

Molecular Genetic Approaches to the Study of Primate Behavior, Social Organization, and Reproduction

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ABSTRACT In the past several decades, the development of novel molecular techniques and the advent of noninvasive DNA sampling, coupled with the ease and speed with which molecular analyses can now be performed, have made it possible for primatologists to directly examine the fitness effects of individual behavior and to explore how variation in behavior and social systems influences primate population genetic structure. This review describes the theoretical connections between individual behavior and primate social systems on the one hand and population genetic structure on the other, discusses the kinds of molecular markers typically employed in genetic studies of primates, and summarizes what primatologists have learned from molecular studies over the past few decades about dispersal patterns, mating systems, reproductive strategies, and the influence of kinship on social behavior. Several important conclusions can be drawn from this overview. First, genetic data confirm that, in many species, male dominance rank and fitness are positively related, at least over the short term, though

this relationship need not simply be a reflection of male-male contest competition over mates. More importantly, genetic research reveals the significance of female choice in determining male reproductive success, and documents the efficacy of alternative mating tactics among males. Second, genetic data suggest that the presumed importance of kinship in structuring primate social relationships needs to be evaluated further, at least for some taxa such as chimpanzees in which demographic factors may be more important than relatedness. I conclude this paper by offering several suggestions of additional ways in which molecular techniques might be employed in behavioral and ecological studies of primates (e.g., for conducting “molecular censuses” of unhabituated populations, for studying disease and host-parasite interactions, or for tracking seed fate in studies of seed dispersal) and by providing a brief introduction to the burgeoning field of nonhuman primate behavioral genetics. *Yrbk Phys Anthropol* 46:62–99, 2003. © 2003 Wiley-Liss, Inc.

INTRODUCTION

Observational studies of the behavior, ecology, and social organization of primates in their natural environments have contributed substantially to our understanding of mammalian social systems and their evolution. Nonetheless, even in the most complete long-term studies of wild primate populations, it is difficult to fully elucidate certain features of social systems such as dispersal patterns, patterns of within-group relatedness, and the effective genetic mating system. Nor is it possible through observational studies alone to fully evaluate the effect of kinship on shaping patterns of social behavior or to examine the link between individual behavior (e.g., dominance interactions, alternative mating tactics) and reproductive success. All of these topics, however, have direct relevance to understanding the evolution of primate social systems, especially since some of the fundamental models forwarded to explain the evolution of primate sociality take either male-male or female-female kinship as a point of

departure for considering the evolutionary consequences of cooperative and competitive behaviors.

In the past several decades, the development of novel molecular techniques (e.g., DNA fingerprinting, PCR-based microsatellite genotyping, and automated DNA sequencing) and the advent of noninvasive DNA sampling, coupled with the new ease and speed with which molecular analyses can be performed, have made it possible for primatologists to investigate some of these issues in greater detail. In fact, the pace with which molecular techniques are being applied as a complement to field observational studies of behavior has quickened substantially in the last 10 years, and researchers now routinely incorporate a molecular component into field research programs.

The purpose of this paper is to broadly review the application of molecular techniques, particularly

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polymerase chain reaction (PCR)-based microsatellite genotyping and mitochondrial DNA sequencing, to examining and understanding the social behavior and social systems of primates. Four major topics will be covered in this review. The first is a theoretical discussion that considers how primate population genetic structure (i.e., the patterning of genetic variation within and between social groups at the local and regional scale and within and between various classes of individuals within social groups) is influenced by individual-level behaviors and by aspects of primate social structure such as dispersal patterns, dominance hierarchies, mating patterns, and group formation processes. Understanding the links between behavior and social structure on the one hand, and population genetic structure on the other, is fundamental to making inferences about primate social organization and behavior from empirical patterns of genetic variation seen in wild primate populations. Secondly, this paper discusses some of the molecular markers and analytical techniques that have been used to examine primate genetic structure and the influence of individual behavior on that structure. Third, I present an overview of studies that have used these markers and methods to investigate specific aspects of primate social organization in wild and select captive populations. Finally, some avenues for future work are discussed, including the emerging discipline of nonhuman behavioral genetics, which promises to become a major area of research and may prove fundamental for understanding the evolutionary significance of the rich behavioral variation we see characterizing nonhuman primates. An online Appendix (<http://www.nyu.edu/projects/difiore/yearbook2003/appendix.html>) accompanies this article and provides a comprehensive list of microsatellite markers that have been used in primate studies and the taxa in which they have been used.

LINKS BETWEEN BEHAVIOR, SOCIAL STRUCTURE, AND POPULATION GENETIC STRUCTURE

Geneticists have long recognized that the genetic variation present within natural biological populations can be partitioned hierarchically into components that reflect underlying population structure (Wright, 1951, 1965; Crow and Kimura, 1970; Nei, 1973). The basic model of population genetic structure by Wright (1943, 1951, 1965) envisions three hierarchical levels of organization: a large total population (T), which can be divided into a set of discrete subpopulations (S), each of which contains a number of individuals (I). In this model, mating takes place within subpopulations, and subpopulations are connected with one another by some degree of gene flow. Practically speaking, additional hierarchical levels of organization are also possible. T might encompass the set of social groups found in a particular geographic area, with each S represent-

ing one of those constituent social groups; alternatively, T might be taken to constitute the entire set of individuals belonging to a particular species, with several hierarchical levels of population organization (e.g., social groups, local populations, or regional populations) between the individual and species levels. In either case, classical population genetics theory describes the genetic consequences of population subdivision and of nonrandom mating within various subpopulations by using Wright's F-statistics, which summarize how the total genetic variation present in a large population is partitioned among different hierarchical levels. Briefly, for the simplest case with three levels of organization, Wright's F_{IS} summarizes the effects of nonrandom mating within subpopulations on average individual heterozygosity. F_{ST} characterizes the reduction in individual heterozygosity expected within subpopulations relative to a total population as a result of genetic drift, effectively measuring the extent of population subdivision and the counteracting evolutionary processes of drift on the one hand and gene flow on the other. Finally, F_{IT} summarizes the extent to which average individual heterozygosity deviates from Hardy-Weinberg expectations due to both nonrandom mating within subpopulations and population subdivision (Hartl and Clark, 1997). Wright's F-statistics and other similar indices that describe the partitioning of genetic variance at different hierarchical levels can be estimated for natural populations using a variety of molecular marker data (Nei, 1973; Weir and Cockerham, 1984; Slatkin, 1985).

Although this classical model for describing the partitioning of population genetic variation does not explicitly link genetic structure to elements of social organization or individual-level behavior (Sugg et al., 1996), it does make a number of implicit connections that interest behavioral ecologists. For example, positive F_{IS} values reflect inbreeding within subpopulations, as mating among close kin results in an increase in homozygosity relative to what would be expected if mating within the subpopulation were random. Negative F_{IS} values, on the other hand, suggest that behavioral mechanisms for avoiding inbreeding may be at play. Additionally, because F_{ST} values reflect the relative importance of gene flow and genetic drift in homogenizing vs. diversifying allele frequencies among subpopulations, they can be used to indirectly infer the minimum number of individuals dispersing between subpopulations in each generation (Wright, 1943; Takahata and Nei, 1984; Slatkin, 1995; Cockerham and Weir, 1993). To summarize, the classical model views genetic differentiation among subpopulations as depending primarily on population-level rates of inbreeding within and migration between subpopulations and on demographic factors, such as effective subpopulation size, that influence the rate of subpopulation diversification through drift. But although rates of subpopulation divergence are ultimately dependent on

individual-level behavioral processes (such as mating patterns within social groups or individual decisions over dispersal), those processes are incorporated into the classical model only indirectly, through a population-level lens that ignores individual decisions and variation in behavior between individuals.

In the last 25 years, prompted in part by observational studies of wild animals, behavioral ecologists and population geneticists have begun to consider more explicitly how individual-level behaviors and other features of animal social systems (e.g., sex-biased dispersal patterns, dominance hierarchies, strong reproductive skew, and processes of new group formation) influence population genetic structure, both theoretically and empirically (Chepko-Sade and Halpin, 1987; Melnick, 1987; Chesser, 1991a,b; Sugg et al., 1996; Storz, 1999; Ross, 2001). Next, I review some of the features of social structure and individual behavior that have particularly important influence on the population genetic structure of natural populations of primates and other social mammals. Understanding how social structure and individual behavior influence the partitioning of genetic variation in natural populations is critical for designing effective conservation programs to manage and conserve that variation. Additionally, such knowledge is essential for behavioral ecologists to make accurate inferences about the social systems and behavior of difficult-to-observe taxa based on population genetic surveys.

Dispersal patterns and genetic structure

Where classical population genetics theory treats gene flow as a deterministic process with no accounting for social structure or variation in behavior among individuals, a behavioral ecological perspective on gene flow highlights several features of dispersal that are likely to influence population genetic structure. First of all, in most species of vertebrates, one sex typically disperses while the other remains philopatric (Greenwood, 1980; Waser and Jones, 1986; Johnson and Gaines, 1990), a pattern that can have marked implications for the structuring of genetic variation within and between populations. Specifically, when dispersal is sex-biased, contrasting patterns of genetic structure are expected for the nuclear genome (which is inherited through both the maternal and paternal lines) vs. the genome that is passed strictly through the philopatric sex (the mitochondrial genome for females, the Y chromosome for males). Avise (1995, 2000) neatly summarized some of the expected patterns. For example, species characterized by high levels of female philopatry are expected to show strong evidence of population genetic substructuring to their mitochondrial genes. In contrast, little to no genetic structure is expected for autosomal markers or Y-linked genes in these species, since males are effectively distributing these as they move out of their natal social groups and begin breeding.

Cercopitheine primates typify this pattern of female philopatry and near-universal male dispersal (Melnick and Pearl, 1987; Pusey and Packer, 1987). For these species, mitochondrial genes are not shuffled among social groups within a local or regional population nearly to the extent seen for nuclear genes, which should theoretically result in contrasting patterns of nuclear vs. mitochondrial genetic structure (Melnick and Hoelzer, 1992, 1996). Moreover, restricted mitochondrial gene flow, combined with the stochastic processes of mutation and genetic drift (by which populations come to diverge from one another genetically) and lineage sorting (the process by which maternally inherited mitochondrial lines are lost from a population due to the fact that some females, by chance, leave no female descendants), should result in relatively low diversity in mitochondrial DNA among females within social groups and within local populations but much greater interpopulational differences, even in the absence of major geographic barriers to gene flow (Melnick and Hoelzer, 1996; Wallman et al., 1996). Thus, most cercopitheine primates should be characterized by very low levels of mitochondrial diversity within groups.

In contrast, for species characterized by female dispersal (whether or not males are philopatric), there is no expectation of low mitochondrial DNA diversity within social groups or of greater geographic substructuring to mitochondrial vs. nuclear diversity. Instead, all else being equal, comparable levels of substructuring are expected for both mitochondrial and autosomal genes, since female-mediated gene flow effectively homogenizes both of these genomes across the landscape. Whether a marked population genetic structure is seen in Y-linked genes depends on the extent of male philopatry and on whether females disperse before breeding or carry with them offspring fertilized by males from their natal groups (Avise, 2000). Thus, for primates in which female dispersal and male philopatry are the norm—spider monkeys (*Ateles*), muriquis (*Brachyteles*), some red colobus (*Procolobus badius*), hamadryas baboons (*Papio hamadryas hamadryas*), and chimpanzees and bonobos (*Pan*)—we would expect to see comparable evidence of structure in the mitochondrial or autosomal genomes, a greater degree of population genetic structure in Y-linked genes, and high mitochondrial DNA diversity within social groups. Finally, for taxa in which both sexes disperse to an appreciable degree, such as in many pair-living primates and highly folivorous taxa such as howler monkeys (*Alouatta*), gorillas (*Gorilla*), and many colobines, comparable levels of population structure are expected in all of these genomes (Avise, 2000).

Sex-biased dispersal patterns also have obvious theoretical implications for patterns of within-group relatedness. In the extreme case, members of one sex are predominantly recruited as new breeding individuals in their natal populations. As a result,

the average genetic relatedness among adults of the nondispersing sex is predicted to be greater than among those of the dispersing sex. Thus, for most cercopithecine primates, we would expect mean pairwise relatedness among females within a social group or among females within a local population to be greater than among males, since almost all males transfer into groups, while female breeders are recruited from within their natal groups. In contrast, we would expect males to show greater average levels of relatedness with one another in species showing male philopatry and a marked female bias in dispersal (e.g., chimpanzees, spider monkeys).

Finally, individual-level decisions over dispersal can also influence patterns of population genetic structure, especially since dispersal between primate social groups within a local population is not a random process, as classical population structure models assume. In some cases, individuals from the same natal social group may transfer together (rhesus macaques: Drickamer and Vessey, 1973; Meikle and Vessey, 1981; Japanese macaques: Sugiyama, 1976; baboons: Cheney and Seyfarth, 1977), or join social groups to which other members of the disperser's previous group have already migrated (Cheney and Seyfarth, 1983). For example, Cheney and Seyfarth (1983) reported that 14 of 16 social group transfers by natal or not yet fully grown male vervet monkeys (*Chlorocebus aethiops*) were to groups containing former members of the disperser's previous group. A biased transfer process results in a nonrandom redistribution of genetic variation among social groups at the population level; if transferring animals then breed successfully in their new groups, the result should be greater differentiation among social groups than predicted by classical population genetic theory (Melnick, 1987).

Mating behavior, reproductive skew, and genetic structure

Classical population genetic models assume random mating within subpopulations, but this assumption is clearly violated in many natural populations. In many primates and other social mammals, mating behavior is strongly skewed within social groups, sometimes to the point where only a single member of one or both sexes is seen to mate. In general, skew in reproductive behavior is greater among males and appears to correlate well with male dominance rank (Cowlshaw and Dunbar, 1991), which reflects a male's ability to consistently win in agonistic encounters with other males. Field observations of this relationship between male rank and male mating success led Altmann (1962) to suggest the priority-of-access model of male dominance, which predicts that the top-ranking male in a social group will monopolize both mating and paternity by guarding females at those times during their estrus cycles when conception is most likely. When multiple females are in estrus, the model predicts that paternity should be shared among males in order of

dominance rank. The priority-of-access model thus predicts a skew within-group paternity towards dominant males, the degree of which is determined by the average number of females simultaneously in estrus, which in turn depends on the number of cycling females and the length of the estrus cycle (Dunbar, 1988).

The existence of such a relationship between male rank and paternity success has implications for genetic structure within and between social groups (Melnick, 1987; Pope, 1990). If a single male or a small set of males is responsible for most of the paternity within a social group over some period of time, then members of cohorts born during those males' tenure are predicted to be more closely related to one another (at least to the level of paternal half siblings, assuming complete monopolization of reproduction by a single male) than they would be to members of the larger social group or to individuals from cohorts sired under a different male's tenure. Depending on male tenure length, this process could dramatically reduce effective social group size and thus increase the likely rate of genetic differentiation between social groups in a local population.

For animals that live in extended family groups, including those such as some callitrichine primates that practice cooperative breeding (Goldizen, 1987; Sussman and Garber, 1987; Tardif et al., 1993), reproductive skew theory suggests a more nuanced relationship between individual-level mating behavior and the structuring of genetic variation (Keller and Reeve, 1994; Emlen, 1995, 1997; Clutton-Brock, 1998). Among cooperative breeders, reproduction within each sex is often strongly biased toward a single, dominant individual who actively suppresses the reproduction of subordinate, same-sex competitors (French, 1997). These subordinate animals nonetheless contribute to the reproductive success of dominants either directly (thorough helping behavior such as infant carrying or provisioning) or indirectly (through group size effects in reducing the likelihood of predation or enhancing the group's ability to compete with other groups) (Koenig, 1995; Tardif, 1997). In some cooperatively breeding callitrichines, subordinate individuals sometimes do reproduce (Digby and Ferrari, 1994; Goldizen et al., 1996). Models of optimal reproductive skew predict that the degree to which a dominant animal concedes reproduction or mating opportunities to subordinates should be inversely related to the degree of relatedness between those individuals, i.e., dominants are predicted to concede more reproduction to individuals who are less closely related to them (Keller and Reeve, 1994; Emlen, 1995, 1997; Clutton-Brock, 1998). This somewhat counterintuitive proposition is based on the fact that more closely related subordinate animals gain greater inclusive fitness benefits from their effect on a dominant's reproduction than do less closely related animals and thus require less of a "staying incentive" in

terms of personal reproduction to keep them from dispersing

At the population level, the rate and extent of genetic differentiation between social groups are expected to be proportional to the degree of reproductive skew seen in the population, which in turn depends on population density. For callitrichines living at high population density, where territories and available breeding positions are limited, offspring are likely to delay dispersal and become reproductively suppressed adult "helpers" within their natal groups, which will lead to extensive genetic differentiation among groups. In contrast, genetic differentiation between groups should be lower at low population density, as maturing offspring are more likely to be able to disperse successfully and begin breeding themselves.

Group formation processes and genetic structure

Classical models of population genetic structure do not typically consider how the subpopulation composition of a larger population may change over time. However, studies of wild primate populations reveal that new social group formation is not a rare occurrence, and the method of new group formation has direct consequences for population genetic structure (Duggleby, 1977; Cheverud et al., 1978; Melnick and Kidd, 1983; Melnick, 1987). Among a number of species of cercopithecine primates, new groups typically form from the fissioning of existing groups along matrilineal lines (free-ranging rhesus macaques, *Macaca mulatta*: Chepko-Sade and Sade, 1979; wild rhesus macaques: Southwick et al., 1965; Japanese macaques, *Macaca fuscata*: Furuya, 1968, 1969; toque macaques, *Macaca sinica*: Dittus, 1988; baboons, *Papio hamadryas*: Nash, 1976). Theoretically, the result of matrilineal fission is that each daughter group will be characterized by a higher average level of within-group relatedness than the parent group; at the same time, the average degree of genetic differentiation among groups in the population should also increase (Melnick and Kidd, 1983; Wade and McCauley, 1988; Whitlock and McCauley, 1990). The extent to which this expectation is met in wild cercopithecine populations, however, depends on the number and size of different matrilineal lines within a fissioning group and on degree of genetic differentiation between matrilineal lines (Melnick and Kidd, 1983; Melnick, 1987). Additionally, because cercopithecine groups are characterized by low mitochondrial DNA diversity and because new females do not immigrate into these groups, geographical population expansion through group fissioning and colonization of new areas can lead to large areas being characterized by very similar mitochondrial haplotypes (Melnick and Hoelzer, 1996). This pattern of new group formation, combined with the stochastic process of lineage sorting at play in groups from across a species' range, can also result in a clear geographic population structure in mito-

chondrial DNA in the absence of any kind of physical barrier to dispersal or of similar structuring to nuclear genetic variation (Hoelzer et al., 1994; Melnick and Hoelzer, 1996).

In other species of primates, new group formation proceeds not through a process of fissioning from existed social groups but rather from the union of dispersing individuals of various source groups. For example, dispersing male and female Venezuelan red howler monkeys (*Alouatta seniculus*) join together in coalitions against existing groups to establish new home ranges and to begin breeding (Pope, 2000). Under this model of new group formation, within-group relatedness is expected to be low initially. The rate and extent to which within-group relatedness increases in these groups over time and to which new groups become further differentiated genetically from existing groups depend on dispersal patterns and mating behavior, as discussed above.

Importance of exploring these links

There are two major reasons why primate behavioral ecologists should be concerned with understanding the links between individual-level behavior and social structure on the one hand and population genetic structure on the other. First, knowledge of population genetic structure in different taxa is crucial for evaluating models of the evolution of social behavior and, indeed, of sociality. Many models of primate social evolution take as a fundamental assumption the importance of kin selection, i.e., the idea that behaviors and patterns of social affiliation can be selected for because of their effects not just on an individual's direct fitness but on the survival and reproduction of relatives as well. As an example, Wrangham's (1980) model for the evolution of "female-bonded" social groups in primates suggests that females should refrain from dispersing from their natal ranges and should form groups preferentially with kin when larger groups of females can more effectively defend access to necessary resources than smaller groups or individuals. Moreover, many affiliative social behaviors are predicted to be manifest more often among relatives than among nonrelatives because of kin selection (Gouzoules and Gouzoules, 1987; Silk, 2002). For example, grooming behavior in primates is hypothesized to be more commonly directed toward kin, and individuals are expected to form coalitions more often with relatives. However, these are, in effect, predictions that in many cases have yet to be tested in natural populations using genetic data.

Additionally, understanding the links between behavior, social structure, and population genetic structure is crucial for using molecular data to infer something about individual-level behaviors and the features of primate social organization that may have given rise to them. For many primate species, it is difficult to conduct the long-term investigations of mating behavior or dispersal patterns that are of such great interest to behavioral ecologists, but mo-

lecular data can provide insights about these features of social systems indirectly, even for species that are unhabituated or difficult to observe. The combining of noninvasive sampling methods with PCR-based genotyping and sequencing has provided primatologists with a powerful tool for investigating primate social systems and the evolutionary significance of individual behavior.

MARKERS AND METHODS

The first step in any analysis of genetic variation involves characterizing individuals using molecular markers. Consequently, before turning to an overview of primate molecular ecological studies, I briefly review some of the markers and analytical techniques that have been used to investigate links between behavior, social structure, and genetic structure in primates. This review is cursory and excludes some classes of genetic markers that have not yet been widely applied in individual-level and population-level studies of nonhuman primates (e.g., SINEs, *Alu* elements, AFLPs, and SNPs). Interested readers should consult Avise (1994), Hillis et al. (1996), and selected chapters in Ferraris and Palumbi (1996), Smith and Wayne (1996), and Baker (2000) for a more detailed overview of different kinds of molecular markers and analyses and their uses in behavioral and ecological field studies.

Allozyme assays

Some of the earliest applications of molecular techniques to the study of primate behavior and genetic structure used allozyme markers. Allozymes are enzymatic proteins that are coded for by DNA, and they can be extracted from a variety of biological tissues. Depending on their size, structure, and net charge (which is dependent on their amino-acid composition), these proteins will migrate at different rates through a gel matrix (typically acrylamide or hydrolyzed potato starch) to which a current is applied, a process called "gel electrophoresis." Once protein variants have been separated from one another by electrophoresis, the gel is treated with a histochemical stain that reacts with a specific protein of interest to produce a visible band or set of bands (a "zymogram") from which an individual's genotype at that particular protein-coding locus can be inferred (Fig. 1A). Many different locus-specific stains have been developed, allowing researchers to easily construct multilocus genotypes suitable for parentage analysis or for characterizing population-level allele frequencies to examine population substructuring. However, a considerable limitation of this process is that fairly large quantities of blood or tissue are needed for analysis, and these are often difficult to obtain from wild primates. Moreover, because allozymes are functional products of coding DNA, they may be under considerable selection pressure, thus violating a basic assumption of most theoretical population genetic models. Even where

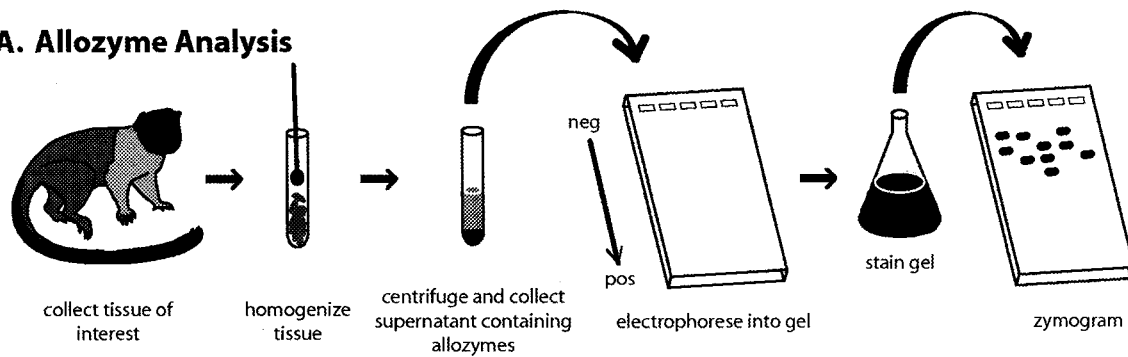
they do not appear to be under selection, allozyme loci also often show very little variation (typically only a few alleles per locus), which requires that many loci be analyzed to provide sufficient resolution for studies of parentage or population structure.

