females may help to explain some of the clear differences in social behavior among same-sexed individuals in these two species. In spider monkeys, males are generally more affiliative with one another than females and cooperate with each other in territory defense (Fedigan and Baxter 1984; Di Fiore and Campbell 2007). In the TBS study population, for example, male spider monkeys often travel together in the same subgroups, and coalitions of males also jointly aggress against females, cooperate in intergroup encounters with males from adjacent groups, and join together to conduct raids or patrols into other groups' territories (Link et al. in review; Di Fiore and Link, unpublished data), as has been reported for chimpanzees (Watts and Mitani 2001) and for spider monkeys at other sites (Aureli et al. 2006).

In woolly monkeys, by contrast, male-male cooperation is rare, although it occasionally occurs in the context of intergroup interactions, and adult males are tolerant but not overly affiliative with one another (Di Fiore 1997; Di Fiore and Fleischer 2005; Di Fiore and Campbell 2007). Interestingly, high intensity aggression among adult male woolly monkeys has been observed on several occasions. In one case, an adult male resident disappeared from one group under observation after he was seen participating in aggression with another male over a period of several days. In a second case, several adult males from a second study group were seen aggressively interacting with an unfamiliar, non-resident adult male over one to two days, after which the unfamiliar animal was not seen again. The fact that adult

males occasionally bear broken canines and/or broken digits on the hands while such injuries are less common among adult females may be due to competition among males for residence in a group, although it is important to stress that overt aggression among males is almost never seen. Nonetheless, the fact that only some of the adult males within a group seem to be close relatives sets up a situation whereby we might expect to see some males be the targets of high intensity aggression and attempted repulsion by coalitions of other males. Whether patterns of affiliative within-group social behavior in woolly monkeys correlate with genetic relatedness among individuals is currently under investigation.

9.7 Conclusions

The molecular genetic techniques discussed above clearly hold great promise for the study of dispersal, kinship, and social organization, but as yet have not been widely applied in primates. Over the past 10 years, the costs of DNA sequencing and multilocus genotyping have dropped dramatically, while laboratory techniques have been refined sufficiently such that it is possible to reliably collect genetic data from many animals using relatively low quality or degraded samples collected non-invasively. At present, the major impediment to broader implementation of the techniques discussed here is the time and money it takes to identify a sufficient number of suitably variable loci within a taxon of interest for unambiguous identification of individuality and for estimating the relatedness between individuals using multilocus genotyping. However, with the growing availability of primate genomic data and the development of new bioinformatic tools for rapidly searching genomes comparatively for points of homology, even the marker identification phase of molecular studies will become much faster. Thus, the use of genetic data as a complement to observational data in field studies is expected to become more common and should be encouraged. Field primatologists must familiarize themselves with the utility of these methods and be encouraged to collect valuable samples (e.g., hair, feces, tissue) from their subjects whenever possible.

9.8 Summary

Among social animals such as primates, "kinship" (i.e., genetic relatedness) has commonly been invoked as a key factor underlying and organizing the expression of social behavior. Patterns of genetic relatedness within groups in turn are linked to individuals' behavior by the effect that behavior has on the distribution of genetic variation. Dispersal and reproductive behavior, in particular, act to shuffle genes across the social and geographic landscapes and to a large extent determine how genetic variation within a population is partitioned within and between social groups. In recent years, a number of analytical techniques have been developed that allow researchers to use molecular genetic data from a variety of markers (e.g., mitochondrial DNA sequences, multilocus microsatellite genotypes, AFLP fingerprints,

etc.) to characterize the kinship relationships among the individuals in a sample, to investigate mating systems, and to make inferences about dispersal patterns. Somewhat surprisingly, however, remarkably few studies of wild primates have taken advantage of these techniques, and fewer still have taken the further critical step of examining whether the genetic relatedness among individuals is in fact a reliable predictor of the social behaviors it has often been invoked to explain. In this chapter, I outline a number of the key theoretical links that can be drawn among between dispersal patterns, genetic relatedness, and population genetic structure and describe some of the analytical methods that can be used to explore these links. I then review the few published studies of New World monkeys that have used genetic data to investigate dispersal and patterns of within-group relatedness. Finally, I supplement this review with results from my own research group's long-term work on two species of sympatric platyrrhines, lowland woolly monkeys (*Lagothrix poeppigii*) and white-bellied spider monkeys (*Ateles belzebuth*).

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