Restriction fragment length assays

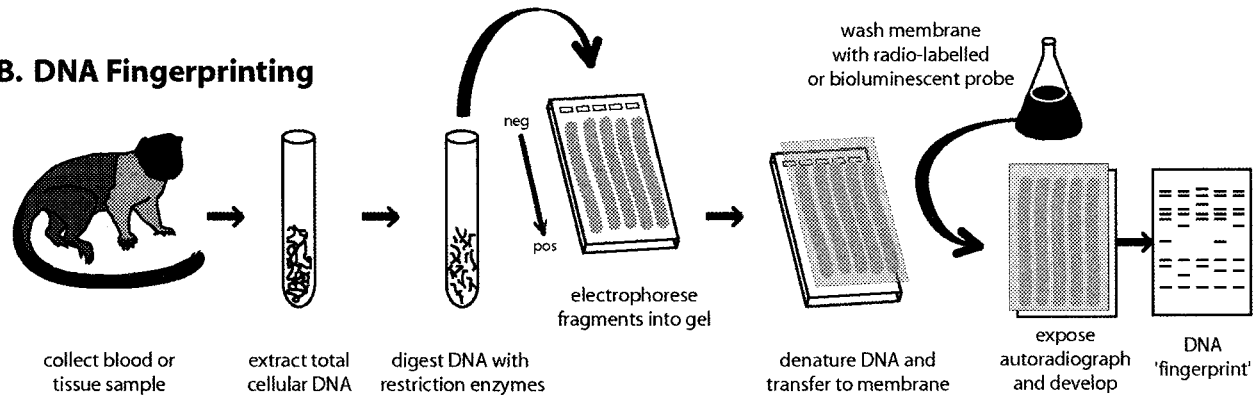
Restriction fragment length assays provide another way to examine genetic variation within populations. Like proteins with different conformations and net charges, DNA fragments of different length also run at different rates through denaturing acrylamide or other electrophoretic gel matrices. Restriction fragment profiles for different individuals are generated by first cutting the individuals' DNA using restriction endonucleases (enzymes isolated from bacteria that recognize and cleave DNA at specific base-pair sequences), and then separating those fragments by electrophoresis and visualizing them. Genetic differences between individuals can result in the loss or gain of a restriction site due to base-pair substitutions, insertions, or deletions in the recognition sequence for an enzyme; this genetic variation is then detectable as polymorphism in the length of resultant restriction fragments.

There are several different ways of visualizing restriction fragment length polymorphism, but, most commonly, electrophoretically separated restriction fragments are first transferred and bound to a nylon or nitocellulose membrane by the process of Southern blotting (Southern, 1975). When this membrane is washed with a radiolabeled or bioluminescently labeled DNA probe that hybridizes specifically to complementary genomic DNA bound on the membrane, the position of those DNA fragments containing complementary sequences can be visualized through autoradiography. Some probes bind to a single location in the genome and thus provide single-locus genotypic data that can be used to characterize population allele frequencies. Other probes are complementary to "minisatellite" DNA, i.e., regions of the genome consisting of tandem repeats of 15–500 base-pair motifs that are present in multiple places in the genome. When a restriction fragment Southern blot is treated with a minisatellite probe, the resultant autoradiograph reveals a complex and individual-specific banding pattern—a multilocus DNA "fingerprint" (Jeffreys et al., 1985a,b) (Fig. 1B)—that, while not appropriate for determining population allele frequencies, can be used in individual identity and parentage assessment: any band present in the fingerprint of offspring must also be present in either the mother or the father. Restriction fragment analysis can also provide direct estimates of sequence deviation between pairs of individuals, since the number of DNA base pairs surveyed essentially equals the product of the number of restriction sites surveyed and the number of base pairs in the recognition sequence. One important limitation of restriction fragment length polymorphism (RFLP) assays is that (at least until the

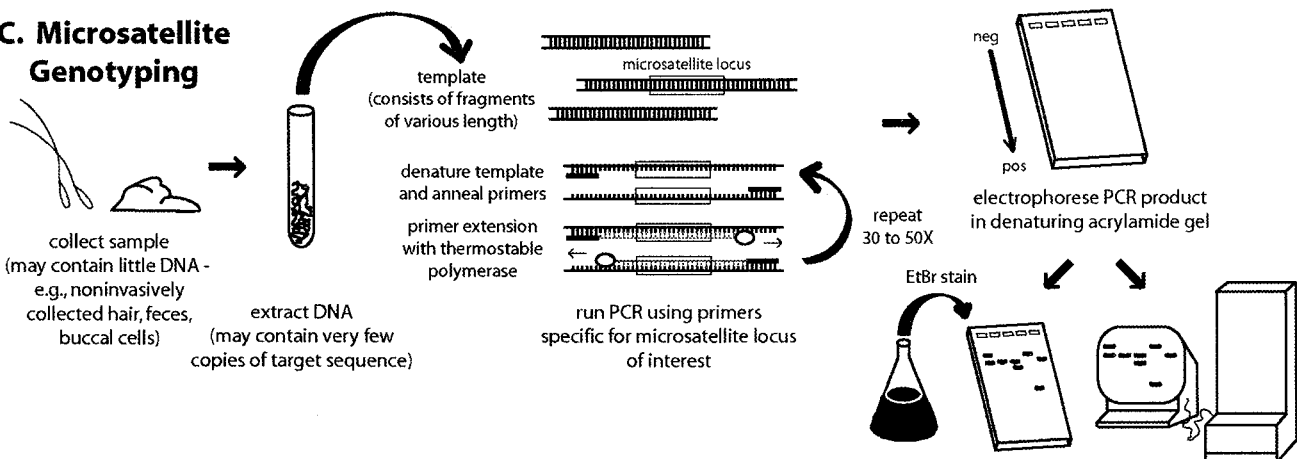
A. Allozyme Analysis



B. DNA Fingerprinting



C. Microsatellite Genotyping



D. RAPD Profile Analysis

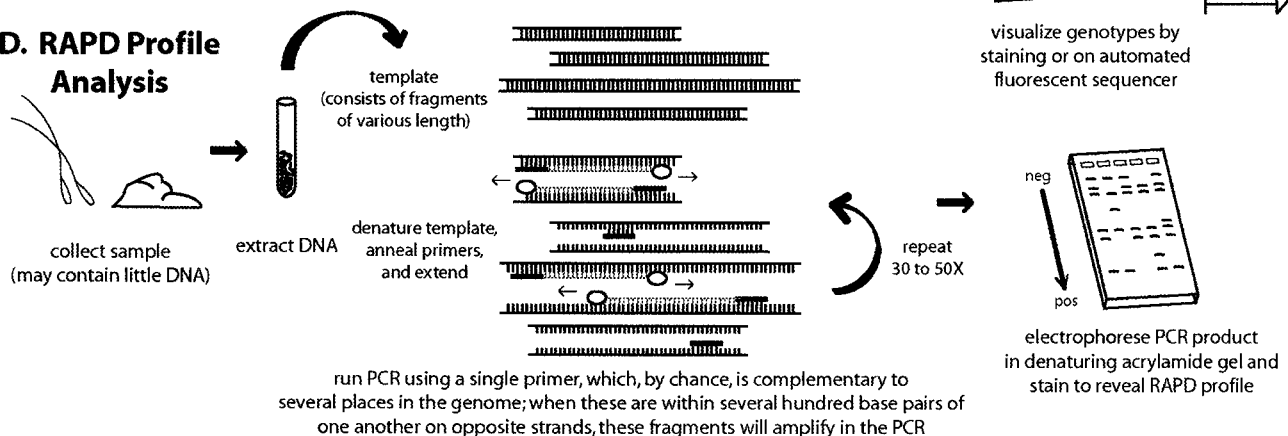


Fig. 1. Summary of standard single-locus and multilocus marker methods used in molecular studies of primate behavior, social organization, and reproduction. **A, B:** Methods are not based on polymerase chain reaction (PCR) and thus require large amounts of high-quality sample (blood, tissue) that may be difficult to obtain in field studies. **C, D:** Methods are PCR-based and can be used with small or degraded samples that can often be collected noninvasively.

advent of PCR) large quantities of high-quality genomic DNA were needed, making their application to hard-to-sample populations of wild primates difficult. Moreover, because a fragment length polymorphism is due principally to the presence vs. absence of particular restriction sites, RFLP markers are typically two-allele systems and show low heterozygosities. As for allozyme loci, this often requires that many loci be analyzed for parentage or population structure studies.

Microsatellite marker genotyping

In the last decade, “microsatellite” loci (also known as simple sequence repeat (SSR) or simple tandem repeat (STR) loci) have become the genetic markers of choice for many kinds of molecular applications, including analysis of population structure and dispersal patterns, assessment of parentage and individual identity, and estimation of degree of relatedness between populations or pairs of individuals. Microsatellites are regions of the genome comprising variable numbers of tandem repeats of a 1–6 base-pair nucleotide motif. Microsatellite markers are ideal for population-level studies for a number of reasons. First, they are randomly distributed throughout the genome, commonly occurring in noncoding regions, and are typically selectively neutral. Second, microsatellite loci are often hypervariable within populations and show much higher mutation rates than other nuclear regions (Weber and Wong, 1993). Variation seen at microsatellite loci arises from differences among alleles in the number of times the basic motif is repeated, with new alleles probably being generated through polymerase slippage and slipped-strand mispairing during DNA replication (Levinson and Gutman, 1987; Kruglyak et al., 1998; Toth et al., 2000), which results in the addition or loss of one or a small number of repeats. Third, microsatellite alleles show codominant inheritance, making them relatively easy to score directly. Finally, and most important for field applications, microsatellite marker genotyping requires only minuscule amounts of template DNA, since it is based on PCR (Mullis and Faloona, 1987). Sufficient DNA for microsatellite analyses can be extracted from small pieces of tissue or minute quantities of blood, as well as from single shed hairs or from the epithelial cells sloughed off in urine, feces, or saliva. Once a microsatellite locus has been identified in the genome, oligonucleotide primers can be designed from the DNA sequences upstream and downstream of the microsatellite to amplify that fragment of the genome by PCR. Then microsatellite marker variation can be assayed directly by electrophoresis and visualization of these PCR products in denaturing polyacrylamide gels; because alleles vary in the number of repeats of the microsatellite motif, heterozygous individuals will show two PCR product bands, while homozygotes will only display a single band (Fig. 1C).

Numerous microsatellite loci have been identified in the genomes of many primate species (see online Appendix at <http://www.nyu.edu/projects/difiore/yearbook2003/appendix.html>). Often, the flanking sequence around a microsatellite has been sufficiently conserved that primers designed for one species also work in closely related taxa (Moore et al., 1991). For catarrhines and hominoids, many useful loci were originally discovered in the human genome, which is estimated to contain roughly one microsatellite per two kilobases of the haploid genome (International Human Genome Sequencing Consortium, 2001). Nonetheless, for other primates (platyrrhines, strepsirrhines, and presumably tarsiers), few microsatellites homologous to those in humans have been found, demanding the expensive and time-consuming identification and optimization of species-specific primers (Table 1). General strategies for building and screening genomic libraries to identify species-specific microsatellites in novel taxa can be found in Strassmann et al. (1996), Hammond et al. (1998), Hamilton et al. (1999), and Paetkau (1999), while Zane et al. (2002) provide a comprehensive overview and comparison of these various microsatellite isolation procedures.

One important caution that must be kept in mind in any microsatellite marker study concerns the problem of “null alleles,” i.e., allelic variants that do not amplify in PCR-based genotyping due to mutations in one or both of the primer binding sites (Pemberton et al., 1995). At some loci, the frequency of null alleles can be quite high, and this frequency can vary substantially from population to population. The existence of null alleles at a locus can make parentage assessment problematic (e.g., a male who truly shares a null allele with an infant can mistakenly be excluded as a potential sire), as well as introduce error into estimates of population allele frequencies and coefficients of pairwise relatedness. At a minimum, researchers should attempt to evaluate the potential problem caused by null alleles at each locus being investigated by looking for mismatches between known parents and offspring and by evaluating the extent to which genotype frequencies at the locus deviate from those expected under Hardy-Weinberg equilibrium conditions.

Random amplified DNA polymorphism analysis

A second kind of PCR-based technique for molecular analysis utilizes a short (ca. 10 base-pair), random oligonucleotide sequence as a single primer for PCR. By chance, these oligonucleotides are complementary to multiple sites in the genome, and where such complementary sites are present on opposite strands of the DNA molecule within a few hundred bases of one another, the bracketed fragment will be amplified by PCR. Electrophoresis and visualization of the PCR product yield a different type of multilocus DNA profile—a random amplified polymorphic DNA or “RAPD” profile (Fig. 1D) that can be used for parentage and individual identity assessment,

TABLE 1. Nonhuman primate taxa for which species-specific microsatellite markers have been developed and published

Species in which loci identified	Number of variable loci reported ¹	Average observed heterozygosity (H_o) per locus (and range)	Average no. of alleles per locus (and range)	Number of chromosomes assayed	Source
<i>Alouatta palliata</i>	3	No data	5.0 (4–6)	80	Ellsworth and Hoelzer (1998)
<i>Callithrix jacchus</i>	9	0.66 (0.38–0.94)	5.9 (2–12)	196	Nievergelt et al. (1998)
<i>Cebus apella</i>	4	No data	6.8 (4–11)	60–148	Escobar-Páramo (2000)
<i>Cheirogaleus medius</i>	7	0.74 (0.63–0.87)	9.3 (5–15)	216	Fietz et al. (2000)
<i>Eulemur fulvus rufus</i>	11	0.59 (0.09–0.82)	6.3 (2–13)	66	Jekielek and Strobeck (1999)
<i>Eulemur fulvus rufus</i>	4	0.77 (0.70–0.92)	9.5 (6–17)	118	Wimmer and Kappeler (2002)
<i>Haplemur griseus alaotrensis</i>	2	0.44 (0.17–0.70)	4 (2–6)	280	Nievergelt et al. (2002)
<i>Haplemur griseus griseus</i> ²	14	R: 0.60 (0.40–0.80) T: 0.69 (0.29–1.00)	R: 6.7 (3–10) T: 4.9 (2–8)	R: 20 T: 14	Sommer et al. (2002)
<i>Leontopithecus rosalia</i> ³	4	0.65 (0.38–0.82)	5.3 (4–6)	54	Gratival et al. (2001)
<i>Macaca fuscata</i>	3	No data	8.0 (6–9)	62	Inoue and Takenaka (1993)
<i>Macaca fuscata</i>	7	No data	7.9 (4–11)	28	Domingo-Roura et al. (1997)
<i>Microcebus murinus</i> ⁴	7	0.72 (0.22–0.93)	17.1 (5–29)	348	Radespiel et al. (2001)
<i>Microcebus murinus</i>	3	0.91 (0.87–0.95)	16.7 (16–18)	158–164	Wimmer et al. (2002)
<i>Pan troglodytes</i>	28	No data	5.7 (2–10)	12	Cooper et al. (1998)
<i>Pan troglodytes</i>	3	No data	10.3 (8–14)	78	Takenaka et al. (1993)
<i>Propithecus verreauxi verreauxi</i> ⁵	16	0.74 (0.63–0.81)	6.6 (2–11)	400+	Lawler et al. (2001a)
<i>Propithecus verreauxi verreauxi</i>	7	0.57 (0.38–0.88)	5.6 (4–7)	16	Mayor et al. (2002)
<i>Saguinus bicolor</i> ⁶	10	0.60 (0.36–0.80)	6.6 (4–12)	4–24	Böhle and Zischler (2002)
<i>Saimiri boliviensis</i>	6	0.59 (0.13–0.73)	6.0 (3–8)	44	Witte and Rogers (1999)

¹ Summarized here are data for only those microsatellite loci that were originally identified in the species listed, although cited source may report data for additional variable loci originally developed in other taxa.

² Heterozygosity and allele number data for two separate populations (R, Ranomafana; T, Tsinjoarivo) are reported.

³ Heterozygosity and allele number data are reported for largest remnant population of this species, living in Poço das Antas Biological Reserve.

⁴ Heterozygosity and allele number data are reported for 162 individuals from a wild population.

⁵ Heterozygosity and allele number data are based on only 7 of 16 loci reported.

⁶ Although reported microsatellite loci were originally identified in *Saguinus bicolor*, variation was assayed in *S. mystax*.

since, again, any band present in an offspring should theoretically appear in one or the other parent (Williams et al., 1990; Welsh et al., 1991). Since the procedure is PCR-based, RAPD analysis needs little DNA and is fast and cheap to perform, requiring little equipment beyond a thermal cycler and electrophoresis rig. Nonetheless, reproducibility of the results is very sensitive to reaction conditions (e.g., template concentration, magnesium concentration, DNA polymerase used, and thermal cycler ramp time) (Ellsworth et al., 1993; Meunier and Grimont, 1993; Ayliffe et al., 1994; Schweder et al., 1995), and artifactual, extraparental bands are common, making the procedure of somewhat suspect utility for parentage analysis (Riedy et al., 1992; Pérez et al., 1998).

Mitochondrial DNA sequencing

Modern DNA sequencing is based on controlled termination of DNA replication (Sanger et al., 1977). The region of the genome of interest is first amplified by PCR to create the sequencing template. This template is then mixed in a PCR-like sequencing reaction with a single primer oligonucleotide, DNA polymerase, and free nucleotide bases, a small fraction of which are modified such that once they have been incorporated into a growing DNA strand, further extension is not possible. The process results in sets of DNA fragments that differ in size by a single base pair, which can then be separated by electro-

phoresis. Initially, the procedure involved using different terminator nucleotides (A, G, T, and C) in four reaction subsamples, which were then electrophoresed in separate lanes, allowing direct manual determination of the DNA sequence from the visualized gel (Sanger et al., 1977). Modern automated DNA sequencing involves modifying the terminator nucleotides with different fluorescent labels so that all can be used in the same reaction and electrophoresed together in the same lane on a gel; the different signals given off by different labels when an electrophoresing fragment is stimulated by laser allow for computerized sequence detection.

Mitochondrial rather than nuclear sequence data are commonly used in population-level assays of genetic variation in primates and other vertebrates, because mitochondrial DNA evolves much more rapidly than most nuclear DNA (Wilson et al., 1985; Mindell and Thacker, 1996) (although the rate of evolution at nuclear microsatellite loci is much faster still). Moreover, mitochondrial DNA is nonrecombining and is inherited strictly through the maternal line (although some examples of “paternal leakage” have been reported). Thus, mitochondrial DNA can theoretically provide direct information about patterns of maternal relatedness and sex-specific population structure, and has not surprisingly become the molecular marker of choice in many phylogenetic and phylogeographic studies (Avise et al., 1987; Avise, 2000; Moritz et al., 1987). Nonethe-

less, researchers have increasingly come to appreciate that substantial caution must be exercised when using mitochondrial markers. In many species of plants and animals, mitochondrial sequences of various lengths have been transposed into the nuclear genome numerous times (Zhang and Hewitt, 1996). During PCR, these nuclear mitochondrial insertions ("numts"; see Lopez et al., 1994), which are nonfunctional, subject to recombination, and more slowly evolving than their true mitochondrial counterparts, may be amplified either preferentially or along with actual mitochondrial sequences, and they can thus yield nonhomologous sequence data that complicate phylogenetic reconstructions. The problem posed by numts may be of particular concern for phylogenetic studies of wild populations, which typically focus on short mitochondrial DNA sequences that are more readily amplified from degraded or low-copy-number DNA sources such as hair or fecal samples. Researchers are increasingly adopting various procedures to avoid or minimize this potential source of error, e.g., by routinely cloning putative mitochondrial PCR products and then sequencing multiple clones to assay for variation within individuals, which can reveal the presence of numts, or by performing initial "long-range" PCR amplifications of large (8,000+ base-pair) segments of mitochondrial DNA before sequencing, since numts of this size are far less common than smaller transpositions.

Basic analytical methods

Four basic types of summary data can be gleaned from these molecular markers: 1) statistics for describing the partitioning of genetic variation among different population organizational levels and for estimating gene flow and effective population size among subpopulations, 2) estimates of relatedness between pairs of individuals or of average relatedness within and between groups of individuals, 3) estimates of gross genetic distance or similarity between individuals or groups of individuals, and 4) parentage exclusions or assignments. A number of computer packages have been developed for calculating these summary statistics and performing parentage analyses (Table 2).

Statistics describing population genetic structure such as Wright's F_{ST} , from which indirect estimates of gene flow can be made, are readily calculated from allele frequency data (Weir and Cockerham, 1984), as are several newer estimators designed specifically for use with microsatellite data that incorporate assumptions about the process of microsatellite evolution (e.g., R_{ST} : Slatkin, 1995; ϕ_{ST} : Michalakis and Excoffier, 1996; ρ_{ST} : Rousset, 1996). One important caveat that should be noted, however, is that our understanding of just how microsatellite loci evolve is limited, and theoretical models of evolutionary change in microsatellites are still being developed and tested (e.g., Estoup and Cornuet, 1999; Feldman et al., 1999). The particular model of evolutionary change assumed for a microsatellite locus,

e.g., "infinite alleles" (Kimura and Crow, 1964) vs. "stepwise mutation" (Kimura and Ohta, 1978) vs. "two-phase mutation" (Di Rienzo et al., 1994) models, and the particular model of population structure subscribed to, e.g., generalized island vs. "stepping-stone" (Kimura and Weiss, 1964), both affect the choice of formulae used to estimate gene flow and genetic distance from microsatellite data. Finally, several likelihood methods based on coalescent theory have also been developed recently for estimating gene flow and effective population size from sequence data (e.g., Beerli, 1998).

Several different estimators of relatedness (R) based on genotype and population allele frequency data have been proposed (e.g., Queller and Goodnight, 1989; Lynch and Ritland, 1999), as have estimators based on multilocus DNA fingerprints (e.g., Lynch, 1988, 1990; Li et al., 1993). Van de Casteele et al. (2001) compared the performance of several microsatellite-based estimators of relatedness using simulation models, and found that, depending on allele frequency distributions at the different loci under investigation, certain estimators more accurately reconstructed "true" relatedness. They recommend that researchers perform simulations to decide which estimator to use in a given study. In general, using numerous unlinked loci each with high heterozygosity yields the best estimates of pairwise relatedness, although heterozygosity appears to be the more important of these two variables: Blouin et al. (1996) found that nearly twice the number of loci with heterozygosities of 0.62 are needed to provide as accurate an estimate of relatedness as a given number of loci each with a heterozygosity of 0.75. In practice, rarefaction analysis (e.g., Altmann et al., 1996; de Ruiter and Geffen, 1998; Wimmer et al., 2002) can be used to evaluate the resolution provided by a given number of loci. Briefly, rarefaction analysis is a bootstrapping procedure in which each iteration involves estimating relatedness values using genotype data from one randomly chosen locus and then examining how those R values change as data from successive random loci are incorporated into the estimate. The difference between R values derived from $N + 1$ vs. N loci (averaged across iterations) will theoretically approach zero as data from more and more loci are added; thus, once the difference between successive R values becomes small enough as an additional locus is added, it means that sufficient loci have been sampled to give a statistically reliable estimate of pairwise relatedness.

Various estimators of genetic distance that can be derived directly from sequence data or indirectly from allele frequency data are overviewed in Graur and Li (2000), while Goldstein et al. (1995), Shriver et al. (1995), and Paetkau et al. (1997) offer several microsatellite-based genetic distance estimators. The assumptions associated with each of these estimators and their particular strengths are beyond the scope of this review, but are discussed in the publications cited.

TABLE 2. Software packages useful for analysis of genetic data in behavioral studies

Program	Description	Reference	Source and platform
GENEPOP	General purpose program for population genetic analysis. Calculates allele frequencies, observed and expected genotype frequencies, various estimators of population subdivision (F_{ST} , R_{ST}) and gene flow (e.g., Nm), performs tests of linkage disequilibrium among loci, etc.	Raymond and Roussett (1995)	wbiomed.curtin.edu.au/genepop/ Web, DOS
MICROSAT	General purpose program for population genetic analysis. Calculates allele frequencies, observed and expected genotype frequencies, various estimators of population subdivision (F_{ST} , R_{ST}), many microsatellite-based estimators of genetic distance (e.g., D_{AD} , D_{SW} , $(d\mu)^2$), etc.	Minch (1996)	hpgl.stanford.edu/projects/microsat/ DOS, Macintosh
FSTAT	General purpose program for population genetic analysis. Calculates allele frequencies, observed and expected genotype frequencies, various estimators of population subdivision and inbreeding (F statistics and R statistics), various estimators of genetic distance from allelic data.	Goudet (1995)	www.unil.ch/izea/software/fstat.html Windows, DOS
ARLEQUIN	General-purpose program for population genetic analysis. Calculates allele frequencies, observed and expected genotype frequencies, various estimators of population subdivision (e.g., AMOVA analysis) and gene flow, various estimators of genetic distance from allelic data. Can also be used to perform assignment tests.	Schneider et al. (2000)	lgb.unige.ch/arlequin/ Windows, Macintosh, Linux (through Java)
RSTCALC	Program for analysis of population structure and gene flow from microsatellite data.	Goodman (1997)	helios.bto.ed.ac.uk/evolgen/rst/rst.html Windows
PAUP*	General purpose program for phylogenetic analysis. Calculates various measures of genetic distance from sequence data. Allows phylogeny estimation using parsimony, distance, or likelihood methods.	Swofford (2002)	Sinauer Associates, Inc., Publishers Windows, Macintosh, UNIX/VMS, DOS
RELATEDNESS	Calculates pairwise relatedness between individuals or average pairwise relatedness between groups using regression.	Queller and Goodnight (1989)	gsoft.smu.edu/GSoft.html Macintosh
KINSHIP	Tests pedigree relationships using likelihood methods and can be used for parentage assignment.	Goodnight and Queller (1999)	gsoft.smu.edu/GSoft.html Macintosh
CERVUS	Conducts likelihood-based parentage assignment.	Marshall et al. (1998)	helios.bto.ed.ac.uk/evolgen/cervus/cervus.htm Windows
DOH	Performs assignment tests.		www2.biology.ualberta.ca/jbrzusto/Doh.php Web
WHICHRUN	Performs assignment tests.	Banks and Eichert (2000)	www-bml.ucdavis.edu/imc/whichrun.htm Windows
GENECLASS	Performs assignment tests.		www.ensam.inra.fr/URLB/geneclass/geneclass.html Windows

Finally, paternity determinations can be made either through parentage exclusion analyses (PEA) (e.g., Chakraborty et al., 1988) or likelihood-based parentage inference (LPI) (Marshall et al., 1998; Goodnight and Queller, 1999). In exclusion analysis, an individual must possess a genotype compatible with its offspring at all of the loci under consideration to remain in contention as a possible parent. Where mother-offspring relationships are known, potential sires must possess each of the

alleles in offspring that are not assigned to the known mother. Likelihood-based parentage inference allows for some genotyping errors (thus relaxing the no-mismatches assumption) and for the fact that some potential parents may have gone unsampled. Parentage is assigned to the individual with the highest likelihood ratio, and a confidence level for this assignment is calculated by simulation, taking in account population allele frequencies.

Practical considerations

Different kinds of noninvasive samples can be used as sources of DNA for molecular ecological studies of wild primates, including feces, hair, urine, and cheek cells shed in saliva. For most species, fecal samples are the easiest noninvasive samples to collect. Two methods appear to work very well for storing fecal samples under field conditions: 1) desiccating the fecal sample thoroughly, using silica gel (e.g., Sigma® Type II 1/8" silica gel beads) to stop hydrolytic degradation of DNA; and 2) mixing the sample with a nucleic-acid stabilization buffer such as RNAlater™ (Ambion®). Samples stored using either of these two methods are stable at room temperature for many months. Hair samples are also relatively easy to acquire for some species. For example, studies of chimpanzee have used shed hairs collected from night nests as a source of DNA for PCR-based microsatellite genotyping or mitochondrial DNA sequencing (Morin et al., 1993, 1994a,b; Gagneux et al., 1997b, 1999; Mitani et al., 2000). For species that do not make nests, more creative methods for collecting hair samples have been used. For example, Oka and Takenaka (2001) hauled "hair traps" covered with sticky tape into the canopy of fruit trees to collect samples from Bornean gibbons (*Hylobates muelleri*), and Valderrama et al. (1999) struck weeper capuchins (*Cebus olivaceus*) with duct tape-covered darts to recover hair. Once collected, hair samples should be stored in as dry an environment as possible (e.g., in separate paper envelopes in airtight canisters containing packets of dessicant) to prevent degradation.

Small tissue samples can also be recovered remotely, without the need to anesthetize animals, by using biopsy darts (Karesh et al., 1987). The advantage of this minimally invasive technique is that it yields a much greater quantity of higher-quality DNA. Biopsy darts are fired from a CO₂-powered rifle and recovered after striking the animal in a large muscle mass such as the thigh or shoulder. This method was used effectively on Malaysian leaf monkeys (*Trachypithecus cristatus*) (Rosenblum et al., 1997b), on several atelin primates (*Lagothrix*, *Ateles*, and *Alouatta*) (Di Fiore, 2002, and unpublished data), and on hamadryas baboons (*Papio hamadryas hamadryas*) (Swedell, personal communication). Tissue samples can be stored in NaCl-saturated DMSO or 90–100% ethanol for months at ambient temperature in the field before extraction. One important drawback of this method, however, is the time investment needed for manufacturing darts and biopsy needles and acquiring proficiency with the rifle.

An additional practical issue concerns several types of genotyping errors that can arise when non-invasively collected samples are used as sources of DNA for PCR-based genotyping (Taberlet et al., 1996, 1999). First, these sources yield extremely low quantities of DNA, and, because of this low template

copy number and stochastic effects in the initial cycles of PCR, only one or the other allele at a heterozygous locus may amplify in a given reaction while the other will "drop out," leading to genotype scoring errors (Gagneux et al., 1997a). Second, DNA extracted from fecal samples is commingled with DNA from plant and animal items in the diet and from intestinal-tract microbes, which may provide a competing template for PCR and produce spurious "alleles" as amplification artifacts (Taberlet et al., 1999; Bradley and Vigilant, 2002). Moreover, some plant secondary compounds present in fecal samples can inhibit PCR. To solve some of the problems associated with using fecal samples, Taberlet et al. (1996) recommended that genotype determinations be replicated at least twice for each putative heterozygous individual and at least seven times for each putative homozygote, and Morin et al. (2001) advocated using quantitative PCR to prescreen fecal DNA extractions to evaluate initial template concentration, genotyping only those samples that meet a particular DNA threshold criterion.

A REVIEW OF MOLECULAR ECOLOGICAL STUDIES OF PRIMATES

Below, I review how primatologists have used molecular markers and methods such as those described above in investigating several fundamental issues about primate behavior and social structure over the last 25 years. I have broken these down into four major areas into which most research can be roughly classified: 1) studies of dispersal and its effects on the distribution of genetic variation within and between groups, 2) studies of mating patterns and male and female reproductive strategies, 3) studies examining patterns of within-group relatedness, and 4) studies of the social organization and behavior of taxa on which only limited observational data have been collected.

Studies of dispersal patterns

Some of the earliest molecular research on wild primates investigated the partitioning of genetic diversity within and between populations of a species and how this partitioning is influenced by patterns of dispersal. As noted above, a contrasting pattern of population genetic structure is predicted for mitochondrial vs. nuclear genetic markers when females are philopatric (Avise, 1995, 2000; Melnick, 1987, 1988). Melnick and Hoelzer (1993, 1996; see also Melnick et al., 1992) found exactly this pattern in their review of mitochondrial and nuclear gene diversity in several species of macaques (rhesus macaques: *Macaca mulatta*; Japanese macaques: *M. fuscata*; long-tailed macaques: *M. fascicularis*; pig-tailed macaques: *M. nemestrina*; and toque macaques: *M. sinica*), using both allozyme and RFLP markers. In brief, for all these species, within-population diversity was very high for the nuclear genome. Local populations (i.e., several social groups)

contained over 90% of the total genetic diversity present within the species for rhesus and toque macaques, and over 50% of the total diversity present within the species in Japanese and long-tailed macaques; for all four species, the average social group contained 96–99% of the genetic diversity present in the larger local population. Mitochondrial DNA diversity, however, showed a very different pattern: within social groups and within local populations, there was very little variation in mitochondrial DNA. For example, only 9% of the total variation in rhesus macaque mitochondrial DNA could be apportioned to differences between individuals within local populations, while 91% was attributable to differences between local populations. A similar pattern was noted in a more recent survey of mitochondrial and nuclear DNA variation within and between five local populations of long-tailed macaques from across western Java. In that study, Perwitasari-Farajallah et al. (1999) found no variation in mitochondrial DNA RFLP haplotypes within either social groups or local populations, but found significant variation between populations. In contrast, over 75% of the nuclear genetic diversity present in the entire western Java sample (assessed using 31 allozyme markers) was also observed within local populations. Together, these studies demonstrate how behavioral processes (female philopatry) combined with stochastic lineage sorting can lead to genetic divergence between local populations in mitochondrial DNA, even in the absence of physical barriers to gene flow, while nuclear gene variation remains geographically unstructured as a result of widespread male dispersal.

Few other studies of primates have explicitly compared the structuring of genetic variation in the mitochondrial vs. nuclear genomes, but a number have documented patterns of mitochondrial DNA diversity similar to those noted above in other species characterized by female philopatry. For example, Rosenblum et al. (1997a) found evidence of population substructuring to the mitochondrial genome of pig-tailed macaques (*Macaca nemestrina*) sampled from across that species' geographic range. Individuals from the same local population had little variation in mitochondrial DNA, while marked variation was apparent between regional populations. Similarly, Shimada (2000) found very low overall mitochondrial DNA diversity in vervets (*Chlorocebus aethiops*) sampled from a number of local populations spanning a 500-km stretch of the Awash River in Ethiopia. Furthermore, this limited diversity was more structured geographically for females than for males, again implicating female philopatry as the underlying explanation for that structure.

Molecular studies comparing mitochondrial vs. nuclear population genetic structure in primates with other dispersal patterns are rare. Nonetheless, there is evidence that within-group variability in mitochondrial DNA tends to be much greater in taxa where female dispersal is common, as would be pre-

dicted. For example, female dispersal characterizes all populations of common chimpanzees (*Pan troglodytes*) studied to date (Goodall, 1986; Nishida, 1990; Boesch and Boesch-Achermann, 2000), and mitochondrial DNA variation is quite high within local chimpanzee populations and communities. Goldberg and Ruvolo (1997) surveyed DNA sequence variation in the mitochondrial control region for 262 eastern chimpanzees (*Pan troglodytes schweinfurthii*) sampled from multiple local populations across the subspecies' geographic range, and found that over 80% of the total mitochondrial DNA variation present within the subspecies was also present within local populations. At the within-community level, Morin et al. (1994a) found 15 different mitochondrial DNA haplotypes in a set of control region sequences from just 19 individuals from the Kasakela community at Gombe. Two other studies focusing primarily on males yielded similar results: Goldberg and Wrangham (1997) found seven haplotypes among a set of 14 chimpanzees from the Kanyawara community in Kibale Forest, Uganda, and Mitani et al. (2000) found 16 distinct sequences in a set of 23 individuals from the nearby Ngogo community. It might be argued that the observed pattern of mitochondrial haplotype diversity in these latter studies does not, in fact, reflect female dispersal, since some diversity among males within groups would also be expected if males were migrating, because these males would carry with them mitochondrial lineages characteristic of their natal groups. However, the extremely high diversity seen among males in the Kanyawara and Ngogo chimpanzees is incompatible with female philopatry and male dispersal, unless the set of community males immigrated from highly differentiated female lineages in numerous other communities, a pattern not supported by long-term behavioral observations. The marked within-community diversity in chimpanzee mitochondrial DNA stands in contrast to the much lower diversity seen in the macaque and vervet populations discussed above that were sampled from across much broader geographic regions. Finally, large-scale phylogeographic studies of mitochondrial DNA variation in chimpanzees (Morin et al., 1994a; Goldberg and Ruvolo, 1997) noted that similar mitochondrial DNA haplotypes can be shared by individuals in populations separated by hundreds of kilometers, suggesting extensive mitochondrial gene flow via female dispersal in the recent past (Gagneux et al., 2001).

Among bonobos (*Pan paniscus*), too, mitochondrial DNA diversity within communities is high among females, consistent with behavioral observations of female dispersal (Idani, 1991; White, 1996). For example, Gerloff et al. (1999) found five different mitochondrial DNA haplotypes in a set of 15 females in the Eyengo community in Lomoko Forest in the Democratic Republic of Congo. Three of these haplotypes were also found in a small number of individuals sampled from neighboring communities, and

there was no evidence of phylogeographic structuring to these haplotypes, as would be predicted if females were philopatric. This study also revealed direct evidence of male philopatry, in that the researchers could confidently assign maternity for 3 of 6 adult males and for 2 adolescent males to older females resident in the community.

A similar pattern of extremely high mitochondrial DNA diversity within social groups, coupled with a lack of geographic structure to that diversity, characterizes a population of lowland woolly monkeys (*Lagothrix lagotricha*) in eastern Ecuador. Woolly monkeys belong to the ateline subfamily of New World primates, a clade apparently characterized by female dispersal (Rosenberger and Strier, 1989; Strier, 1994). However, although female transfer was confirmed for some populations (Nishimura, 1990; Stevenson et al., 1994), solitary adult and subadult males (as well as an all-male group of five individuals) were also noted at one study site (Di Fiore, unpublished data). Nonetheless, in a study of mitochondrial DNA variation in woolly monkeys, Di Fiore (2002, unpublished data) found 17 different mitochondrial control region haplotypes in a set of 25 female woolly monkeys sampled from several social groups at one site in lowland Ecuador and eight different haplotypes among nine females sampled in another local population 35 km away. Moreover, the phylogenetic relationship among these mitochondrial DNA haplotypes shows no evidence of being structured geographically, consistent with a pattern of female dispersal. Mitochondrial DNA variation in hamadryas baboons, a cercopithecine primate also characterized by female dispersal (Stammback, 1987), has a very similar pattern. Hapke et al. (2001) sampled 74 individual hamadryas baboons from 12 troops (sleeping associations comprising several bands, each made up of multiple one-male units) from across Eritrea and sequenced a portion of their mitochondrial D loops. As with chimpanzees and woolly monkeys, hamadryas baboons showed substantial within-troop variation in their mitochondrial DNA and little between-troop variation, and there was no evidence that the variation present was structured geographically.

Finally, as expected, taxa characterized primarily by male dispersal but also showing some dispersal by females (e.g., many species of colobines; Moore, 1984) also lack geographic population structuring in their mitochondrial DNA. For example, Rosenblum et al. (1997b) examined mitochondrial DNA diversity within populations of two species of leaf monkeys from Java and Malaysia, and found substantial variation within some populations; this variation, however, showed no evidence of being geographically structured, presumably reflecting the effects of female dispersal on homogenizing the distribution of mitochondrial DNA variation across broad geographic regions.

Studies of mating systems and reproductive strategies

The study of primate mating systems and male and female reproductive strategies is another area where molecular data have been frequently applied to understanding the behavior of primates and the fitness consequences of those behaviors. Mating behavior is not easily observed in the wild, especially for arboreal primate species living in tropical forests with less than ideal observation conditions. Moreover, it is well-known from studies of other vertebrates that observed mating behavior does not always correlate with the actual pattern of paternity in population (e.g., Coltman et al., 1998), and that extragroup mating and paternity, even among socially monogamous taxa, are not uncommon (e.g., mammals: African wild dogs, *Lycaon pictus*, Girman et al., 1997; alpine marmots, *Marmota marmota*, Goossens et al., 1998; birds: blue tits, *Parus caeruleus*; Kempenaers et al., 1992; reed buntings, *Emberiza schoeniclus*; Dixon et al., 1994). Some of the earliest applications of molecular techniques in primate behavioral studies were thus directly concerned with evaluating the genetic mating system realized in a population and with investigating the effects of behavioral variables (e.g., dominance rank, mating tactics) and demographic variables (e.g., number of competitors, estrus synchrony among females) on individual fitness. In fact, the question of whether and how male dominance rank and reproductive success are linked has long been of central interest to primatologists, since male dominance hierarchies were so conspicuous among the species of cercopithecine primates that were the focus of many early primatological studies (e.g., Altmann, 1962; Hall and DeVore, 1965; Sade, 1967; Struhsaker, 1967).

The first molecular studies of mating systems in both wild and captive populations of primates assessed parentage using either allozyme markers or traditional DNA fingerprints (Jeffreys et al., 1985a,b) derived from minisatellite-probed genomic DNA digests. In one seminal study, Melnick (1987) used seven allozyme markers (in combination with cell surface antigen immunological assays) to assess paternity in two small groups of wild rhesus macaques (*Macaca mulatta*), and found that the dominant male in each group was the likeliest sire of most of the infants born during a 2-year period. Pope (1990) also used a suite of allozyme markers to investigate the mating system of red howler monkeys (*Alouatta seniculus*) living in the central llanos region of Venezuela. Red howler monkeys in this population live either in single-male or in age-graded multimale groups that typically contain 1–4 females (Crockett and Eisenberg, 1987). In her sample of five single-male and four multimale groups, Pope (1990) found no evidence that extragroup males ever sired offspring. Moreover, in each of the multimale troops, only the dominant male appeared to sire offspring

conceived during his tenure, providing genetic evidence of a clear link between dominance and fitness for this taxon. In another early molecular study of primate mating systems, Periera and Weiss (1991) used minisatellite DNA fingerprints to assess paternity in two groups of free-ranging ring-tailed lemurs (*Lemur catta*) at the Duke University Primate Center. Over a 5-year period, offspring were sired by multiple males in at least some years, and a male's likelihood of siring offspring appeared to be highly dependent on female mate choice rather than on male dominance rank, a result consistent with previous behavioral observations of female dominance over males in this species (Richard, 1987).

Soon thereafter, de Ruiter et al. (1992, 1994; see also de Ruiter and van Hooff, 1993) used a combination of allozyme marker analysis and DNA fingerprinting to conduct one of the first molecular studies of the mating system of a wild catarrhine primate. Their study evaluated the link between male dominance rank, copulation success, and paternity in three social groups of long-tailed macaque (*Macaca fascicularis*) in northern Sumatra. These groups contained between 2 and 10 adult males, and paternity was strongly skewed, with the dominant male in each social group responsible for siring 52–92% of offspring produced during his tenure and the beta male responsible for most of the remaining conceptions. Alpha and beta males were presumed to have secured paternity by monopolizing females during periods of likely conception, since the proportion of offspring sired by each of these classes of males was greater than the proportion of matings in which they participated. Variation in the proportion of offspring sired by alpha males in different groups was attributed to a female strategy of mating promiscuously during a prolonged receptive period to promote paternity uncertainty (de Ruiter et al., 1994).

The mating systems of a number of other cercopithecin species have also been investigated using traditional DNA fingerprinting, in part to examine the putative link between dominance rank and reproductive success and to test the dominance priority-of-access model (Altmann, 1962). For example, Bauers and Hearn (1994) used DNA fingerprinting to assign paternity to offspring born in a captive colony of stump-tailed macaques (*Macaca arctoides*) at the Wisconsin Regional Primate Center and found that the alpha male was responsible for siring all but one of 27 offspring born in an 8.5-year period. Similarly, Paul et al. (1993) found a clear, positive association between male rank and reproductive success during 3 of 4 mating seasons in a semifree-ranging group of Barbary macaques (*Macaca sylvanus*). Dixson et al. (1993) also found that male dominance rank strongly determined reproductive success in a semifree-ranging colony of mandrills (*Mandrillus sphinx*): over a 5-year period, only the two most dominant adult males in the colony sired infants. Finally, Gust et al. (1998) used DNA fingerprints derived from two minisatellite probes to in-

vestigate the link between male dominance rank and reproductive success in two captive groups of sooty manglebeys (*Cercocebus torquatus atys*). In this 2-year study, the dominant of two adult males sired all the offspring born in the smaller of the two study groups, which contained six adult females. In the larger social group, with 4–8 males and 31 females, there was a significant relationship between male dominance rank and reproductive success only during the 2 years of stable tenure of one of two alpha males.

Other DNA fingerprinting studies of cercopithecines found no clear association between male dominance rank and reproductive success and instead demonstrated the efficacy of alternative male mating tactics. For example, Inoue et al. (1991) found no correlation between rank and reproductive success in a captive population of Japanese macaques (*Macaca fuscata*). Similarly, among free-ranging rhesus macaques (*Macaca mulatta*), Berard et al. (1993, 1994) found that although the two highest-ranking males in one social group sired proportionally more infants than other males during the single breeding season analyzed, there was no clear correlation between male rank and reproductive success. In this population, some infants were sired by both lower-ranking and extragroup males, typically those following a "furtive" tactic of mating during very brief consort associations. Ohsawa et al. (1993) also concluded that furtive mating between females and subordinate (i.e., nonharem-holding) males results in conceptions in wild patas monkeys (*Erythrocebus patas*); DNA fingerprinting analysis (in combination with microsatellite genotyping), revealed that roughly one-third of infants had to have been sired by males other than the dominant harem-holder.

In recent years, DNA fingerprinting and allozyme marker-based assessments of parentage have been largely superseded by PCR-based techniques. The primary PCR-based techniques that have been used in primates include RAPD profile analysis and microsatellite marker genotyping. For example, Neveu et al. (1996, 1999) used PCR-based RAPD profiles to assess paternity in captive groups of a variety of prosimians, including grey mouse lemurs (*Microcebus murinus*), brown lemurs (*Eulemur fulvus*), and black lemurs (*Eulemur macaco*). However, as noted above, drawbacks to this method (e.g., the extreme sensitivity of the procedure to PCR reaction conditions) have limited its application in studies of primate mating systems (Riedy et al., 1992), especially when compared with PCR-based microsatellite genotyping. Most recent applications of RAPD analysis in the primate literature involve estimating the degree of genetic variation within and between selected primate taxa (e.g., Lan et al., 1995; Neveu et al., 1998; Bachmann et al., 2000; Fausser et al., 2000; Ravaoarimanana et al., 2001) rather than as a tool for parentage analysis.

Over the past decade, PCR-based microsatellite genotyping, combined with either paternity exclusion analysis or likelihood-based parentage assessment, has become the molecular tool of choice for use in studies of primate mating systems and reproductive strategies. Among the first studies of this type were those of Morin et al. (1993, 1994b; see also Morin and Woodruff, 1992) for chimpanzees (*Pan troglodytes*) from the Kasakela community at Gombe, Tanzania; see also Sugiyama et al. (1993), a similar, though much smaller-scale study conducted on a chimpanzee population in Bossou, Guinea. All living members of the Gombe community were sampled in 1991 and genotyped at up to eight microsatellite loci, using DNA extracted from noninvasively collected hairs as the template in PCR reactions. These genotype data allowed partial paternity exclusions to be conducted for 25 individuals born in the community. Although the researchers were only able to confidently assign paternity to two of these individuals (one to each of two males), the pool of potential sires could be narrowed substantially for a number of remaining offspring by excluding males with incompatible paternal genotypes. This study was one of the first clear demonstrations of the potential for coupling noninvasive sampling techniques (important for wild populations of primates), PCR, and microsatellite genotyping to understanding the links between behavior and population structure in natural primate populations.

Soon thereafter, Altmann et al. (1996) conducted a more comprehensive genetic analysis of the mating system of wild savanna baboons (*Papio hamadryas cynocephalus*) living in Amboseli National Park, Kenya. Given the multimale grouping pattern, this study specifically tested the hypothesis that a male's dominance rank determined his priority-of-access to estrus females and thereby his fitness. Altmann et al. (1996) used genotype data from 10 microsatellite and two allozyme loci to evaluate paternity for 27 offspring born in one troop of savanna baboons (*Papio hamadryas cynocephalus*) during a 4-year period in which male dominance ranks were stable. They found that the top-ranking male sired over 80% of these offspring, and that the distribution of paternity among males fit well with that predicted based on the dominance priority-of-access model and with observed patterns of mating during females' fertile periods that resulted in conception.

A study of the mating system of toque macaques (*Macaca sinica*) at Polonnaruwa, Sri Lanka also used microsatellite and allozyme marker-based paternity analysis (Keane et al., 1997). Toque macaques live in groups containing either a single or, more commonly, multiple adult males (Dittus, 1975). Based on genotype data from four microsatellite loci and one allozyme locus, Keane et al. (1997) conducted partial paternity exclusions for 140 offspring born into 13 different social groups over a 12-year period. While paternity could only be assigned with confidence for around half of these off-

spring, the researchers were able to estimate the minimum number of sires reproducing per year per group based on the number of different alleles that appeared at each locus among the set of offsprings' genotypes once maternal alleles had been accounted for. They found that multiple males typically sired the set of offspring born in each group during each birth season. Moreover, in both unimale and multimale groups, some paternity was assigned to extra-group males, hinting that some males in this population pursued alternative routes to reproductive success.

Launhardt et al. (2001) further explored the consequences of alternative male reproductive strategies among gray langurs (*Semnopithecus entellus*) occupying different social positions in a population at Ramnagar, Nepal. Both single-male and multimale groups are common in this population, and breeding is seasonal (Koenig et al., 1997). Launhardt et al. (2001) determined likely paternity for 13 infants born in three unimale groups and for 29 infants born in three multimale groups, using genotype data for a battery of five microsatellite loci. For the unimale groups, the resident male could never be excluded as the possible sire, suggesting complete monopolization of paternity by harem-holders. Alpha males sired 57% of infants born into multimale groups, while other resident males sired 22%; the remaining 21% of infants had to have been sired by nonresident males. Combining these short-term data on reproductive success with long-term demographic data on the same population, Launhardt et al. (2001) concluded that the difference in lifetime reproductive success between harem-holders, alpha males in multimale groups, and nonalpha males is likely to be substantial. Thus, selection for behavioral characteristics that influence a males' likelihood of assuming a position as a harem-holder is expected to be quite strong.

Borries et al. (1999a,b) used these same paternity data to investigate the possible adaptive value of the male behavioral strategies of infanticide and infant protection. Infanticide by males has long been proposed as an adaptive male reproductive strategy (e.g., Hrdy, 1974, 1977, 1979), and the risk of infanticide is increasingly recognized as an important selective pressure underlying the evolution of primate social systems in general and male-female associations in particular (Kappeler, 1997; van Schaik and Kappeler, 1997). Infanticide as a sexually selected, adaptive reproductive strategy for males engenders two predictions: 1) that males should only kill infants whom they had little chance of siring, and 2) that infanticidal males should have an increased chance of siring a female's subsequent offspring (Hrdy and Hausfater, 1984; van Schaik, 2000). Borries et al. (1999a) analyzed paternity for 16 known or suspected cases of infanticide and attacks by adult males. In all cases, the attacking male was excluded as a potential father of the victim by possessing an incompatible microsatellite geno-

type, thus providing support for prediction 1; Soltis et al. (2000) found the same to be true for male attacks against infants in Japanese macaques (*Macaca fuscata*). Additionally, for 4 of 5 cases of presumed infanticide among the langurs, a male suspected of killing the infant was identified as the likely father of the mother's next offspring, consistent with prediction 2. Finally, adult male grey langurs sometimes defend infants against attacks by other males; if infant protection represents an adaptive male strategy, then males are predicted to primarily defend infants for whom they are potential sires. Using microsatellite marker genotypes to effect paternity exclusion analysis for eight infants who were protected during 17 attacks by one or more adult males, Borries et al. (1999b) indeed found that all protectors were either fathers of the infant or males who were resident in the group when the infant was conceived; in no case were males who were not resident in the group at the time of the infant's conception observed protecting those infants.

The potential importance of alternative male reproductive strategies has also been investigated in Sumatran orangutans (*Pongo pygmaeus*) (Utami et al., 2002). Adult male orangutans are dimorphic in their expression of secondary sexual characteristics: "flanged" males possess large, fibrous cheek pads and a large laryngeal sac used in vocal communication, while "unflanged" but nonetheless sexually mature males do not. One of the hypotheses proposed to explain this pattern of bimaturism suggests that the two morphotypes represent males following alternative reproductive strategies (Mitani, 1985), with "flanged" males producing long calls as honest signals of male quality that are designed to attract females mates, and with "unflanged" males roving in search of females to mate with, sometimes through forceful coercion. Using microsatellite marker genotypes for both paternity exclusion and likelihood-based paternity analyses, Utami et al. (2002) determined probable sires for 10 of 11 offspring born into their study population over a 15-year period. Six of these offspring were fathered by "unflanged" males, suggesting the efficacy of this alternative tactic in securing fitness.

Another alternative reproductive tactic that males might pursue is to cultivate "friendships" with females as a strategy for increasing the likelihood of future mating with those females (Smuts, 1985; Smuts and Gubernick, 1992). This hypothesis may explain the caretaking behavior seen in Barbary macaques (Taub, 1980), although alternatively, males could be investing in offspring they believe may be their own. Ménard et al. (2001) examined the relationship between male caretaking behavior, genetic paternity, and male mating behavior in two wild Barbary macaque groups in Algeria to test between these alternatives, and rejected the paternal care hypothesis based on two results. First, males in the set of "main caretakers" (i.e., the male who pro-

vided the greatest amount of care plus other all other males who provided at least one-third of that amount) were no more likely than other males to have sired the infants for whom they provided care. Second, the main mating partners of females in the breeding season were no more likely than other males to be caretakers of the females' next infants. However, the "care as mating effort" hypothesis received strong support: main caregivers were more likely to mate with the mothers of infants they cared for during the following breeding season than were other males. Unfortunately, no data are reported on whether caretaker males also produced offspring with those females, making it difficult to draw conclusions about the efficacy of male caregiving as a reproductive strategy.

Finally, since the original work by Morin et al.'s (1993, 1994b) on the Kasakela chimpanzees, a number of research groups have analyzed paternity in several communities of chimpanzees from the Tai Forest, Côte d'Ivoire (Gagneux et al., 1997b, 1999; Vigilant et al., 2001), expanded on the work from Gombe (Constable et al., 2001), and examined paternity success in one population of bonobos (*Pan paniscus*) from the Lomoko Forest, Democratic Republic of Congo (Gerloff et al., 1999). Each of these studies confirmed that multiple males sire the offspring born within communities. Additionally, Constable et al. (2001) documented the effectiveness of several different male mating strategies among common chimpanzees. At Gombe, two different alpha males and one high-ranking male sired 50% of 14 offspring for whom paternity could be determined through a combination of "possessive" mate-guarding (where males broke up copulations involving other males and behaved aggressively towards potential competitors) and "opportunistic" matings (where groups of two or more males mated with estrus females with no overt competition). Five different middle- and low-ranking males sired the remaining seven offspring, and five of these conceptions took place though either opportunistic matings or during "consortships" in which a male-female pair ranged apart from other individuals in the community for a period of several days.

The distribution of mating success among bonobo males appears similar. Gerloff et al. (1999) used DNA extracted from noninvasively collected fecal samples to assess paternity for 10 offspring born in a single bonobo community. Although all community males were observed mating, higher-ranking male bonobos sired more offspring than lower-ranking males, and middle-ranking males sired up to 50% of offspring. Finally, recent studies also suggest some evidence of extragroup paternity, at least among common chimpanzees, although the community appears to be the primary social unit within which reproduction occurs. In an analysis of paternity in one community of chimpanzees from the Tai Forest, Gagneux et al. (1997b, 1999) concluded that the rate of extragroup paternity might

exceed 50%, and suggested that females actively seek extracommunity mating. Subsequent reanalysis of Gagneux et al.'s (1997b, 1999) genotype data, using an alternative, likelihood-based method of paternity estimation (Marshall et al., 1998; Constable et al., 2001), and repetition of the genotyping and paternity exclusion analysis using additional loci (Vigilant et al., 2001), revealed that the original study Gagneux et al.'s (1997b, 1999) suffered from serious genotyping errors (presumably caused by allelic dropout and sample contamination or mix-up), which resulted in a far higher estimate of extragroup paternity than was warranted. Vigilant et al. (2001) revised that estimate substantially downward, to just one likely case out of 13 offspring for whom all potential within-group sires were sampled and genotyped. This example appropriately highlights the technical problems and challenges associated with the use of noninvasive samples in molecular ecology studies (Vigilant, 2002) and emphasizes the need for researchers to follow exacting guidelines concerning DNA template quality and replication standards for verification (e.g., Taberlet et al., 1996; Morin et al., 2001) to ensure the accuracy of their results. Nonetheless, despite the revised conclusions, the suggestive initial results of Gagneux et al.'s (1997b, 1999) stress how important molecular studies may be for examining the evolutionary significance of female as well as male mating strategies.

Some recent research on captive cercopithecines highlights extragroup paternity further, but also raises an important issue concerning what researchers and readers should make of highly unexpected results. Smith et al. (1999) found a high degree of extragroup paternity (7 of 25 births) among offspring born into five one-male units comprising a captive band of hamadryas baboons, a finding then replicated in a second band. If this pattern were confirmed in the wild, where virtually all observed mating takes place within one-male units which males compete fiercely to defend (Kummer, 1968; Swedell, 2000), it would indeed demonstrate the potential for female choice to counteract male reproductive strategies. Interestingly, for 25 of 45 offspring born in these two bands, the putative mother could be excluded from possible maternity on the basis of the genotype data (hinting at an unprecedented level of infant kidnapping occurring in this captive population, a behavior with no ready explanation). Given that the genetic data on maternity yield a dramatically different picture of hamadryas baboon offspring care than would have been expected on the basis of behavioral observations (with close to 50% of mothers seemingly raising offspring that were not their own), it seems prudent to replicate the entire study before accepting the results with confidence.

Finally, outside of the Old World monkeys and great apes, there have been few genetic studies of primate mating systems since the early work by

Pope (1990) on howler monkeys. Nievergelt et al. (2000) used microsatellite markers to examine parentage for 11 infants born into three wild groups of common marmosets (*Callithrix jacchus*) in northern coastal Brazil using hair samples collected noninvasively. Although sires for these infants were not assigned definitively, the socially dominant male in each group could not be excluded as the father for 9 of 11 infants born into the population, while at least some group males other than dominants could be. Interestingly, in one of the two remaining cases, both possible within-group males could be excluded as sires if the resident female was presumed to be the infant's mother; this result suggests either that the infant was sired by an unsampled extragroup male, or that a second breeding female who subsequently disappeared was present in the group at the time of the infant's birth. Together, these genetic parentage data are wholly consistent with observed reproductive behavior, in which mating is heavily skewed towards the dominant male with occasional cases of extragroup mating by females (Digby, 1999) and where occasional cases of multiple breeding females within the same social group have been reported (Digby and Ferrari, 1994; Ferrari and Digby, 1996). Oka and Takenaka (2001) investigated parentage in a small sample of Bornean gibbons (*Hylobates muelleri*), using noninvasively collected hair and fecal samples as a source of DNA for microsatellite genotyping. Maternity and paternity for three offspring born into different social groups were assigned to the adult female and adult male residents, thus finding no evidence for extragroup paternity despite observations of extragroup copulations in other gibbon species (Reichard, 1995). Interestingly, the genetic data revealed that two subadults (one male and one female) living in two different family groups were not the offspring of the breeders in those groups. Radespiel et al. (2002) investigated the mating system of a captive population of seven groups of grey mouse lemurs (*Microcebus murinus*) using 13 microsatellite marker loci and found no relationship between male dominance rank and reproductive success within groups. Finally, Wimmer and Kappeler (2002) used seven microsatellite markers to determine paternity in multimale groups of red-fronted lemurs (*Eulemur fulvus rufus*) and found that socially dominant, central males fathered 9 of the 12 offspring born into four social groups over a 2-year period.

Several general points can be made, given the results reviewed above. First, molecular data can shed considerable light onto the genetic breeding system that characterizes a taxon, even in the absence of extensive behavioral data. Second, for many primate species where genetic data on paternity are available, both in captivity and in the wild, it does seem that dominant males enjoy somewhat greater fitness, at least over the short term, than do subordinates. Nevertheless, a clear relationship between male dominance rank and reproductive success is

not always seen, and even where the relationship between these two variables is positive, it is unclear whether that pattern reflects the outcome of male-male competition or some other aspect of sexual selection such as female choice. For example, despite the fact that dominant males enjoyed greater overall fitness than subordinates during a 15-year study of captive rhesus macaques, Smith (1994) found significant positive associations between male dominance rank and reproductive success during only two individual breeding seasons, reflecting the fact that peaks in male dominance rank and reproductive success need not correspond temporally over the course of a reproductive career. In this study, per annum fitness for males typically peaked prior to those males' achieving their highest dominance rank (the opposite pattern to what the priority-of-access model predicts), and male reproductive success might reflect female preference for young males who are rising in rank more than male rank per se. The extent to which observed patterns of paternity in the other taxa discussed above can be attributed to female choice remains an area for future research. Third, a number of the studies reviewed above clearly demonstrate the efficacy of alternative reproductive tactics among males, reiterating the significance of female choice as an important determinant of male fitness. Finally, several of the studies reviewed above clearly highlight the technical and interpretive challenges involved in molecular studies of primate mating systems and stress the importance of exacting laboratory methods and replication.

Studies of within-group relatedness, affiliation, and cooperation

One of the stalwart assumptions underlying attempts to understand the expression of social behavior in primates is that individuals should preferentially direct affiliative and cooperative behavior toward close kin because of the influence that kin can have on increasing an individual's inclusive fitness (Hamilton, 1964a,b; Gouzoules and Gouzoules, 1987; Chapais, 2001; Silk, 1987, 2002). Until recently, however, testing the extent to which behavioral indices of affiliation and cooperation reflect patterns of relatedness between individuals has proven difficult, especially for wild populations of long-lived primates where detailed pedigrees are often impossible to record. Molecular techniques offer an alternative method for estimating genetic relatedness between individuals directly, based on the sharing of genetic markers (Pamilo and Crozier, 1982; Queller and Goodnight, 1989; Lynch and Ritland, 1999).

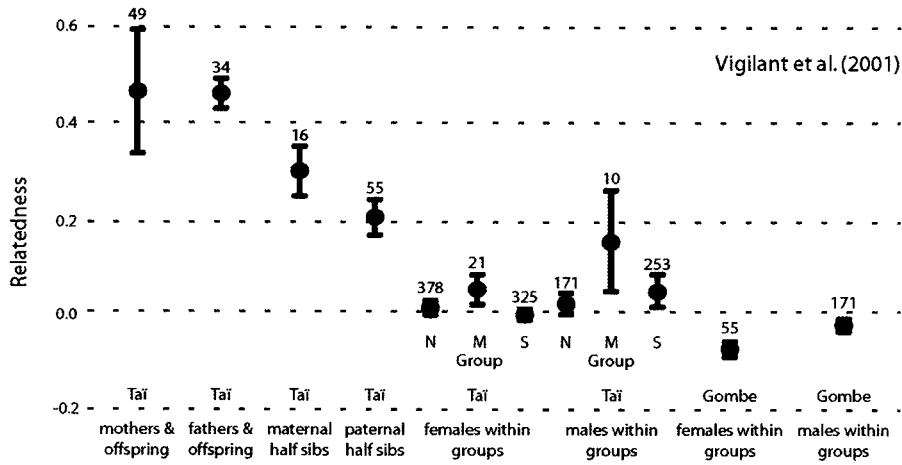
The most comprehensive sets of data for comparing patterns of affiliation and cooperation with assessments of within-group relatedness come from studies of chimpanzees. Chimpanzees generally live in large social groups or communities ranging in size from 10 to more than 100 adult individuals (Goodall,

1986; Nishida, 1990; Mitani and Watts, 1999; Boesch and Boesch-Achermann, 2000). Within these communities, individuals associate with one another in temporary subgroups that vary in size and composition over time (Goodall, 1986; Boesch, 1996). Long-term studies of chimpanzee social behavior have consistently revealed the existence of strong affiliative and cooperative relationships, or bonds, among males (Goodall, 1986; Nishida, 1990; Watts, 1998; Watts and Mitani, 2001). Males within a community also have been commonly reported to hunt cooperatively (Boesch and Boesch, 1989; Boesch, 1994; Stanford et al., 1994; Stanford, 1998; Mitani and Watts, 1999), to jointly patrol community borders looking for and attacking intruders from neighboring communities (Goodall et al., 1979; Nishida et al., 1985; Wrangham and Peterson, 1996; Watts and Mitani, 2001), and to form coalitions with other males in contests over rank or mating access to females (Watts, 1998). The presumed explanation for these patterns of behavior is that they have evolved through kin selection, because male chimpanzees are likely to be more closely related to one another within a community than are females by virtue of the fact that males are typically philopatric and dispersal is female-biased.

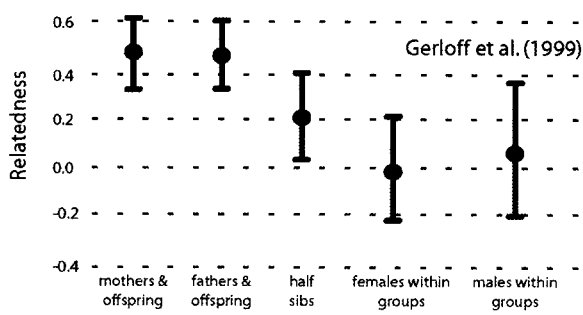
Until recently, few data were available to test the assumption of greater average male-male relatedness within chimpanzee communities or to evaluate whether affiliative and cooperative behavior among males do, in fact, reflect patterns of kinship. The first molecular evidence bearing on these issues came from the pioneering molecular work of Morin et al. (1993, 1994a,b). Using shed hairs collected from night nests, Morin et al. (1993, 1994a,b) genotyped 43 members of the Kasakela chimpanzee community in Gombe National Park at eight microsatellite loci and found that the mean number of alleles per locus shared between males was, in fact, significantly greater than among females, an observation consistent with the expectation based on observations of female-biased dispersal. However, more recent analyses of average male-male and female-female relatedness among chimpanzees from the

Fig. 2. Molecular estimates of average pairwise relatedness (R) (\pm SE) among different subsets of individuals within populations of several species of nonhuman primates. **A:** Chimpanzees. **B:** Bonobos. **C:** Savanna baboons. **D:** Long-tailed macaques. **E:** Alaotran gentle lemurs. **F:** Mouse lemurs. **G:** Common marmosets. Figures are redrawn from sources as noted. Relatedness values are based on microsatellite marker genotype data for all taxa except long-tailed macaques (for which R values were derived using allozyme loci) and savanna baboons (for which a combination of microsatellite and allozyme loci was used). Numbers above each data point reflect number of pairwise comparisons upon which each data point is based, where such data are presented in source. Note higher average R among females within groups compared to among males within groups (or to between females and the breeding male) for those species presumably characterized by female philopatry (C to G). There is little difference between average female-female and male-male pairwise relatedness within groups among chimpanzees and bonobos.

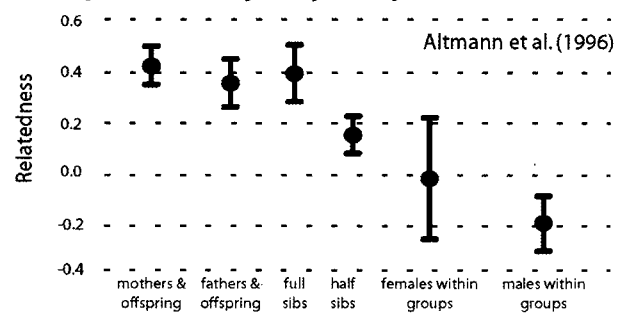
A. *Pan troglodytes*



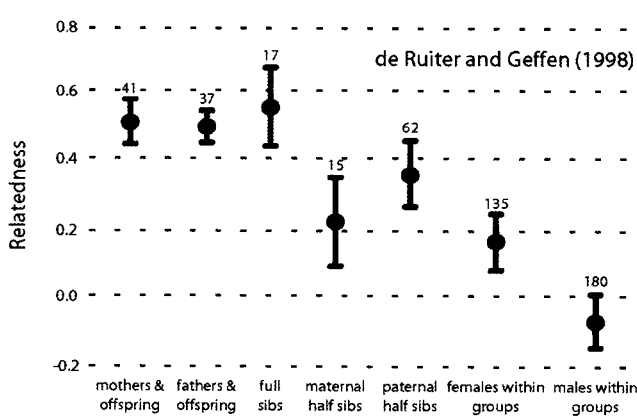
B. *Pan paniscus*



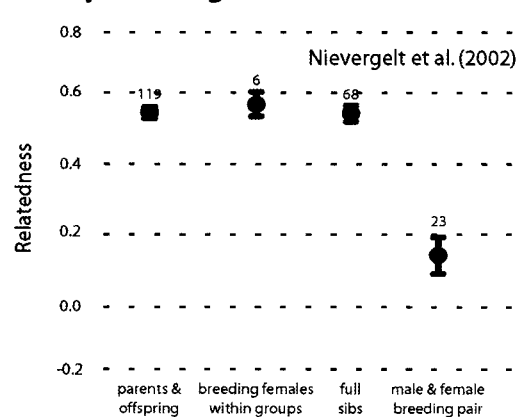
C. *Papio hamadryas cynocephalus*



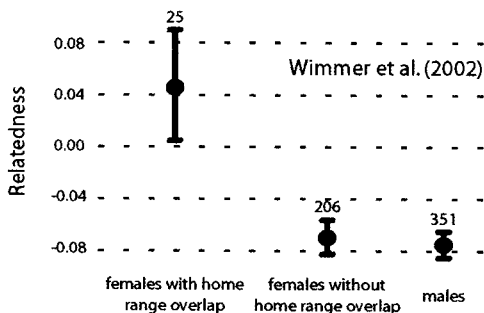
D. *Macaca fascicularis*



E. *Hapalemur griseus alaotrensis*



F. *Microcebus murinus*



G. *Callithrix jacchus*

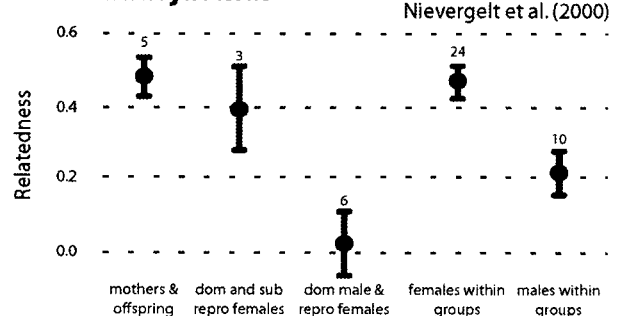


Fig. 2.

Kasakela community at Gombe (Vigilant et al., 2001) and from three communities in the Tai Forest, Côte d'Ivoire (Gagneux et al., 1999; Vigilant et al., 2001) suggest a somewhat different picture. Gagneux et al. (1999) used nine microsatellite loci to derive multilocus genotypes for 55 individuals in one well-sampled community in the Tai Forest and found that the average degree of relatedness among adult males was not significantly different from the average degree of relatedness among adult females. Despite the genotyping errors present in Gagneux et al. (1999), this result was later corroborated by Vigilant et al. (2001) for the same community and two others found in the same forest (Fig. 2A). Vigilant et al. (2001) also reanalyzed the genotype data by Constable et al. (2001) for the Kasakela chimpanzees to reevaluate the results of Morin et al. (1993, 1994a,b), and found no significant difference between male-male and female-female relatedness (Fig. 2A). Consequently, despite early molecular evidence to the contrary, it appears that males are no more closely related than are females among these chimpanzee populations. This conclusion challenges the hypothesis that male affiliative and cooperative behaviors arose as a result of kin selection and suggests that other evolutionary mechanisms (e.g., mutualism, reciprocal altruism) may be responsible for male behavior patterns, at least in chimpanzees.

Because these molecular data on the Gombe and Tai Forest chimpanzees reflect only community-level estimates of average relatedness among males and among females, it is possible that a more narrow focus, examining relatedness among affiliative vs. nonaffiliative pairs of individuals, might still reveal that kin selection is an important force structuring social bonds. Two recent studies directly compared behavioral measures of affiliation among males with molecular estimates of matrilineal relatedness. Goldberg and Wrangham (1997) determined mitochondrial DNA haplotypes for 14 chimpanzees (8 adult males, 5 subadult males, and one adult female) from the Kanyawara community in Kibale National Park, Uganda by amplifying and sequencing 368 base pairs of the hypervariable first region of the mitochondrial control region, using DNA extracted from shed hairs. They then examined whether closely affiliated individuals shared a mitochondrial DNA haplotype, which would indicate matrilineal relatedness (e.g., brothers sharing the same mother). None of the five closely affiliative dyads within this set of animals comprised matrilineal kin. Moreover, when they compared matrices summarizing the strength of pairwise affiliative relationships among their subjects based on several behavioral indices to the matrix of pairwise genetic distance, they found no significant correlation and concluded that chimpanzees' choices of affiliative social partners was not influenced by matrilineal kinship. The results of Goldberg and Wrangham (1997) were replicated by Mitani et al. (2000), who examined 23 male chimpanzees from the much larger Ngogo com-

munity also found in Kibale National Park. They too found little concordance among dendrograms summarizing patterns of pairwise affiliation (association, grooming, and proximity) and mitochondrial DNA similarity. Likewise, they found no correlation between genetic distance among pairs of individuals and any behavioral measure of affiliation or cooperation, despite the fact that some subsets of males within the community did share mitochondrial haplotypes. An obvious and interesting next step would be to repeat these analyses using Y-chromosome markers to evaluate whether cooperative and affiliative male partners are patrilineal kin.

In bonobos, which are also characterized by female dispersal but where male-male bonds tend to be less developed, molecular data suggest a similar pattern of within-group relatedness to that seen in common chimpanzees (Fig. 2B). In a study of one bonobo community from the Democratic Republic of Congo, Gerloff et al. (1999) found that average relatedness among adult males and among adult females determined from genotype data for five microsatellite loci was, in both cases, close to zero and not significantly different from one another. If these estimates of relatedness based on only five loci are statistically reliable (ideally more loci would be included), then they support the idea that kinship may not be as important as other factors for structuring same-sex social relationships in some primate taxa. Nonetheless, some of the strongest and most persistent associations apparent among the Lomoko bonobos did involve close relatives (e.g., mothers and sons and maternal half-brothers) (Hohmann et al., 1999).

Outside of chimpanzees and bonobos, few studies have been done of within-group patterns of relatedness, so the importance of kin selection as a general explanation for patterns of primate social affiliation and cooperation needs further testing. Among cercopithecine primates, female social relationships tend to be highly differentiated, and affiliative and coalitionary behaviors are most commonly seen among members of the same matriline. As was the case for male chimpanzee bonds, kin selection is a hypothesized explanation for these female cooperative relationships, in that females within cercopithecine groups are presumed to more closely related to one another than are males as a result of female philopatry. Again, few data were actually available to test this presumption in wild cercopithecines until recently. In a seminal study, Altmann et al. (1996) used microsatellite and allozyme marker genotypes to examine relatedness among males and among females for one troop of savanna baboons (*Papio hamadryas cynocephalus*) from Amboseli National Park, Kenya. Their results confirmed that within groups, as expected, females were on average more closely related to one another than were males (Fig. 2C). De Ruiter and Geffen (1998) similarly compared average pairwise relatedness among different subgroups of individuals in

three social groups of long-tailed macaques (*Macaca fascicularis*) from Ketambe, Sumatra. Using 11 allozyme markers to genotype individuals and DNA fingerprinting to determine paternity, which allowed them to evaluate the extent to which their relatedness estimates conformed to expected patterns (e.g., father-offspring $R_{\text{expected}} = 0.5$, half sibling $R_{\text{expected}} = 0.25$), de Ruiter and Geffen (1998) found that male-male relatedness within social groups, on average, was lower than average female-female relatedness: adult males were essentially unrelated, while females were related to one another at the level of first cousins (Fig. 2D). These genetic data are consistent with the pattern of male-biased dispersal and female philopatry seen in this species, and when coupled with behavioral data from other sources, provide some support for the hypothesis that female within-group social relationships develop through kin selection within female matriline. Nonetheless, alternative explanations based on other evolutionary mechanisms such as reciprocal altruism cannot be discounted. Interestingly, de Ruiter and Geffen (1998) also revealed that average pairwise relatedness was higher within higher-ranking matriline in the lone social group comprising more than one female lineage. This appeared to be a consequence of assortative mating between higher-ranking females and the alpha male, who sired 50% of offspring born in the group but an even higher proportion of those born into higher-ranking matriline (i.e., offspring in higher-ranking matriline are more likely to be related through both the maternal and paternal lines).

For strepsirrhines, results of an investigation of within-group relatedness were reported for one species of Malagasy lemur, the white sifaka (*Propithecus verreauxi verreauxi*). Lawler et al. (2001b, 2003) genotyped over 200 individual sifakas from a number of social groups living in the Beza Mahafaly Special Reserve, Madagascar, at seven species-specific microsatellite loci, and estimated average relatedness among males and among females at several different hierarchical levels of grouping. They found that relatedness among females was greater than among males, both within social groups and within larger neighborhoods, a pattern consistent with behavioral observations of female philopatry and male-biased dispersal. Studies of several other lemurs (reviewed below) revealed a similar pattern (Nievergelt et al., 2002; Wimmer and Kappeler, 2002) (Fig. 2E,F). Among platyrrhines, Nievergelt et al. (2000) also found greater average relatedness among adult females than among adult males for several groups of wild common marmosets (Fig. 2G). Interestingly, there have been no other studies to date that have examined average male vs. female relatedness in other female-philopatric cercopithecines or strepsirrhines, nor in either of the larger-bodied female-philopatric platyrrhines (i.e., *Cebus*, and some populations of *Saimiri*). Recently, however, Di Fiore (2003) reported greater average

relatedness among males vs. among females for several social groups of a putatively male-philopatric platyrrhine, the lowland woolly monkey.

Although some of the studies reviewed above suggest that the affiliative and cooperative relationships among females in some female-philopatric cercopithecine and strepsirrhine taxa may, in fact, arise through kin selection, no study of wild populations of either of these groups of primates has demonstrated the evolutionary consequences of directing cooperative behavior preferentially towards kin. Instead, the clearest examples of the fitness consequences of kin-biased cooperation come from work by Pope (1990, 2000) on the mating system and population structure of Venezuelan red howler monkeys (*Alouatta seniculus*), a taxon in which both males and females are known to disperse. In this population, there is fierce competition among males and among females for membership in social groups as breeding appears to only occur within established troops (Crockett, 1984; Pope, 1990, 2000). Male howler monkeys may form coalitions to take over existing groups from resident males or else to defend their own group against takeovers. Pope (1990) used genotype data from multiple allozyme loci to assess relatedness and mating success among males in a number of social groups, and combined these with long-term observational data on the demographic histories of those groups. She found that coalitions comprising related males (typically fathers and sons or full siblings) lasted longer and enjoyed greater overall reproductive success than did coalitions formed between unrelated males. Within coalitions, paternity was always monopolized by the dominant coalition partner, and subordinate coalition members were presumed to participate because of the indirect fitness benefits they received through the reproduction of their male kin. Female red howler monkeys that emigrate from their natal troops also must form coalitions with one another (and with one or more males) to establish new social groups in which they can begin breeding, but invariably must do so with unrelated animals (Pope, 2000). As these groups grow, coalitions among founding females and their kin prevent additional females from immigrating into the group (Crockett and Pope, 1993; Crockett, 1984, 1996) such that female recruitment into breeding groups is only by natal individuals. At the same time, founding females and their female kin attempt to expel other founders and their kin from the group. Using allozyme marker data, Pope (2000b) documented that the average degree of relatedness among group females was much greater in established groups than in newly formed ones (mean $R \geq 0.25$ vs. mean $R = 0$, respectively), reflecting the genetic outcome of this process of cooperation among matrilineal kin to evict unrelated competitors. Moreover, the per capita reproductive output of females in established groups greatly exceeded that of females in new groups, even when other factors such

as group size were controlled for, indicating a clear fitness benefit to females of cooperating with kin.

Finally, a very few studies of primates have examined the influence of kinship through the male lineage on primate social behavior. Theoretically, animals should behave just as affiliatively and cooperatively toward patrilineal as matrilineal kin of the same degree of relatedness. To test this hypothesis, Widdig et al. (2001) analyzed parentage in a group of free-ranging rhesus macaques using both microsatellite genotyping and DNA fingerprinting and identified pairs of females who were paternal vs. maternal half-siblings; they then compared levels of affiliative behavior (e.g., frequency of grooming, time spent in proximity) among maternal half-sibling, paternal half-sibling, and nonkin dyads. Among both peers (animals close to one another in age or members of the same birth cohort) and non-peers, maternal half-siblings were the most affiliative dyads, but paternal half-siblings were also significantly more affiliative than nonkin, suggesting both paternal kin discrimination and the potential importance of kin-directed nepotism. Alberts (1999) also demonstrated the potential for baboons to recognize patrilineal kin. While male-female paternal half-sibling dyads did not refrain from consorting with each other, these consortships involved less sexual and affiliative behavior than those involving nonkin.

It is surprising that more studies have not sought to evaluate whether patterns of social affiliation and cooperation are, in fact, directed more commonly towards relatives in primates, as this is one of the fundamental assumptions underlying most sociobiological theories of primate social relationships. Given the efficacy of noninvasive methods of genetic sampling, it should be relatively easy to incorporate a molecular component into more traditional observational analyses of primate behavior and to begin to evaluate this assumption and its implications in a wider array of taxa. Furthermore, it is important to note that kin selection may not always play the strong role it has long been presumed to play in structuring primate social relationships, as is apparently the case in chimpanzees. In fact, for chimpanzees this may not be that surprising: there may be only a very low probability that any given male chimpanzee, as an adult, actually has any male maternal kin living in his community at the same time, given the more than 5-year interbirth interval, the relatively high level of juvenile mortality, and the possible secondary dispersal of his mother after giving birth to him. Obviously, far more data on patterns of within-group relatedness are needed to evaluate whether the chimpanzee results also characterize any other primate taxa.

Studies of primate social organization in less-studied taxa

Molecular data have also been used to examine fundamental questions about the social systems of

primates that are difficult to observe in typical field studies. Several recent studies of nocturnal and cathemeral lemurs, in particular, exemplify this trend. Radespiel et al. (2001) and Wimmer et al. (2002) used molecular techniques to examine dispersal patterns, neighborhood structure, and social group composition in two separate populations of gray mouse lemurs (*Microcebus murinus*). Mouse lemurs are small-bodied, nocturnal primates who live in a “dispersed” or “noyau” social system thought to be primitive for primates (Martin, 1972; Di Fiore and Rendall, 1994; Müller and Thalmann, 2000; Kappeler and van Schaik, 2002), where individuals typically forage independently in somewhat overlapping ranges, and the ranges used by adult males tend to overlap those of several females (Bearder, 1987). Among mouse lemurs, adult females typically share daytime nesting sites with several other females with whom their ranges overlap (Radespiel, 2000); during the nonmating season, males typically sleep apart from females, singly or in pairs (Martin, 1972; Radespiel, 2000), although mixed-sex sleeping associations are common during the mating season (Martin, 1972). Martin (1972, 1973) hypothesized that groups of co-sleeping adult females might comprise matrilineally related individuals and that adult males in an area were immigrants and unrelated to resident females.

Radespiel et al. (2001) tested these hypotheses using genotype data for 166 individuals at seven lemur-specific microsatellite loci, and found that co-sleeping females were, on average, significantly more closely related to one another than females from different sleeping associations. Using microsatellite marker data for 85 individuals typed at six loci, Wimmer et al. (2002) also found support for the model for Martin’s (1972, 1973): while the average pairwise relatedness among wild adults (both males and females) within their 9-hectare study area was close to zero (as would be expected in a large, panmictic population), the average relatedness among females whose home ranges overlapped was significantly higher (Fig. 2F). Wimmer et al. (2002) also sequenced a 530-base-pair fragment of the mitochondrial control region and found strikingly different patterns of diversity among males vs. females. Most of the 33 adult and juvenile females in their population shared a single, common mitochondrial DNA haplotype, while most of the other haplotypes in the population were only seen in adult males. Moreover, haplotypes appeared spatially clustered: while the ranges of females with the same mitochondrial haplotypes overlapped, there was little geographic overlap among the ranges of females with different haplotypes.

Kappeler et al. (2002) found exactly the same pattern of geographical clustering of mitochondrial DNA haplotypes among females in a population of Coquerel’s dwarf lemurs (*Mirza coquereli*), another nocturnal prosimian with a “dispersed” social system but one in which individuals seldom form sleep-

ing associations like those seen in *Microcebus*. Male mitochondrial DNA variation showed no such structuring, and several adult males bearing common female haplotypes were found within geographic areas characterized by a different female haplotype. As in mouse lemurs, the clear geographic structuring to female mitochondrial DNA variation reflects a strong bias towards female philopatry and male dispersal, although Kappeler et al. (2002) noted that not all males dispersed, nor did all females remain close to their natal ranges as adults. Finally, Kappeler et al. (2002) also shed light on the mating systems of dwarf lemurs. For over 30% of offspring for whom it was possible to determine maternity, exclusion analysis ruled out all of the adult males resident in the study area as possible fathers, suggesting that offspring were conceived with males who briefly entered the area during the mating season. Moreover, paternity within the study population was divided among five different males, and individual offspring in 2 out of 4 sets of twins were sired by different males. The mating system of dwarf lemurs is best characterized as “scramble competition” polygyny, since it does not appear that individual males are able to effectively monopolize paternity on even a limited scale (Kappeler et al., 2002).

Fietz et al. (2000) investigated the mating system of another nocturnal prosimian, the fat-tailed dwarf lemur (*Cheirogaleus medius*), which, unlike Coquerel's dwarf lemur, is pair-living with males displaying paternal care. Using microsatellite genotypes for seven species-specific loci, Fietz et al. (2000) found that 44% of a pair's offspring were sired by males other than the resident male. Typically, paternity was assigned to a paired male in a nearby social group, and in no case was a floater male identified as a sire. Fietz et al. (2000) also found that males in the population tended to be slightly inbred, as revealed by a positive F_{IS} value; thus, through kin selection, cuckolded males might not suffer as great a fitness loss as expected by raising offspring other than their own. A corresponding study of the distribution of mitochondrial DNA variation in this population would reveal how closely males in the area are related matrilineally.

Finally, two studies of cathemeral strepsirrhines, the red-fronted lemur (*Eulemur fulvus rufus*) and the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*) also exemplify how molecular studies can shed broad light on primate social systems and, in combination with the other studies mentioned above, point to some emerging commonalities about lemur social organization. Red-fronted lemurs typically live in multimale-multifemale groups with a roughly even sex ratio (Overdorff et al., 1999). Wimmer and Kappeler (2002) sequenced a portion of the mitochondrial control region of 59 individual red-fronted lemurs from multiple social groups, and genotyped these individuals at seven microsatellite loci. Analysis of the mitochondrial data revealed that females are more philopatric than males and

that social groups are organized along lines of matrilineal kinship. First, male mitochondrial DNA diversity was far greater than female diversity: 12 distinct haplotypes were found among males and only four among females. Second, all the adult females resident in each of the social groups shared identical mitochondrial DNA haplotypes, and one haplotype characterized females in six different groups. A group's adult males, in contrast, typically had haplotypes distinct from both females and one another. Not surprisingly, adult females within groups were closely related (at the level of half to full siblings), while average relatedness among males within groups was lower. Paternity analysis for 12 offspring born into the study population revealed that socially “central” males (Ostner and Kappeler, 1999) who dominated other resident males were responsible for most conceptions, suggesting an influence of male dominance rank on reproductive success. Nonetheless, about one-third of offspring were sired by noncentral males.

Like red-fronted lemurs, Alaotran gentle lemurs typically live in multimale-multifemale social groups with a small number of adult individuals of each sex. Nievergelt et al. (2002) genotyped and sequenced a portion of the mitochondrial control region for 99 Alaotran gentle lemurs from 22 social groups found at three different sites around Lac Alaotra in northeastern Madagascar. As in red-fronted lemurs (Wimmer and Kappeler, 2002), breeding females in each gentle lemur social group invariably shared the same mitochondrial DNA haplotype and were closely related to one another, at the level of mother-daughter or full-sib pairs. Average relatedness between reproductive-age males and females within groups was significantly lower and was not statistically different from the average relatedness between members of different groups. Furthermore, paternity analyses revealed that just one of the resident males in each group was reproductively active; nonbreeding adult and subadult males within groups were typically maturing offspring of the breeding animals and never bred themselves. Additionally, over 21% of offspring in the population were sired by former rather than current resident males (who nonetheless tolerated these older juveniles), suggesting a frequent turnover among male residents. Finally, Nievergelt et al. (2002) found that about 8.5% of offspring in the population (five individuals) were sired by extragroup males; several of these appeared to be cases of inbreeding avoidance, as the resident breeding male was a close relative of the female involved.

What emerges from all these studies, and from work on *Propithecus* (Lawler et al., 2001b; 2003) is the clear matrilineal underpinnings to lemur sociality. In all these taxa, except for *Cheirogaleus medius* for which data are not available, there appears to be considerable geographic structuring to mitochondrial DNA variation, consistent with the typical mammalian pattern of female philopatry and male-

biased dispersal (Greenwood, 1980; Johnson and Gaines, 1990). Moreover, among all these taxa (again with the exception of *Cheirogaleus*), females within social groups or within local areas are more closely related to one another than are males, and in fact appear to be close matrilineal kin. Nonetheless, lemurs differ fundamentally from matrilineally organized cercopithecines in many other aspects of social organization, such as in their general lack of highly differentiated female-female social relationships and strong female bonds, even in the face of close kinship among females.

SOME FUTURE DIRECTIONS

I want to close this review by pointing to a couple of areas beyond those outlined above where PCR-based molecular techniques seem likely to play an important role in future studies of primate behavior, ecology, social organization, and conservation. Given the versatility of PCR, there is no doubt that many additional novel applications of molecular techniques will also be developed in the near future. Indeed, in *Making PCR*, an ethnographic account of the discovery and patenting of the polymerase chain reaction at the Cetus Corporation, social anthropologist Paul Rabinow (1996) recounted one insider's view that "the truly astonishing thing about PCR is precisely that it *wasn't* designed to solve a problem; once it existed, problems began to emerge to which it could be applied" (Rabinow, 1996, p. 7).

Conservation applications

Many species of primates are currently threatened by various anthropogenic activities including deforestation, habitat fragmentation and conversion, and hunting. Within the realm of primate conservation biology, molecular genetic techniques have myriad applications (e.g., characterizing genetic diversity in threatened species and how it is structured geographically, estimating effective population size, informing management decisions over breeding in captive colonies). Though a review of these applications is beyond the scope of this paper, several books (Loeschcke et al., 1994; Avise and Hamrick, 1996; Smith and Wayne, 1996) and a new journal, *Conservation Genetics*, provide excellent overviews of conservation applications for the molecular methods outlined here.

One particular conservation application of likely interest to behavioral ecologists is the potential to conduct population surveys and demographic studies of specific species through fecal sample collection and PCR-based sex determination and genotyping. In essence, these methods can be used to effect genetic "mark-recapture" studies, which can yield estimates of population size and sex composition. Kohn et al. (1999) provide a nice overview of the relevant procedures, and demonstrate how they can be used to estimate population size, sex ratio, home range use, and patterns of relatedness using coyotes

(*Canis latrans*) as a model. Similar studies have not yet been conducted for primates, but all of the molecular tools are in place. With respect to PCR-based sex determination, for example, Bradley et al. (2001) recently verified that the sexing assay commonly employed in human forensic cases (which is based on a 6-base-pair difference in length between homologous regions of the amelogenin gene on the human X and Y chromosomes; Sullivan et al., 1993) is likewise effective for sexing noninvasively collected samples of gorillas, chimpanzees, and gibbons. Although not broadly tested in other catarrhines, preliminary data suggest that this assay will not work without modification outside of the hominoids (Ensminger and Hoffman, 2002; Di Fiore, unpublished data). Nonetheless, Wilson and Erlandsson (1998) developed a general PCR-based sexing assay for anthropoid primates which takes advantage of a several hundred base-pair size difference between the X and Y homologues of the zinc finger protein gene, and this assay has been used successfully in studies of wild populations of several New World primates (e.g., *Lagothrix*: Di Fiore, 2002, 2003; *Aotus*: Gagneux, personal communication).

Novel ways of studying diets, parasitic infection, and seed dispersal

DNA extractions from primate fecal samples contain genetic material of many other organisms besides the defecating animal, e.g., plants, insects, and vertebrates that were eaten, as well as intestinal parasites and pathogens. This provides an excellent opportunity for primatologists to study primate diets and disease in a novel way, one that need not involve excellent observation conditions or even extensive contact with animals in the field. For instance, with appropriate primers, researchers could use PCR to amplify DNA from specific insects or specific plants that are potentially in the diet from a set of opportunistically collected fecal samples to determine whether or not those items are eaten. For primates such as chimpanzees that hunt and kill vertebrate prey, feces could be assayed using PCR primers designed for specific prey species, to see what kinds of prey are being eaten at what times of the year. Additionally, by combining individual genotyping of fecal samples with conventional fecal diet analysis, primate researchers could have a powerful tool for studying individual variation in foraging strategies and diet choice, even where detailed observations of feeding behavior are impossible, as Fedriani and Kohn (2001) have attempted for coyotes.

PCR of nucleic acids extracted from fecal samples could also be used to test for the presence of specific microbial pathogens, which could allow remote monitoring of infectious diseases in wild primate populations. For example, Ling et al. (2003) and Santiago et al. (2003) recently used PCR to amplify viron RNA from simian immunodeficiency virus (SIV) from the feces of captive sooty manglebeys and wild chimpan-

zees, demonstrating the feasibility of such noninvasive epidemiological surveys.

Finally, molecular techniques offer a novel way for primatologists to examine seed dispersal. Primates play a major ecological role as dispersers of seeds in many tropical forests. In the New World, for example, up to 90% of woody plant species produce fruits that are dispersed by frugivores (Howe and Smallwood, 1982; Jordano, 1995; Taberelli and Peres, 2002), and primates comprise from 25% to over 50% of the total frugivore biomass (Eisenberg et al., 1979; Terborgh, 1983; Glanz, 1990). From the plant's point of view, effective seed dispersal normally requires that dispersers move seeds away from the parent tree, as seedling mortality is generally high underneath parents (e.g., Howe, 1980; Howe et al., 1985). Thus, one of the goals of primate seed dispersal studies is to evaluate "seed shadows" of different plant species to investigate the effectiveness of primates as dispersers. However, determining the seed shadows of important primate fruit trees is difficult, particularly if an animal feeds in multiple individuals of the same species in the course of a day, as this makes it impossible to infer the "correct" parent tree that defecated seeds come from. Molecular techniques provide a possible solution to this problem. With appropriate genetic markers, researchers can genotype defecated seeds and match them back to the appropriate parent tree to get a precise estimate of dispersal distance. Such a project was recently initiated to examine seed dispersal by sympatric woolly and spider monkeys in Ecuador (Di Fiore, unpublished data).

Primate behavioral genetics

Finally, one of the most exciting new areas where molecular methods are beginning to be applied is in the burgeoning field of nonhuman primate behavioral genetics. In both human and nonhuman primates, there is a substantial hereditary component to many aspects of behavior, including such "complex" individual behaviors as temperament, personality, and cognitive ability (Plomin et al., 2001). One major aspect of behavioral genetic research involves the search for specific genes or gene systems that have significant effects on individual behavior. In the natural world, genetic differences that are, in part, responsible for the behavioral variation we see among individuals could have substantial evolutionary effects. Even though behavioral genetic studies of nonhuman primates are just beginning, it is already apparent that dramatic behavioral differences may be the product of relatively modest genetic polymorphism.

A series of recent studies exemplifies the potential for behavioral genetics research to broaden our understanding of the behavioral variation seen in nonhuman primate populations. Differences between individual rhesus macaques in the concentration of cerebrospinal fluid 5-hydroxyindoleacetic acid (CSF 5-HIAA), the primary metabolite of the neurotrans-

mitter serotonin, were shown to be associated with marked differences in behavior: animals with low CSF 5-HIAA concentrations (indicative of low central serotonin activity) were associated with impulsivity, unrestrained aggressive behavior, and "risk-taking" (Mehlman et al., 1995; Fairbanks et al., 1999; Fairbanks, 2001); low CSF 5-HIAA individuals were also less social than their counterparts, spent more time alone, and were likely to migrate earlier from their natal groups (Kaplan et al., 1995; Mehlman et al., 1995). Recently, Lesch et al. (1996, 1997) identified a genetic polymorphism in a tandem repeat motif in the promoter region of the serotonin transporter gene (SLC6A4) that is apparently responsible for this variation in CSF 5-HIAA levels (Heils et al., 1996). There are two major alleles for the SLC6A4 gene, *l* (long form) and *s* (short form), which are associated with relatively higher and lower transcriptional efficiency, respectively, and Bennett et al. (2002) have demonstrated that *ls* heterozygotes raised in peer groups (rather than parent-reared animals) have lower CSF 5-HIAA levels than *ll* homozygotes. Trefilov et al. (2000) genotyped 532 male rhesus macaques born into various social groups on Cayo Santiago and examined the relationship between age at dispersal and SLC6A4 genotype. They found that homozygous *ss* males left their natal groups an average of 14.4 months earlier than *ll* individuals and 6.4 months earlier than *ls* heterozygotes. The maintenance of this polymorphism in the population may be due to heterozygote advantage, and genetic paternity data demonstrated that heterozygous individuals sired more offspring per capita than either homozygote, although the difference in reproductive output only approached significance (Trefilov et al., 2000). Gerald et al. (2002) examined the reproductive consequences of variation in CSF 5-HIAA level and found that in breeding groups containing two reproductive males of differing CSF 5-HIAA levels, males with higher levels sired more offspring. They suggested that this polymorphism may be maintained in the population because the early migration associated with low CSF 5-HIAA levels results in those males gaining sexual opportunities and reproducing sooner than high CSF 5-HIAA males. Among rhesus macaques on Cayo Santiago, females prefer novel mating partners (Manson, 1995) and newly immigrated males enjoy high mating success (Berard, 1999), which suggests that these explanations for maintenance of the SLC6A4 polymorphism are plausible. It is not at all difficult to imagine the evolutionary implications of heritable variation in a gene that influences such a fundamental primate behavior as dispersal. In the next few years, research on nonhuman primate behavioral genetics is sure to be expanded, beginning with screening other primate species (e.g., Trefilov et al., 1999) for variation at the SLC6A4 locus and other loci known to be associated with complex behavioral traits in humans or laboratory animals, e.g., genes for GABA benzodiazepam receptors, cho-

lecystokinin-tetrapeptide (CCK4) receptors, catechol-O-methyltransferase (COMT), monoamine oxidase A (MAOA), tryptophan hydroxylase (TPH), and various serotonin and dopamine receptor and transporters (Ebstein et al., 1996; Benjamin et al., 1996; Lesch and Merschdorf, 2000; Alsobrook et al., 2002; Flint, 2002; Goldman and Mazzanti, 2002).

CONCLUSIONS

The studies discussed above and reviewed in Table 3 demonstrate the myriad ways in which researchers can incorporate molecular genetic techniques into field studies of primate behavior and ecology. These techniques are, first and foremost, valuable tools for addressing many of the major topics that have occupied primatologists for the last several decades, e.g., the significance dominance rank, the influence of kinship on patterns of social behavior, the effectiveness of alternative mating strategies for males, the extent to which dispersal is a strategy to avoid inbreeding or the product of mating competition, and the influence of female mating strategies on male fitness. Additionally, the studies discussed in this review exemplify the new links being forged between field-based behavioral ecology and laboratory-based population genetics, and they highlight our developing understanding of the genetic consequences of social structure and individual behavior (e.g., Chesser, 1991a,b; Sugg et al., 1996; Ross, 2001).

Several conclusions can be drawn from this review with respect to the influence of primate social structure and individual behavior on population genetic structure. First, sex-biased dispersal indeed has the effect on population genetic structure that is predicted by theory. Among cercopithecines and several strepsirrhines characterized by female philopatry, a contrasting structure is seen in mitochondrial vs. nuclear genetic diversity, with mitochondrial diversity typically quite low at the social group and local population levels. In contrast, among chimpanzees, hamadryas baboons, and woolly monkeys (taxa in which female dispersal is common), mitochondrial DNA diversity is high within groups and shows no evidence of being geographically structured. Additionally, recently developed "assignment tests" (Paetkau et al., 1995; Favre et al., 1997) now allow researchers to evaluate dispersal on a more individual level and to move beyond the relatively crude assessments described above. In brief, assignment tests use microsatellite marker or other allelic data to evaluate the likelihood that a particular individual represents an immigrant into a population or to assign an individual to a particular source population (Waser and Strobeck, 1998). The basic procedure is remarkably simple: for any individual, an assignment index (AI) is calculated that reflects the probability that its genotype occurred by chance, given observed population allele frequencies (Paetkau et al., 1995). Subtracting the individual's AI from the population average after each is log-trans-

formed yields a corrected index (AI_C) (Favre et al., 1997). Since the mean AI_C in any population would be zero, negative values indicate those individuals more likely to have been born outside of the local population. Indices calculated for an individual using allele frequencies from different potential source populations can be compared and the individual "assigned" to the most likely source population. Furthermore, at the population level, comparisons of the distribution of AI_C values among different demographic classes (e.g., females vs. males, dominant animals vs. subordinates) can reveal whether there are any demographic biases in dispersal behavior. Rannala and Mountain (1997) described a similar statistical test for detecting immigration and identifying a likely source population for immigrants where population allele frequencies are estimated using Bayesian methods. Thus far, these tests have not been applied to primates, but they have been used to reveal identify dispersal patterns in other mammals (e.g., monogamous white-toothed shrews, *Crocodyra russula*, Favre et al., 1997; white-footed mice, *Peromyscus leucopus*, Mossman and Waser, 1999).

A second important conclusion that emerges from this review is that although there is a clear relationship between male dominance rank and reproductive success in many taxa, female choice and alternative male reproductive tactics also have important evolutionary consequences. Genetic data reveal that the rate of extragroup paternity may be high in some taxa (e.g., *Cheirogaleus*), and that males using alternative mating strategies are often quite successful at siring offspring. For species in which strong linear dominance hierarchies characterize male-male relationships, alternative male mating strategies and female choice may reduce the degree of reproductive skew that would be presumed based on observations of dominance-based mating. In this case, effective population size would be greater than that suggested by behavior patterns alone, which could slow the loss of diversity due to genetic drift and reduce the rate of differentiation among subpopulations. Studies on a wider array of taxa are necessary to further explore how individual decisions over mating affect an individual's reproductive success and, in turn, population genetic structure.

The third conclusion to draw from this review is that far more research is needed on the importance of kin selection vs. other factors in shaping primate social behavior and social relationships. Genetic data suggest an association between relatedness on the one hand and affiliative and cooperative social behavior on the other for taxa such as howler monkeys and some cercopithecines, but no such an association is seen in other taxa (e.g., chimpanzees). Despite the close male bonds among chimpanzees, male social partners are no more likely to be maternal kin than nonkin, and average male-male relatedness within communities is no greater than aver-

TABLE 3. Summary of molecular studies of primate mating systems, reproductive strategies, patterns of within-group relatedness, and dispersal

Species	Molecular technique used	Population type	Relationship between male rank and RS ¹	Success of alternative male mating strategies demonstrated ¹	Extragroup paternity ²	Influence of female choice ³	Within-group relatedness and dispersal pattern ³	References
<i>Alouatta seniculus</i>	Allozyme genotyping	Wild	Strong	No	No	No	Ms sometimes related, F relatedness low initially and increases with time	Pope (1990, 2000)
<i>Callithrix jacchus</i>	Microsatellite genotyping	Wild	Strong	No	Possible	Yes, Fs mate with extragroup Ms	F > M, groups are extended families	Nievergelt et al. (2000)
<i>Callithrix jacchus</i>	mtDNA sequencing	Wild	No data	No data	No data	No data	Both sexes disperse, multiple matriline per group	Faulkes et al. (2003)
<i>Cercopithecus torquatus atys</i>	DNA fingerprinting	Captive	Moderate to strong	No data	Not applicable	No data	No data	Gust et al. (1998)
<i>Cheirogaleus medius</i>	Microsatellite genotyping	Wild	Not applicable	Not applicable	Yes	Yes, high level of EGP	M > F	Fietz et al. (2000)
<i>Erythrocebus patas</i>	DNA fingerprinting, microsatellite genotyping	Wild	None	Yes	Yes	Yes	No data	Ohsawa et al. (1993)
<i>Eulemur fulvus rufus</i>	Microsatellite genotyping, mtDNA sequencing	Wild	Moderate	One-third of offspring sired by noncentral males	No	Implied	F > M, matrilineal structure, M dispersal	Wimmer and Kappeler (2002)
<i>Haplemur griseus alaotrensis</i>	Microsatellite genotyping, mtDNA sequencing	Wild	Strong	No	Little	Implied for few cases of EGP	F > M, matrilineal structure, M dispersal	Nievergelt et al. (2002)
<i>Hylobates muelleri</i>	Microsatellite genotyping	Wild	Not applicable	Not applicable	No	No data	Some subadults not related to breeding pair	Oka and Takenaka (2000)
<i>Lagothrix lagotricha</i>	Microsatellite genotyping, mtDNA sequencing	Wild	No data	No data	No data	No data	M > F, multiple matriline per group, F dispersal implicated	Di Fiore (2002, 2003, unpublished data)
<i>Lemur catta</i>	DNA fingerprinting	Captive	None	Implied	No data	Yes, Fs consistently mated with unrelated Ms, Fs dominant over Ms	No data	Periera and Weiss (1991)
<i>Macaca arctoides</i>	DNA fingerprinting	Captive	Strong	No	No	Perhaps, offspring not sired by alpha M may be case of incest avoidance	No data	Bauers and Hearn (1994)
<i>Macaca cyclopis</i>	Microsatellite genotyping	Captive	Strong	No	No	No	No data	Chu et al. (1999)
<i>Macaca fascicularis</i>	DNA fingerprinting	Wild	Strong	No	No data	Implied by long period of receptivity	F > M	de Ruiter et al. (1992, 1994); de Ruiter and Geffen (1998)

(continued)

TABLE 3. Continued

Species	Molecular technique used	Population type	Relationship between male rank and RS ¹	Success of alternative male mating strategies demonstrated ¹	Extragroup paternity ²	Influence of female choice ³	Within-group relatedness and dispersal pattern ³	References
<i>Macaca fuscata</i>	DNA fingerprinting	Wild	None	No data	Not applicable	No data	No data	Inoue et al. (1991); Inoue (1995)
<i>Macaca mulatta</i>	Allozyme genotyping, immunological assays	Wild	Strong	No data	No data	No data	M dispersal	Melnick (1987); Melnick and Hoelzer (1996)
<i>Macaca mulatta</i>	DNA fingerprinting	Free-ranging	None	Yes	Yes	Yes	No data	Berard et al. (1993, 1994)
<i>Macaca mulatta</i>	Allozyme genotyping, immunological assays, DNA fingerprinting	Captive	None in most years, moderate in some years, moderate overall	No data	No data	Implied	Not applicable	Smith (1994)
<i>Macaca sinica</i>	Microsatellite genotyping	Wild	Some	No data	Yes	Implied	No data	Keane et al. (1997)
<i>Macaca sylvanus</i>	DNA fingerprinting	Free-ranging	Moderate, in 3 of 4 seasons	No data	No data	No data	No data	Paul et al. (1993)
<i>Macaca sylvanus</i>	DNA fingerprinting microsatellite genotyping	Wild	None	Perhaps, caretaking appears to be mating effort and increases mating success	No data	Yes	No data	Ménard et al. (1992)
<i>Mandrillus sphinx</i>	DNA fingerprinting	Captive	Strong	No	Not applicable	No	No data	Dixson et al. (1993)
<i>Microcebus murinus</i>	Microsatellite genotyping, mtDNA sequencing	Wild, captive	None	Mating system = scramble polygyny	Not applicable	No data	F co-sleepers > Ms and > Fs in different sleeping groups, M dispersal	Radespiel et al. (2001, 2002)
<i>Microcebus murinus</i>	Microsatellite genotyping, mtDNA sequencing	Wild	No data	No data	No data	No data	Fs with overlapping home ranges > Ms and > other Fs, matrilineal structure, M dispersal	Wimmer et al. (2002)
<i>Mirza coquereli</i>	Microsatellite genotyping, mtDNA sequencing	Wild	None	Mating system = scramble polygyny	Not applicable	No data	F > M, matrilineal structure, M dispersal	Kappeler et al. (2002)
<i>Pan paniscus</i>	Microsatellite genotyping, mtDNA sequencing	Wild	Moderate, skewed somewhat to high-ranking males	No data	Yes	Yes, Fs observed mating with outside Ms	M = F, some evidence that some Ms are matrilineal kin, F dispersal implicated	Gerloff et al. (1999); Hohmann et al. (1999)
<i>Pan troglodytes schweinfurthii</i>	Microsatellite genotyping, mtDNA sequencing	Wild	Moderate, skewed somewhat to high-ranking males	Yes	No (Gombe), yes (Bossou)	Yes, some EGP and Fs observed mating with outside Ms	M > F reported initially, later M = F, some evidence that some Ms are matrilineal kin, F dispersal implicated	Sugiyama et al. (1993); Morin et al. (1994); Goldberg and Wrangham (1997); Mitani et al. (2000); Constable et al. (2001)

(continued)

TABLE 3. Continued

Species	Molecular technique used	Population type	Relationship between male rank and RS ¹	Success of alternative male mating strategies demonstrated ¹	Extragroup paternity ²	Influence of female choice ³	Within-group relatedness and dispersal pattern ³	References
<i>Pan troglodytes verus</i>	Microsatellite genotyping, mtDNA sequencing	Wild	No data	No data	Yes	Yes, some EGP and Fs observed mating with outside Ms	M = F, F dispersal implicated	Gagneux et al. (1997b, 1999); Vigilant et al. (2001)
<i>Papio hamadryas cynocephalus</i>	Microsatellite and allozyme genotyping	Wild	Strong	No	No	No data	F > M	Altmann et al. (1996)
<i>Papio hamadryas hamadryas</i>	Microsatellite genotyping	Captive	None	Implied	Yes	Implied	No data	Smith et al. (1999)
<i>Papio hamadryas hamadryas</i>	mtDNA sequencing	Wild	No data	No data	No data	No data	Multiple matriline per group, F dispersal implicated	Hapke et al. (2001)
<i>Pongo pygmaeus</i>	Microsatellite genotyping	Wild	None, both morphotypes sire about same proportion of offspring	Yes	Not applicable	No data	No data	Utami et al. (2002)
<i>Propithecus verreauxi</i>	Microsatellite genotyping	Wild	No data	No data	Yes	Yes	F > M, M dispersal, some Ms disperse to groups with M kin	Lawler et al. (2001b, 2003)
<i>Semnopithecus entellus</i>	Microsatellite genotyping	Wild	Moderate, RS for harem holder > alpha in MM group > other in MM group	Implied	Some	Implied	No data	Launhardt et al. (2001)

¹ Pair-living taxa are scored as not applicable; RS, reproductive success.

² Captive social groups not in contact with other groups and taxa with “dispersed” social systems are scored as “Not applicable.”

³ F, female; Fs, females; M, male; Ms, males; EGP, extra group paternity.

age female-female relatedness. Additionally, even though several lemur species appear to be organized along matrilineal kin lines, female social bonds in these taxa appear to be poorly developed, at least in comparison to many female-philopatric cercopithecines. In general, genetic data have yet to be widely applied to examining links between kinship and social behavior in many other primates, so this should be a priority of future research. Moreover, the role that patrilineal vs. matrilineal kinship plays in shaping primate social dynamics has yet to be explored in any detail for nonhuman primates, though the growing use of Y-chromosome markers as a counterpart to mitochondrial DNA in human population genetics studies (e.g., Hammer, 1995; Hammer et al., 1998; Seielstad et al., 1998; Shen et al., 2000; Thomson et al., 2000) represents a promising avenue for future work (Hurles and Jobling, 2001).

Finally, a cautionary comment should be made concerning the generality of the insights provided by limited genetic studies into the social organization and behavior of particular primate species. Most of the case studies reviewed here focused on a single or a small number of social groups, sampled within a relatively short window of time; yet the more we learn about the social behavior, mating patterns, and group dynamics of wild primates through long-term observational research, the more we come to appreciate the impressive temporal and population variation possible in these features of primate biology (see Strier, this volume). Before making final conclusions about individual behavioral processes or features of a species' social organization on the basis of molecular data, multiple genetic studies should be conducted that sample a range of groups, environments, and demographic backgrounds.

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LITERATURE CITED

- Alberts SC. 1999. Paternal kin discrimination in wild baboons. *Proc R Soc Lond [Biol]* 266:1501–1506.

- Alsobrook JP, Zohar AH, Leboyer M, Chabane N, Ebstein RP, Pauls DL. 2002. Association between the COMT locus and obsessive-compulsive disorder in females but not males. *Am J Med Genet* 114:116–120.
- Altmann J, Alberts SC, Haines SA, Bubach J, Muruthi P, Coote T, Geffen E, Cheesman DJ, Mututa RS, Saiyalel SN, Wayne RK, Lacy RC, Bruford MW. 1996. Behavior predicts genetic structure in a wild primate group. *Proc Natl Acad Sci USA* 93:5797–5801.
- Altmann SA. 1962. A field study of the sociobiology of the rhesus monkey, *Macaca mulatta*. *Ann NY Acad Sci* 102:338–435.
- Avise JC. 1994. Molecular markers, natural history and evolution. New York: Chapman and Hall.
- Avise JC. 1995. Mitochondrial DNA polymorphism and a connection between genetics and demography of relevance to conservation. *Conserv Biol* 9:686–690.
- Avise JC. 2000. Phylogeography: the history and formation of species. Cambridge, MA: Harvard University Press.
- Avise JC, Hamrick JL, editors. 1996. Conservation genetics: case histories from nature. New York: Chapman and Hall.
- Avise JC, Arnold J, Ball RM, Bermingham E, Lamb T, Neigel JE, Reeb CA, Saunders NC. 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annu Rev Ecol Syst* 18:489–522.
- Ayliffe MA, Lawrence GJ, Ellis JG, Pryor AJ. 1994. Heteroduplex molecules formed between allelic sequences cause nonparental RAPD bands. *Nucleic Acids Res* 7:1632–1636.
- Bachmann L, Rumpler Y, Ganzhorn JU, Tomiuk J. 2000. Genetic differentiation among natural populations of *Lepilemur rufigaudatus*. *Int J Primatol* 21:853–864.
- Baker AJ, editor. 2000. *Molecular Methods in Ecology*. Oxford: Blackwell Scientific.
- Banks MA, Eichert W. 2000. WHICHRUN (version 3.2) a computer program for population assignment of individuals based on multilocus genotype data. *J Hered* 91:87–89.
- Bauers KA, Hearn JP. 1994. Patterns of paternity in relation to male social rank in the stump-tailed macaque, *Macaca arcoides*. *Behaviour* 129:149–176.
- Bearder SK. 1987. Lorises, bushbabies, and tarsiers: diverse societies in solitary foragers. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 11–24.
- Berli P. 1998. Estimation of migration rates and population sizes in geographically structured populations. In: Carvalho GR, editor. *Advances in molecular ecology*. Amsterdam: IOS Press. p 39–53.
- Benjamin J, Li L, Patterson C, Greenburg BD, Murphy DL, Hamer DH. 1996. Population and familial association between the D4 dopamine receptor gene and measures of novelty seeking. *Nat Genet* 12:81–84.
- Bennett AJ, Lesch KP, Heils A, Long JC, Lorenz JG, Shoaf SE, Champoux M, Suomi SJ, Linnoila MV, Higley DG. 2002. Early experience and serotonin transporter gene variation interact to influence primate CNS function. *Mol Psychiatry* 7:118–122.
- Berard J. 1999. A four-year study of the association between male dominance rank, residency status, and reproductive activity in rhesus macaques (*Macaca mulatta*). *Primates* 40:159–175.
- Berard JD, Nürnberg P, Epplen JT, Schmidtke J. 1993. Male rank, reproductive behavior, and reproductive success in free-ranging rhesus macaques. *Primates* 34:481–489.
- Berard JD, Nürnberg P, Epplen JT, Schmidtke J. 1994. Alternative reproductive tactics and reproductive success in male rhesus macaques. *Behaviour* 129:177–201.
- Blouin MS, Parsons M, Lacaille V, Lotz S. 1996. Use of microsatellite loci to classify individuals by relatedness. *Mol Ecol* 5:393–401.
- Boesch C. 1994. Cooperative hunting in wild chimpanzees. *Anim Behav* 48:653–667.
- Boesch C. 1996. Social grouping in Tai chimpanzees. In: McGrew WC, Marchant LF, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 101–113.
- Boesch C, Boesch H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *Am J Phys Anthropol* 78:547–573.

- Boesch C, Boesch-Achermann H. 2000. The chimpanzees of the Tai Forest. Oxford: Oxford University Press.
- Böhle U-R, Zischler H. 2002. Polymorphic microsatellite loci for the mustached tamarin (*Saguinus mystax*) and their cross-species amplification in other New World monkeys. *Mol Ecol Notes* 2:1–3.
- Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P. 1999a. DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. *Proc R Soc Lond [Biol]* 266:901–904.
- Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P. 1999b. Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups—defence pattern, paternity and sexual behaviour. *Behav Ecol Sociobiol* 46:350–356.
- Bradley BJ, Vigilant L. 2001. The evolutionary genetics and molecular ecology of chimpanzees and bonobos. In: Boesch C, Hohmann G, Marchant LF, editors. Behavioural diversity in chimpanzees and bonobos. New York: Cambridge University Press. p 259–276.
- Bradley BJ, Vigilant L. 2002. False alleles derived from microbial DNA pose a potential source of error in microsatellite genotyping of DNA from faeces. *Mol Ecol Notes* 2:602–605.
- Bradley BJ, Chambers KE, Vigilant L. 2001. Accurate DNA-based sex identification of apes using non-invasive samples. *Conserv Genet* 2:179–181.
- Chakraborty R, Meagher T, Smouse P. 1988. Parentage analysis with genetic markers in natural populations. I. The expected proportion of offspring with unambiguous paternity. *Genetics* 118:527–536.
- Chapais B. 2001. Primate nepotism: what is the explanatory value of kin selection? *Int J Primatol* 22:203–229.
- Cheney DL, Seyfarth RM. 1977. Behavior of adult and immature male baboons during inter-group encounters. *Nature* 269:404–406.
- Cheney DL, Seyfarth RM. 1983. Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *Am Nat* 122:392–412.
- Chepko-Sade BD, Halpin ZT, editors. 1987. Mammalian dispersal patterns: the effects of social structure on population genetics. Chicago: University of Chicago Press.
- Chepko-Sade BD, Sade DS. 1979. Patterns of group splitting within matrilineal kinship groups: a study of social group structure in *Macaca mulatta* (Cercopithecidae, Primates). *Behav Ecol Sociobiol* 5:67–86.
- Chesser RK. 1991a. Gene diversity and female philopatry. *Genetics* 127:437–447.
- Chesser RK. 1991b. Influence of gene flow and breeding tactics on gene diversity within populations. *Genetics* 129:573–583.
- Cheverud JM, Buettner-Janusch J, Sade DS. 1978. Social group fission and the origin of intergroup genetic differentiation among the rhesus monkeys of Cayo Santiago. *Am J Phys Anthropol* 49:449–456.
- Chu J-H, Wu H-Y, Yang Y-J, Takenaka O, Lin Y-O. 1999. Polymorphic microsatellite loci and low-invasive DNA sampling in *Macaca cyclopis*. *Primates* 40:573–580.
- Clutton-Brock TH. 1998. Reproductive skew, concessions and limited control. *Trends Ecol Evol* 13:288–292.
- Cockerham CC, Weir BS. 1993. Estimation of gene flow from F-statistics. *Evolution* 47:855–863.
- Coltman DW, Bancroft DR, Robertson A, Smith JA, Clutton-Brock TH, Pemberton JM. 1998. Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Mol Ecol* 8:1199–1209.
- Constable JL, Ashley MV, Goodall J, Pusey AE. 2001. Noninvasive paternity assignment in Gombe chimpanzees. *Mol Ecol* 10:1279–1300.
- Cooper G, Rubinsztein DC, Amos W. 1998. Ascertainment bias cannot entirely account for human microsatellites being longer than their chimpanzee homologues. *Hum Mol Genet* 7:1425–1429.
- Cowlishaw G, Dunbar RIM. 1991. Dominance rank and mating success in male primates. *Anim Behav* 41:1045–1056.
- Crockett CM. 1984. Emigration by female red howler monkeys and the case for female competition. In: Small MF, editor. Female primates: studies by women primatologists. New York: Alan R. Liss. p 159–173.
- Crockett CM. 1996. The relation between red howler monkey (*Alouatta seniculus*) troop size and population growth in two habitats. In: Norconk MA, Rosenberger AL, Garber PA, editors. Adaptive radiations of neotropical primates. New York: Plenum. p 489–510.
- Crockett CM, Eisenberg JF. 1987. Howlers: variations in group size and demography. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 54–68.
- Crockett CM, Pope TR. 1993. Consequences of sex differences in dispersal for juvenile red howler monkeys. In: Pereira ME, Fairbanks LA, editors. Juvenile primates: life history, development, and behavior. New York: Oxford University Press. p 104–118.
- Crow JF, Kimura M. 1973. An introduction to population genetics theory. New York: Harper & Row.
- de Ruiter JR, Geffen E. 1998. Relatedness of matrilineal, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*). *Proc R Soc Lond [Biol]* 265:79–87.
- de Ruiter JR, van Hooff JARAM. 1993. Male dominance rank and reproductive success in primate groups. *Primates* 34:513–523.
- de Ruiter JR, Scheffrhan W, Trommelen GJJM, Uitterlinden AG, Martin RD. 1992. Male social rank and reproductive success in wild long-tailed macaques. In: Martin RD, Dixon AF, Wickings EJ, editors. Paternity in primates: genetic tests and theories. Basel: Karger. p 175–191.
- de Ruiter JR, van Hooff JARAM, Scheffrhan W. 1994. Social and genetic aspects of paternity in wild long-tailed macaques (*Macaca fascicularis*). *Behaviour* 129:203–223.
- Di Fiore A. 2002. Molecular perspectives on dispersal in lowland woolly monkeys (*Lagothrix lagotricha poeppigii*). *Am J Phys Anthropol [Suppl]* 34:63.
- Di Fiore A. 2003. Social and reproductive strategies of lowland woolly monkeys (*Lagothrix lagotricha*). *Am J Phys Anthropol [Suppl]* 36:89.
- Di Fiore A, Rendall D. 1994. Evolution of social organization: a reappraisal for primates by using phylogenetic methods. *Proc Natl Acad Sci USA* 91:9941–9945.
- Di Rienzo A, Peterson AC, Garza JC, Valdes AM, Slatkin M, Freimer NB. 1994. Mutational processes of simple-sequence repeat loci in human populations. *Proc Natl Acad Sci USA* 91:3166–3170.
- Digby LJ. 1999. Sexual behavior and extra-group copulations in a wild population of common marmosets (*Callithrix jacchus*). *Folia Primatol (Basel)* 70:136–145.
- Digby L, Ferrari S. 1994. Multiple breeding females in free-ranging groups of *Callithrix jacchus*. *Int J Primatol* 15:389–397.
- Dittus WPJ. 1975. Population dynamics of the toque macaque, *Macaca sinica*. In: Tuttle RH, editor. Sociobiology and psychology of primates. The Hague: Mouton. p 125–151.
- Dittus WPJ. 1988. Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. *Anim Behav* 36:1626–1645.
- Dixon A, Ross D, O'Malley SLC, Burke T. 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature* 371:698–700.
- Dixon AF, Bossi T, Wickings EJ. 1993. Male dominance and genetically determined reproductive success in the mandrill (*Mandrillus sphinx*). *Primates* 34:525–532.
- Domingo-Roura X, López-Giráldez T, Shinohara M, Takenaka O. 1997. Hypervariable microsatellite loci in the Japanese macaque (*Macaca fuscata*) conserved in related species. *Am J Primatol* 43:357–360.
- Drickhamer LC, Vessey SH. 1973. Group changing in free-ranging male rhesus monkeys. *Primates* 14:359–368.
- Duggleby CR. 1977. Blood group antigens and the population genetics of *Macaca mulatta* on Cayo Santiago. II. Effects of social group division. *Yrbk Phys Anthropol* 20:263–271.
- Dunbar RIM. 1988. Primate social systems. Ithaca, NY: Cornell University Press.

- Ebstein RP, Novick O, Umansky R, Priel B, Osher Y, Blaine D, Bennett ER, Nemanov L, Katz M, Belmaker RH. 1996. Dopamine D4 receptor (D4DR) exon III polymorphism associated with the human personality trait of novelty seeking. *Nat Genet* 12:78–80.
- Eisenberg JF, O'Connell MA, August PV. 1979. Density, productivity, and distribution of mammals in two Venezuelan habitats. In: Eisenberg JF, editor. *Vertebrate ecology in the northern neotropics*. Washington, DC: Smithsonian Institution Press. p 187–207.
- Ellsworth DL, Rittenhouse D, Honeycutt RL. 1993. Artifactual variation in randomly amplified polymorphic DNA banding patterns. *Biotechniques* 7:214–217.
- Ellsworth JA, Hoelzer GA. 1998. Characterization of microsatellite loci in a New World primate, the mantled howler monkey (*Alouatta palliata*). *Mol Ecol* 7:657–666.
- Emlen ST. 1995. An evolutionary theory of the family. *Proc Natl Acad Sci USA* 92:8092–8099.
- Emlen ST. 1997. Predicting family dynamics in social vertebrates. In: Krebs JR, Davies NB, editors. *Behavioural ecology: an evolutionary approach* (4th edition). Cambridge, MA: Blackwell Scientific Publications. p 228–253.
- Ensminger AL, Hoffman SMG. 2002. Sex identification assay useful in great apes is not diagnostic in a range of other primate species. *Am J Primatol* 56:129–134.
- Escobar-Parámo P. 2000. Microsatellite primers for the wild brown capuchin monkey, *Cebus apella*. *Mol Ecol* 9:107–118.
- Estoup A, Cornuet J-M. 1999. Mutation and migration in models of microsatellite evolution. In: Goldstein DB, Schlotterer C, editors. *Microsatellites: evolution and applications*. Oxford: Oxford University Press. p 49–65.
- Fairbanks LA. 2001. Individual differences in response to a stranger: social impulsivity as a dimension of temperament in vervet monkeys (*Chlorocebus aethiops sabeus*). *J Comp Psychol* 115:22–28.
- Fairbanks LA, Fontenot MB, Phillips-Conroy JE, Jolly CJ, Kaplan JR, Mann JJ. 1999. CSF monoamines, age, and impulsivity in wild grivet monkeys (*Cercopithecus aethiops aethiops*). *Brain Behav Evol* 53:305–312.
- Faulkes CG, Arruda MF, de Cruz MAOM. 2003. Matrilineal genetic structure within and among populations of the cooperatively breeding common marmoset, *Callithrix jacchus*. *Mol Ecol* 12:1101–1108.
- Fausser JL, Rabarivola C, Meier B, Hahn T, Rumpler Y. 2000. Genetic comparison between different populations of *Eulemur macaco flavifrons* in northwest Madagascar using RAPD markers. *Am J Primatol* 51:249–255.
- Favre L, Balloux F, Goudet J, Perrin N. 1997. Female-biased dispersal in the monogamous mammal *Crocidura russula*: evidence from field data and microsatellite patterns. *Proc R Soc Lond [Biol]* 264:127–132.
- Fedriani JM, Kohn MH. 2001. Genotyping faeces links individuals to their diet. *Ecol Lett* 4:477–483.
- Feldman MW, Kumm J, Pritchard J. 1999. Mutation and migration in models of microsatellite evolution. In: Goldstein DB, Schlotterer C, editors. *Microsatellites: evolution and applications*. Oxford: Oxford University Press. p 98–115.
- Ferrari S, Digby L. 1996. Wild *Callithrix* groups: stable extended families? *Am J Primatol* 38:19–27.
- Ferraris JD, Palumbi SR, editors. 1996. *Molecular zoology: advances, strategies, and protocols*. New York: Wiley-Liss, Inc.
- Fietz J, Zischler H, Schwegk C, Tomiuk J, Dausmann KH, Ganzhorn J. 2000. High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. *Behav Ecol Sociobiol* 49:8–17.
- Flint J. 2002. Animal models of personality. In: Benjamin J, Ebstein RP, Belmaker RH, editors. *Molecular genetics and the human personality*. Washington, DC: American Psychiatric Publishing, Inc. p 63–90.
- French JA. 1997. Proximate regulation of singular breeding in callitrichid primates. In: Solomon NG, French JA, editors. *Cooperative breeding in mammals*. Cambridge: Cambridge University Press. p 34–75.
- Furuya Y. 1968. On the fission of troops of Japanese monkeys. *Primates* 9:323–349.
- Furuya Y. 1969. On the fission of troops of Japanese monkeys (part II). *Primates* 10:47–60.
- Gagneux P, Woodruff DS, Boesch C. 1997a. Microsatellite scoring errors associated with noninvasive genotyping based on nuclear DNA amplified from shed hair. *Mol Ecol* 6:861–868.
- Gagneux P, Woodruff DS, Boesch C. 1997b. Furtive mating by female chimpanzees. *Nature* 387:327–328.
- Gagneux P, Boesch C, Woodruff DS. 1999. Female reproductive strategies, paternity and community structure in wild West African chimpanzees. *Anim Behav* 57:19–32.
- Gagneux P, Gonder MK, Goldberg TL, Morin PA. 2001. Gene flow in wild chimpanzee populations: what genetic data tell us about chimpanzee movement over space and time. *Philos Trans R Soc Lond [Biol]* 356:889–897.
- Gerald MS, Higley S, Lussier ID, Westergaard GC, Suomi SJ, Higley DG. 2002. Variation in reproductive outcomes for captive male rhesus macaques (*Macaca mulatta*) differing in CSF 5-hydroxyindoleacetic acid concentrations. *Brain Behav Evol* 60:117–124.
- Gerloff U, Hartung B, Fruth B, Hohmann G, Tautz D. 1999. Intra-community relationships, dispersal pattern, and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proc R Soc Lond [Biol]* 266:1189–1195.
- Girman DJ, Mills MGL, Geffen E, Wayne RK. 1997. A molecular genetic analysis of social structure, dispersal, and interpack relationships of the African wild dog (*Lycan pictus*). *Behav Ecol Sociobiol* 40:187–198.
- Glanz WE. 1990. Neotropical mammal densities: how unusual is the community on Barro Colorado Island, Panama? In: Gentry AH, editor. *Four neotropical rainforests*. New Haven: Yale University Press. p 287–313.
- Goldberg TL, Ruvolo M. 1997. The geographic apportionment of mitochondrial genetic diversity in east African chimpanzees, *Pan troglodytes schweinfurthii*. *Mol Biol Evol* 14:976–984.
- Goldberg TL, Wrangham RW. 1997. Genetic correlates of social behaviour in wild chimpanzees: evidence from mitochondrial DNA. *Anim Behav* 54:559–570.
- Goldizen AW. 1987. Tamarins and marmosets: communal care of offspring. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 69–82.
- Goldizen AW, Mendelson J, Terborgh J. 1996. Saddle-back tamarin (*Saguinus fuscicollis*) reproductive strategies: evidence from a thirteen-year study of a marked population. *Am J Primatol* 38:57–84.
- Goldman D, Mazzanti C. 2002. From phenotype to gene and back. In: Benjamin J, Ebstein RP, Belmaker RH, editors. *Molecular genetics and the human personality*. Washington, DC: American Psychiatric Publishing, Inc. p 273–291.
- Goldstein DB, Ruiz Linares A, Cavalli-Sforza LL, Feldman MA. 1995. An evaluation of genetic distances for use with microsatellite loci. *Genetics* 139:463–471.
- Goodall J. 1986. *The chimpanzees of Gombe: patterns of behavior*. Cambridge, MA: Belknap Press.
- Goodall J, Bandora A, Bergmann E, Busse C, Matama H, Mpongo E, Pierce A, Riss D. 1979. Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: Hamburg D, McCown E, editors. *The great apes*. Menlo Park: Benjamin/Cummings. p 13–54.
- Goodman SJ. 1997. R_{ST} CALC: a collection of computer programs for calculating unbiased estimates of genetic differentiation and gene flow from microsatellite data and determining their significance. *Mol Ecol* 6:881–886.
- Goodnight KF, Queller DC. 1999. Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Mol Ecol* 8:1231–1234.
- Goossens B, Graziani L, Waits LP, Farand E, Magnolon S, Coulon J, Bel M-C, Taberlet P, Allainé D. 1998. Extra-pair paternity in the monogamous alpine marmot revealed by nuclear DNA microsatellite analysis. *Behav Ecol Sociobiol* 43:281–288.

- Goudet J. 1995. FSTAT (version 1.2): a computer program to calculate F-statistics. *J Hered* 86:485–486.
- Gouzoules H, Gouzoules S. 1987. Kinship. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struthsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 299–305.
- Grativol AD, Ballou JD, Fleischer RC. 2001. Microsatellite variation within and among recently fragmented populations of the golden lion tamarin (*Leontopithecus rosalia*). *Conserv Genet* 2:1–9.
- Graur D, Li W-H. 2000. Fundamentals of molecular evolution (2nd edition). Sunderland, MA: Sinauer Associates, Inc.
- Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162.
- Gust DA, McCaster T, Gordon TP, Gergits WF, Casna NJ, McClure HM. 1998. Paternity in sooty manglebeys. *Int J Primatol* 19:83–94.
- Hall KRL, DeVore I. 1965. Baboon social behavior. In: DeVore I, editor. Primate behavior: field studies of monkeys and apes. New York: Holt, Rinehart and Winston. p 53–110.
- Hamilton MB, Pincus EL, Di Fiore A, Fleischer RC. 1999. Universal linker and ligation procedures for construction of genomic DNA libraries enriched for microsatellites. *Biotechniques* 27:500–507.
- Hamilton WD. 1964a. The genetical evolution of social behavior I. *J Theol Biol* 7:1–16.
- Hamilton WD. 1964b. The genetical evolution of social behavior II. *J Theol Biol* 7:17–52.
- Hammer M. 1995. A recent common ancestry for human Y chromosomes. *Nature* 378:376–378.
- Hammer MF, Karafet T, Rasanayagam A, Wood ET, Altheide TK, Jenkins T, Griffiths RC, Templeton AR, Zegura SL. 1998. Out of Africa and back again: nested cladistic analysis of human Y chromosome variation. *Mol Biol Evol* 15:427–441.
- Hammond RL, Saccheria LJ, Ciofi C, Coote T, Funk SM, McMillan WO, Bayes MK, Taylor E, Bruford MW. 1998. Isolation of microsatellite markers in animals. In: Karp A, Isaac PG, Ingram DS, editors. Molecular tools for screening biodiversity: plants and animals. London: Chapman & Hall. p 279–285.
- Hapke A, Zinner D, Zischler H. 2001. Mitochondrial DNA variation in Eritrean hamadryas baboons (*Papio hamadryas hamadryas*): life history influences population genetic structure. *Behav Ecol Sociobiol* 50:483–492.
- Hartl DL, Clark AG. 1997. Principles of population genetics (3rd edition). Sunderland, MA: Sinauer Associates, Inc.
- Heils A, Teufel A, Petri S, Stöber G, Riederer P, Bengel D, Lesch K-P. 1996. Allelic variation of human serotonin transporter gene expression. *J Neurochem* 66:2621–2624.
- Hillis DM, Moritz C, Mable BK, editors. 1996 Molecular systematics. Sunderland, MA: Sinauer Associates, Inc.
- Hoelzer GA, Dittus WPJ, Ashley MV, Melnick DJ. 1994. The local distribution of highly divergent mitochondrial DNA haplotypes in toque macaques *Macaca sinica* at Polonnaruwa, Sri Lanka. *Mol Ecol* 3:451–458.
- Hohmann G, Gerloff U, Tautz D, Fruth B. 1999. Social bonds and genetic ties: kinship, association, and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour* 136:1219–1235.
- Howe HF. 1980. Monkey dispersal and waste of a neotropical fruit. *Ecology* 61:944–959.
- Howe HF, Smallwood J. 1982. Ecology of seed dispersal. *Annu Rev Ecol Syst* 3:201–228.
- Howe HF, Schupp EW, Westley LC. 1985. Early consequences of seed dispersal for a neotropical tree (*Viola surinamensis*). *Ecology* 66:781–791.
- Hrdy SB. 1974. Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol (Basel)* 22:19–58.
- Hrdy SB. 1977. Infanticide as a primate reproductive strategy. *Am Sci* 65:40–49.
- Hrdy SB. 1979. Infanticide among animals: a review, classification and examination of the implications for the reproductive strategies of females. *Ethol Sociobiol* 1:1–13.
- Hrdy SB, Hausfater B. 1984. Comparative and evolutionary perspectives on infanticide: introduction and overview. In: Hausfater G, Hrdy SB, editors. Infanticide: comparative and evolutionary perspectives. New York: Aldine. p. xiii–xxxv.
- Hurles ME, Jobling MA. 2001. Haploid chromosomes in molecular ecology: lessons from the human Y. *Mol Ecol* 10:1599–1613.
- Idani G. 1991. Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia Primatol (Basel)* 57:83–95.
- Inoue M. 1995. Application of paternity discrimination by DNA polymorphism to the analysis of social behavior in primates. *Hum Evol* 10:53–62.
- Inoue M, Takenaka O. 1993. Japanese macaque microsatellite PCR primers for paternity testing. *Primates* 34:37–45.
- Inoue M, Mitsunaga F, Ohsawa N, Takenaka A, Sugiyama Y, Soumah AG, Takenaka O. 1991. Male mating behavior and paternity discrimination by DNA fingerprinting in a Japanese macaque group. *Folia Primatol (Basel)* 56:202–210.
- International Human Genome Sequencing Consortium. 2001. Initial sequencing and analysis of the human genome. *Nature* 409:860–921.
- Jeffreys AJ, Wilson V, Thein SL. 1985a. Hypervariable “minisatellite” regions in human DNA. *Nature* 314:67–73.
- Jeffreys AJ, Wilson V, Thein SL. 1985b. Individual-specific “fingerprints” of human DNA. *Nature* 316:76–79.
- Jekielek J, Strobeck C. 1999. Characterization of polymorphic brown lemur (*Eulemur fulvus*) microsatellite loci and their amplification in the family Lemuridae. *Mol Ecol* 8:895–906.
- Johnson ML, Gaines MS. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annu Rev Ecol Syst* 21:449–480.
- Jordano P. 1995. Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *Am Nat* 145:163–191.
- Kaplan JR, Fontenot MB, Berard J, Manuck SB, Mann JJ. 1995. Delayed dispersal and elevated monoamine activity in free-ranging rhesus monkeys. *Am J Primatol* 35:229–234.
- Kappeler PM. 1997. Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. *Biol Rev Camb Philos Soc* 72:111–151.
- Kappeler PM, van Schaik CP. 2002. Evolution of primate social systems. *Int J Primatol* 23:707–740.
- Kappeler PM, Wimmer B, Zinner D, Tautz D. 2002. The hidden matrilineal structure of a solitary lemur: implications for primate social evolution. *Proc R Soc Lond [Biol]* 269:1755–1763.
- Karesh WB, Smith F, Frazier-Taylor H. 1987. A remote method for obtaining skin biopsy samples. *Conserv Biol* 1:261–262.
- Keane B, Dittus WPJ, Melnick DJ. 1997. Paternity assessment in wild groups of toque macaques *Macaca sinica* at Polonnaruwa, Sri Lanka using molecular markers. *Mol Ecol* 6:267–282.
- Keller L, Reeve HK. 1994. Partitioning reproduction in animal societies. *Trends Ecol Evol* 9:98–102.
- Kempnaers B, Verheyen GR, van den Broeck M, Burke T, van Broeckhoven C, Dhondt AA. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature* 357:494–496.
- Kimura M, Crow JF. 1964. The number of alleles that can be maintained in a finite population. *Genetics* 49:725–738.
- Kimura M, Ohta T. 1978. Stepwise mutation model and distribution of allele frequencies in a finite population. *Proc Natl Acad Sci USA* 75:2868–2872.
- Kimura M, Weiss GH. 1964. The stepping stone model of population structure and decrease of genetic correlation with distance. *Genetics* 49:561–576.
- Koenig A. 1995. Group size, composition, and reproductive success in wild common marmosets (*Callithrix jacchus*). *Am J Primatol* 35:31–317.
- Koenig A, Borries C, Chalise MK, Winkler P. 1997. Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *J Zool Lond* 243:215–235.
- Kohn MH, York EC, Kamradt DA, Haught G, Sauvajot RM, Wayne RK. 1999. Estimating population size by genotyping faeces. *Proc R Soc Lond [Biol]* 266:657–663.
- Kruglyak S, Durrett RT, Schug MD, Aquadro CF. 1998. Equilibrium distribution of microsatellite repeat length resulting from

- a balance between slippage events and point mutations. *Proc Natl Acad Sci USA* 95:10774–10778.
- Kummer H. 1968. Social organization of hamadryas baboons. Chicago: University of Chicago Press.
- Lan H, Zhang W-Y, Wang W, Su B, Shi L-M. 1995. Genetic diversity in the snub-nosed monkey (*Rhinopithecus bieti*) based on random amplified polymorphic DNA. *Folia Primatol (Basel)* 65:154–158.
- Launhardt K, Borries C, Hardt C, Epplen JT, Winkler P. 2001. Paternity analysis of alternative male reproductive routes among the langurs (*Semnopithecus entellus*) of Ramnagar. *Anim Behav* 61:53–64.
- Lawler RR, Richard AF, Riley MA. 2001a. Characterization and screening of microsatellite loci in a wild lemur population (*Propithecus verreauxi verreauxi*). *Am J Primatol* 55:253–259.
- Lawler RR, Richard AF, Riley MA. 2001b. Genetic and demographic structure in a population of white sifaka (*Propithecus verreauxi verreauxi*). *Am J Phys Anthropol [Suppl]* 32:96.
- Lawler RR, Richard AF, Riley MA. 2003. Genetic population structure of the white sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, southwest Madagascar (1992–2001). *Mol Ecol* 12:2307–2317.
- Lesch KP, Merschedorf U. 2000. Impulsivity, aggression, and serotonin: a molecular psychobiological perspective. *Behav Sci Law* 18:581–604.
- Lesch K-P, Bengel D, Heils A, Sabol SZ, Greenberg BD, Petri S, Benjamin J, Muller CR, Hamer DH, Murphy DL. 1996. Association of anxiety-related traits with a polymorphism in the serotonin transporter gene regulatory region. *Science* 274:1527–1531.
- Lesch KP, Meyer J, Glatz K, Flugge G, Hinney A, Hebebrand J, Klauck S, Poustka F, Bengel D, Mössner R, Riederer P, Heils A. 1997. The 5-HT transporter gene-linked polymorphic region (5-HTTLPR) in evolutionary perspective: alternative biallelic variation in rhesus monkeys. *J Neural Transm* 104:1259–1266.
- Levinson G, Gutman GA. 1987. Slipped-strand mispairing: a major mechanism for DNA sequence evolution. *Mol Biol Evol* 4:203–221.
- Li CC, Weeks DE, Chakravarti A. 1993. Similarity of DNA fingerprints due to chance and relatedness. *Hum Hered* 43:45–52.
- Ling B, Santiago ML, Meleth S, Gormus B, McClure HM, Apetrei C, Hahn BH, Marx PA. 2003. Noninvasive detection of new simian immunodeficiency virus lineages in captive sooty mangabeys: ability to amplify virion RNA from fecal samples correlates with viral load in plasma. *J Virol* 77:2214–2226.
- Loeschcke V, Tomiuk J, Jain SK, editors. 1994. Conservation genetics. Basel: Birkhäuser Verlag.
- Lopez JV, Yuhki N, Masuda R, Modi W, O'Brien SJ. 1994. Numt, a recent transfer and tandem amplification of mitochondrial DNA to the nuclear genome of the domestic cat. *J Mol Evol* 39:174–191.
- Lynch M. 1988. Estimation of relatedness by DNA fingerprinting. *Mol Biol Evol* 5:584–599.
- Lynch M. 1990. The similarity index and DNA fingerprinting. *Mol Biol Evol* 7:478–484.
- Lynch M, Ritland K. 1999. Estimation of pairwise relatedness with molecular markers. *Genetics* 152:1753–1766.
- Manson JH. 1995. Do female rhesus macaques choose novel mates? *Am J Primatol* 37:285–296.
- Marshall TC, Slate J, Kruuk LEB, Pemberton JM. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Mol Ecol* 7:639–655.
- Martin RD. 1972. A preliminary field-study of the lesser mouse lemur (*Microcebus murinus* J F Miller, 1777). *Z Tierpsychol* 9:43–89.
- Martin RD. 1973. A review of the behaviour and ecology of the lesser mouse lemur (*Microcebus murinus* J F Miller 1777). In: Michael RP, Crook JH, editors. Comparative ecology and behaviour of primates. London: Academic Press. p 1–68.
- Mayor MI, Sommer JA, Huebinger RM, Barber RC, Louis Jr. EE. 2002. Characterization of seven microsatellite marker loci in a genus of Malagasy lemurs (*Propithecus*). *Mol Ecol Notes* 2:385–388.
- Mehlman P, Higley JD, Faucher I, Lilly AA, Taub DM, Vickers JH, Suomi S, Linnoila M. 1995. Correlation of CSF 5-HIAA concentration with sociality and the timing of emigration in free-ranging primates. *Am J Psychiatry* 152:907–913.
- Meikle DB, Vessey SH. 1981. Nepotism among rhesus monkey brothers. *Nature* 294:160–161.
- Melnick DJ. 1987. The genetic consequences of primate social organization: a review of macaques, baboons, and vervet monkeys. *Genetica* 73:117–135.
- Melnick DJ. 1988. Genetic structure of a primate species: rhesus macaques and other cercopithecine monkeys. *Int J Primatol* 9:195–231.
- Melnick DJ, Hoelzer GA. 1992. Differences in male and female macaque dispersal lead to contrasting distributions of nuclear and mitochondrial DNA variation. *Int J Primatol* 13:379–393.
- Melnick DJ, Hoelzer GA. 1993. What is mtDNA good for in the study of primate evolution? *Evol Anthropol* 2:2–10.
- Melnick DJ, Hoelzer GA. 1996. The population genetic consequences of macaque social organization and behaviour. In: Fa JE, Lindburg DG, editors. Evolution and ecology of macaque societies. Cambridge: Cambridge University Press. p 413–443.
- Melnick DJ, Kidd KK. 1983. The genetic consequences of social group fission in a wild population of rhesus monkeys (*Macaca mulatta*). *Behav Ecol Sociobiol* 12:229–236.
- Melnick DJ, Pearl MC. 1987. Cercopithecines in multi-male groups: genetic diversity and population structure. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 121–134.
- Melnick DJ, Hoelzer GA, Honeycutt RL. 1992. Mitochondrial DNA: its uses in anthropological research. In: Dover EJ, editor. Molecular applications in biological anthropology. Cambridge: Cambridge University Press. p 179–233.
- Ménard N, Scheffrahn W, Vallet D, Zidane C, Reber C. 1992. Application of blood protein electrophoresis and DNA fingerprinting to the analysis of paternity and social characteristics of wild Barbary macaques. In: Martin RD, Dixon AF, Wickings EJ, editors. Paternity in primates: genetic tests and theories. Basel: Karger. p 155–174.
- Ménard N, van Segesser F, Scheffrahn W, Pastorini J, Valleta D, Gaci B, Martin RD, Gautier-Hion A. 2001. Is male-infant caretaking related to paternity and/or mating activities in wild Barbary macaques (*Macaca sylvanus*)? *C R Acad Sci [III]* 324: 601–610.
- Meunier J-R, Grimont PAD. 1993. Factors affecting reproducibility of random amplified polymorphic DNA fingerprinting. *Res Microbiol* 144:373–379.
- Michalakis Y, Excoffier L. 1996. A generic estimation of population subdivision using distances between alleles with a special reference for microsatellite loci. *Genetics* 142:1061–1064.
- Minch E. 1996. MICROSAT (v. 1.5). Stanford, CA: Stanford University Medical Center.
- Mindell DP, Thacker CE. 1996. Rates of molecular evolution: phylogenetic issues and applications. *Annu Rev Ecol Syst* 27: 279–303.
- Mitani J. 1985. Mating behavior of male orangutans in the Kutai Reserve, East Kalimantan, Indonesia. *Anim Behav* 33:392–403.
- Mitani JC, Watts DP. 1999. Demographic influences on the hunting behavior of chimpanzees. *Am J Phys Anthropol* 109:439–454.
- Mitani JC, Merriwether A, Zhang C. 2000. Male affiliation, cooperation and kinship in wild chimpanzees. *Anim Behav* 59:885–893.
- Moore J. 1984. Female transfer in primates. *Int J Primatol* 5:537–589.
- Moore SS, Sargeant LL, King TJ, Mattick JS, Georges M, Hetzel DJS. 1991. The conservation of dinucleotide microsatellites among mammalian genomes allows the use of heterologous PCR primer pairs in closely related species. *Genomics* 10:654–660.
- Morin PA, Woodruff DS. 1992. Paternity exclusion using multiple hypervariable microsatellite loci amplified from nuclear DNA of hair cells. In: Martin RD, Dixon AF, Wickings EJ, editors.

- Paternity in primates: genetic tests and theories. Basel: Karger. p 63–81.
- Morin PA, Wallis J, Moore JJ, Chakaborty R, Woodruff DS. 1993. Non-invasive sampling and DNA amplification for paternity exclusion, community structure, and phylogeography in wild chimpanzees. *Primates* 34:347–356.
- Morin PA, Moore JJ, Chakaborty R, Jin L, Goodall J, Woodruff DS. 1994a. Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science* 265:1193–1201.
- Morin PA, Wallis J, Moore JJ, Woodruff DS. 1994b. Paternity exclusion in a community of wild chimpanzees using hypervariable simple sequence repeats. *Mol Ecol* 3:469–478.
- Morin PA, Chambers KE, Boesch C, Vigilant L. 2001. Quantitative polymerase chain reaction analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes*). *Mol Ecol* 10:1835–1844.
- Moritz C, Dowling TE, Brown WM. 1987. Evolution of animal mitochondrial DNA: relevance for population biology and systematics. *Annu Rev Ecol Syst* 18:269–292.
- Mossman CA, Waser PM. 1999. Genetic detection of sex-biased dispersal. *Mol Ecol* 8:1063–1067.
- Müller AE, Thalmann U. 2000. Origin and evolution of primate social organisation: a reconstruction. *Biol Rev Camb Philos Soc* 75:405–435.
- Mullis K, Faloona F. 1987. Specific synthesis of DNA in vitro via a polymerase catalyzed chain reaction. *Methods Enzymol* 155:335–350.
- Nash LT. 1976. Troop fission in free-ranging baboons in the Gombe Stream National Park, Tanzania. *Am J Phys Anthropol* 48:63–77.
- Nei M. 1973. Analysis of gene diversity in subdivided populations. *Proc Natl Acad Sci USA* 70:3321–3323.
- Neveu H, Montagnon D, Rumpler Y. 1996. Paternity discrimination in four prosimian species by the random amplified polymorphic DNA method. *Folia Primatol (Basel)* 67:157–162.
- Neveu H, Hafen T, Zimmermann E, Rumpler Y. 1998. Comparison of the genetic diversity of wild and captive groups of *Microcebus murinus* using the random amplified polymorphic DNA method. *Folia Primatol (Basel)* 69:127–135.
- Neveu H, Petit M, Roeder JJ. 1999. Paternity discrimination in two groups of *Eulemur fulvus mayottensis*: implications for understanding mating strategies. *Int J Primatol* 20:107–119.
- Nievergelt CM, Mundy NI, Woodruff DS. 1998. Microsatellite primers for genotyping common marmosets (*Callithrix jacchus*) and other callitrichids. *Mol Ecol* 7:1431–1439.
- Nievergelt CM, Digby LJ, Ramakrishnan U, Woodruff DS. 2000. Genetic analysis of group composition and breeding system in a wild common marmoset (*Callithrix jacchus*) population. *Int J Primatol* 21:1–20.
- Nievergelt CM, Mutschler T, Feistner ATC, Woodruff DS. 2002. Social system of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*): genetic characterization of group composition and mating system. *Am J Primatol* 57:157–176.
- Nishida T, editor. 1990. The chimpanzees of the Mahale Mountains. Tokyo: Tokyo University Press.
- Nishida T, Hiraiwa-Hasegawa M, Hasegawa T, Takahata Y. 1985. Group extinction and female transfer in wild chimpanzees in the Mahale Mountains National Park, Tanzania. *Z Tierpsychol* 67:281–301.
- Nishimura A. 1990. Mating behavior of woolly monkeys (*Lagothrix lagotricha*) at La Macarena, Colombia (II): mating relationships. *Field Stud New World Monkeys Macarena Colombia* 3:7–12.
- Ohsawa H, Inoue M, Takenaka O. 1993. Mating strategy and reproductive success of male pata monkeys (*Erythrocebus patas*). *Primates* 34:533–544.
- Oka T, Takenaka O. 2001. Wild gibbons' parentage tested by non-invasive DNA sampling and PCR-amplified polymorphic microsatellites. *Primates* 42:67–73.
- Ostner J, Kappeler PM. 1999. Central males instead of multiple pairs in redfronted lemurs, *Eulemur fulvus rufus* (Primates: Lemuridae)? *Anim Behav* 58:1069–1078.
- Overdorff DJ, Merenlender A, Talata P, Telo A, Forward Z. 1999. Life history of *Eulemur fulvus rufus* from 1988–1998 in south-eastern Madagascar. *Am J Phys Anthropol* 105:153–166.
- Paetkau D. 1999. Microsatellites obtained using strand extension: an enrichment protocol. *Biotechniques* 26:690–697.
- Paetkau D, Calvert W, Stirling I, Strobeck C. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Mol Ecol* 4:347–354.
- Paetkau D, Waits LP, Clarkson PI, Craighead L, Strobeck C. 1997. An empirical evaluation of genetic distance statistics using microsatellite data from bear (Ursidae). *Genetics* 147:1943–1957.
- Pamilo P, Crozier RH. 1982. Measuring genetic relatedness in natural populations: methodology. *Theor Popul Biol* 21:171–193.
- Paul A, Kuester J, Timme A, Arnemann J. 1993. The association between rank, mating effort, and reproductive success in male Barbary macaques (*Macaca sylvanus*). *Primates* 34:491–502.
- Pemberton JM, Slate J, Bancroft DR, Barrett JA. 1995. Nonamplifying alleles at microsatellite loci: a caution for parentage and population studies. *Mol Ecol* 4:249–252.
- Pereira ME, Weiss ML. 1991. Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behav Ecol Sociobiol* 28:141–152.
- Pérez T, Alborozoj J, Domínguez A. 1998. An evaluation of RAPD fragment reproducibility and nature. *Mol Ecol* 7:1347–1357.
- Perwitasari-Farajallah D, Kawamoto Y, Suryabroto B. 1999. Variation in blood proteins and mitochondrial DNA within and between local populations of longtail macaques, *Macaca fascicularis* on the island of Java, Indonesia. *Primates* 40:581–595.
- Plomin R, DeFries JC, McClearn GE, McGuffin P. 2001. Behavioral genetics (4th edition). New York: Worth Publishers.
- Pope TR. 1990. The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. *Behav Ecol Sociobiol* 27:439–446.
- Pope TR. 2000. Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behav Ecol Sociobiol* 48:253–267.
- Pusey AE, Packer C. 1987. Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 250–266.
- Queller DC, Goodnight KF. 1989. Estimating relatedness using genetic markers. *Evolution* 43:258–275.
- Rabinow P. 1996. Making PCR: a story of biotechnology. Chicago: University of Chicago Press.
- Radespiel U. 2000. Sociality in the grey mouse lemur (*Microcebus murinus*) in northwestern Madagascar. *Am J Primatol* 46:77–84.
- Radespiel U, Funk SM, Zimmermann E, Bruford MW. 2001. Isolation and characterization of microsatellite loci in the grey mouse lemur (*Microcebus murinus*) and their amplification in the family Cheirogaleidae. *Mol Ecol* 1:16–18.
- Radespiel U, dal Secco V, Drögemüller C, Braune P, Labes E, Zimmermann E. 2002. Sexual selection, multiple mating and paternity in grey mouse lemurs, *Microcebus murinus*. *Behaviour* 63:259–268.
- Rannala B, Mountain JL. 1997. Detecting immigration by using multilocus genotypes. *Proc Natl Acad Sci USA* 94:9197–9201.
- Ravaoarimanana B, Fausser JL, Rumpler Y. 2001. Genetic comparison of wild populations of *Lepilemur septentrionalis* and *Lepilemur dorsalis* using RAPD markers. *Primates* 42:221–231.
- Raymond M, Rousset M. 1995. GENEPOP (version 1.2), a population genetics software for exact tests and ecumenicism. *J Hered* 86:248–249.
- Reichard U. 1995. Extra-pair copulations in a monogamous gibbon (*Hylobates lar*). *Ethology* 100:99–112.
- Richard AF. 1987. Malagasy prosimians: female dominance. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 25–33.

- Riedy MF, Hamilton WJ III, Aquadro CF. 1992. Excess of non-parental bands in offspring from known primate pedigrees assayed using RAPD PCR. *Nucleic Acids Res* 20:918.
- Rosenberger AL, Strier KB. 1989. Adaptive radiation of the ateline primates. *J Hum Evol* 18:717–750.
- Rosenblum LL, Supriatna J, Melnick DJ. 1997a. Phylogeographic analysis of pigtail macaque populations (*Macaca nemestrina*) inferred from mitochondrial DNA. *Am J Phys Anthropol* 104:35–45.
- Rosenblum LL, Supriatna J, Hasan MN, Melnick DJ. 1997b. High mitochondrial DNA diversity with little structure within and among leaf monkey populations (*Trachypithecus cristatus* and *Trachypithecus auratus*). *Int J Primatol* 18:1005–1028.
- Ross KG. 2001. Molecular ecology of social behaviour: analyses of breeding systems and genetic structure. *Mol Ecol* 10:265–284.
- Rousset F. 1996. Equilibrium values of measures of population subdivision for stepwise mutation processes. *Genetics* 142:1356–1362.
- Sade DS. 1967. Determinants of dominance in a group of free-ranging rhesus monkeys. In: Altmann SA, editor. *Social communication among primates*. Chicago: University of Chicago Press. p 99–114.
- Sanger F, Nicklen S, Coulson AR. 1977. DNA sequencing with chain-terminating inhibitors. *Proc Natl Acad Sci USA* 74:5463–5467.
- Santiago ML, Bibollet-Ruche F, Bailes E, Kamenya S, Muller MN, Lukasik M, Pusey AE, Collins DA, Wrangham RW, Goodall J, Shaw GM, Sharp PM, Hahn BH. 2003. Amplification of a complete simian immunodeficiency virus genome from fecal RNA of a wild chimpanzee. *J Virol* 77:2233–2242.
- Schneider S, Roessli D, Excoffier L. 2000. Arlequin: a software for population genetics data analysis (version 2.000). Geneva: Genetics and Biometry Laboratory, Department of Anthropology, University of Geneva.
- Schweder MEE, Shatters RGJ, West SH, Smith RL. 1995. Effect of transition interval between melting and annealing temperatures on RAPD analyses. *Biotechniques* 7:40–42.
- Seielstad MT, Minch E, Cavalli-Sforza LL. 1998. Genetic evidence for a higher female migration rate in humans. *Nat Genet* 20:278–280.
- Shen P, Wang F, Underhill PA, Franco C, Yang W-H, Roxas A, Sung R, Lin AA, Hyman RW, Vollrath D, Davis RW, Cavalli-Sforza LL, Oefner PJ. 2000. Population genetic implications from sequence variation in four Y chromosome genes. *Proc Natl Acad Sci USA* 97:7354–7359.
- Shimada MK. 2000. Geographic distribution of mitochondrial DNA variations among grivet (*Cercopithecus aethiops aethiops*) populations in central Ethiopia. *Int J Primatol* 21:113–129.
- Shriver MD, Jin L, Boerwinkle E, Deka R, Ferrell RE, Chak-aborty R. 1995. A novel measure of genetic distance for highly polymorphic tandem repeat loci. *Mol Biol Evol* 12:457–462.
- Silk JB. 1987. Social behavior in evolutionary perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 318–329.
- Silk JB. 2002. Kin selection in primate groups. *Int J Primatol* 23:849–875.
- Slatkin M. 1985. Gene flow in natural populations. *Annu Rev Ecol Syst* 16:393–430.
- Slatkin M. 1995. A measure of population subdivision based on microsatellite allele frequencies. *Genetics* 139:457–462.
- Smith DG. 1994. Male dominance and reproductive success in a captive group of rhesus macaques (*Macaca mulatta*). *Behaviour* 129:225–242.
- Smith DG, Kanthaswamy S, Disbrow M, Wagner JL. 1999. Reconstruction of parentage in a band of captive hamadryas baboons. *Int J Primatol* 20:415–429.
- Smith TB, Wayne RK, editors. 1996 *Molecular genetic approaches in conservation*. New York: Oxford University Press.
- Smuts BB. 1985. Sex and friendship in baboons. New York: Aldine de Gruyter.
- Smuts B, Gubernick DJ. 1992. Male-infant relationships in non-human primates: paternal investment or mating effort? In: Hewlett BS, editor. *Father-child relations: cultural and biosocial context*. Hawthorne: Aldine Publishing Co.
- Soltis J, Thomsen R, Matsubayashi K, Takenaka O. 2000. Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behav Ecol Sociobiol* 48:195–202.
- Sommer JA, Barber RC, Huebinger RM, Grassi C, Williamson JE, Louis EE Jr. 2002. Characterization of 14 microsatellite marker loci in the grey bamboo lemur (*Haplemur griseus*). *Mol Ecol Notes* 2:161–163.
- Southern EM. 1975. Detection of specific sequences among DNA fragments separated by gel electrophoresis. *J Mol Biol* 98:503–517.
- Southwick CH, Beg MA, Siddiqi MR. 1965. Rhesus monkeys in north India. In: DeVore I, editor. *Primate behavior: field studies of monkeys and apes*. New York: Holt, Rinehart and Winston. p 115–159.
- Stammach E. 1987. Desert, forest, and montane baboons: multilevel societies. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 112–120.
- Stanford CB. 1998. Chimpanzee and red colobus: the ecology of predator and prey. Cambridge, MA: Harvard University Press.
- Stanford CB, Wallis J, Mpongo E, Goodall J. 1994. Hunting decisions in wild chimpanzees. *Behaviour* 131:1–18.
- Stevenson PR, Quiñones MJ, Ahumada JA. 1994. Ecological strategies of woolly monkeys (*Lagothrix lagotricha*) at Tinigua National Park, Colombia. *Am J Primatol* 32:123–140.
- Storz JF. 1999. Genetic consequences of mammalian social structure. *J Mammal* 80:553–569.
- Strassmann JE, Solís CR, Peters JM, Queller DC. 1996. Strategies for finding and using highly polymorphic DNA microsatellite loci for studies of genetic relatedness and pedigrees. In: Ferraris JD, Palumbi SR, editors. *Molecular zoology: advances, strategies, and protocols*. New York: Wiley-Liss, Inc. p 163–180.
- Strier KB. 1994. The myth of the typical primate. *Yrbk Phys Anthropol* 37:233–271.
- Struhsaker TT. 1967. Social structure among vervet monkeys (*Cercopithecus aethiops*). *Behaviour* 29:83–121.
- Sugg DW, Chesser RK, Dobson FS, Hoogland JL. 1996. Population genetics meets behavioral ecology. *Trends Ecol Evol* 11:338–342.
- Sugiyama Y. 1976. Life history of male Japanese monkeys. *Adv Stud Behav* 7:255–284.
- Sugiyama Y, Kawamoto S, Takenaka O, Kumazaki K, Miwa N. 1993. Paternity discrimination and inter-group relationships of chimpanzees at Bossou. *Primates* 34:545–552.
- Sullivan K, Walton A, Kimpton C, Tully G, Gill P. 1993. A rapid and quantitative DNA sex test: fluorescence-based PCR analysis of X-Y homologous gene amelogenin. *Biotechniques* 15:637–641.
- Sussman RW, Garber PA. 1987. A new interpretation of the social organization and mating system of the Callitrichidae. *Int J Primatol* 8:73–92.
- Swedell L. 2000. Social behavior and reproductive strategies of female hamadryas baboons, *Papio hamadryas hamadryas*, in Ethiopia. New York: Columbia University Press.
- Swofford DL. 1998. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sunderland, MA: Sinauer Associates.
- Tabarelli M, Peres CA. 2002. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration. *Biol Conserv* 106:165–176.
- Taberlet P, Griffin S, Goossens B, Questiau S, Manceau V, Escaravage N, Waits L, Bouvet J. 1996. Reliable genotype of samples with very low DNA quantities using PCR. *Nucleic Acids Res* 24:3189–3194.
- Taberlet P, Waits LP, Luikart G. 1999. Noninvasive genetic sampling: look before you leap. *Trends Ecol Evol* 14:321–325.
- Takahata N, Nei M. 1984. F_{ST} and G_{ST} statistics in the finite island model. *Genetics* 107:501–504.
- Takenaka O, Takasaki H, Kawamoto S, Arakawa M, Takenaka A. 1993. Polymorphic microsatellite DNA amplification customized for chimpanzee paternity testing. *Primates* 34:27–35.

- Tardif SD. 1997. The bioenergetics of parental behavior and the evolution of alloparental care in marmosets and tamarins. In: Solomon NG, French JA, editors. Cooperative breeding in mammals. Cambridge: Cambridge University Press. p 11–33.
- Tardif SD, Harrison ML, Simek MA. 1993. Communal infant care in marmosets and tamarins: relation to energetics, ecology, and social organization. In: Rylands A, editor. Marmosets and tamarins: systematics, behaviour, and ecology. Oxford: Oxford University Press. p 220–234.
- Taub DM. 1980. Female choice and mating strategies among wild Barbary macaques (*Macaca sylvanus* L.). In: Lindberg DG, editor. The macaques: studies in ecology, behavior, and evolution. New York: Van Nostrand Reinhold Co. p 287–344.
- Terborgh J. 1983. Five New World primates: a study in comparative ecology. Princeton, NJ: Princeton University Press.
- Thomson R, Pritchard JK, Shen P, Oefner PJ, Feldman MW. 2000. Recent common ancestry of human Y chromosomes: evidence from DNA sequence data. *Proc Natl Acad Sci USA* 97: 7360–7365.
- Toth G, Gaspari Z, Jurka J. 2000. Microsatellites in different eukaryotic genomes: survey and analysis. *Genome Res* 10:967–981.
- Trefilov A, Krawczak M, Berard J, Schmidtke J. 1999. DNA sequence polymorphisms in genes involved in the regulation of dopamine and serotonin metabolism in rhesus macaques. *Electrophoresis* 20:1771–1777.
- Trefilov A, Berard J, Krawczak M, Schmidtke J. 2000. Natal dispersal in rhesus macaques is related to serotonin transporter gene promoter variation. *Behav Genet* 30:295–301.
- Utami SS, Goossens B, Bruford MW, de Ruiter JR, van Hooff JARAM. 2002. Male bimaturism and reproductive success in Sumatran orang-utans. *Behav Ecol* 13:643–652.
- Valderrama X, Karesh WB, Wildman DE, Melnick DJ. 1999. Noninvasive methods for collecting fresh hair tissue. *Mol Ecol* 8:1749–1752.
- van de Castele T, Galbusera P, Matthysen E. 2001. A comparison of microsatellite-based pairwise relatedness estimators. *Mol Ecol* 10:1539–1549.
- van Schaik CP. 2000. Infanticide by male primates: the sexual selection hypothesis revisited. In: van Schaik CP, Janson CH, editors. Infanticide by males and its implications. Cambridge: Cambridge University Press. p 27–60.
- van Schaik CP, Kappeler PM. 1997. Infanticide risk and the evolution of male-female association in primates. *Proc R Soc Lond [Biol]* 264:1687–1694.
- Vigilant L. 2002. Technical challenges in the microsatellite genotyping of a wild chimpanzee population using feces. *Evol Anthropol [Suppl]* 1:162–165.
- Vigilant L, Hofreiter M, Siedel H, Boesch C. 2001. Paternity and relatedness in wild chimpanzee communities. *Proc Natl Acad Sci USA* 98:12890–12895.
- Wade MJ, McCauley DE. 1988. Extinction and recolonization: their effects on the genetic differentiation of local populations. *Evolution* 42:995–1005.
- Wallman J, Hoelzer GA, Melnick DJ. 1996. The effects of social structure, geographical structure, and population size on the evolution of mitochondrial DNA: I. A simulation model. *Comput Appl Biosci* 12:481–489.
- Waser PM, Jones WT. 1983. Natal philopatry among solitary mammals. *Q Rev Biol* 58:355–390.
- Waser PM, Strobeck C. 1998. Genetic signatures of interpopulation dispersal. *Trends Ecol Evol* 13:43–44.
- Watts D. 1998. Coalitionary mate-guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behav Ecol Sociobiol* 44:43–55.
- Watts D, Mitani J. 2001. Boundary patrols and intergroup encounters among wild chimpanzees. *Behaviour* 138:299–327.
- Weber JL, Wong C. 1993. Mutation of human short tandem repeats. *Hum Mol Genet* 2:1123–1128.
- Weir BS, Cockerham CC. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 38:1358–1370.
- Welsh J, Petersen C, McClelland M. 1991. Polymorphisms generated by arbitrarily primed PCR in the mouse: application to strain identification and genetic mapping. *Nucleic Acids Res* 19:303–306.
- White FJ. 1996. Comparative socio-ecology of *Pan paniscus*. In: McGrew WC, Marchant LF, Nishida T, editors. Great ape societies. Cambridge: Cambridge University Press. p 29–41.
- Whitlock MC, McCauley DE. 1990. Some population genetic consequences of colony formation and extinction: genetic correlations within founding groups. *Evolution* 44:1717–1724.
- Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch FB. 2001. Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proc Natl Acad Sci USA* 98:13769–13773.
- Williams JGW, Kubelik AR, Livak KJ, Rafalski JA, Tingey SV. 1990. DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. *Nucleic Acids Res* 7:6531–6535.
- Wilson AC, Cann RL, Carr SM, George M Jr, Gyllensten UB, Helm-Bychowski KM, Higuchi RG, Palumbi SR, Prager EM, Sage RD, Stoneking M. 1985. Mitochondrial DNA and two perspectives on evolutionary genetics. *Biol J Linn Soc* 26:375–400.
- Wilson JF, Erlandsson R. 1998. Sexing of human and other primate DNA. *Biol Chem* 379:1287–1288.
- Wimmer B, Kappeler PM. 2002. The effects of sexual selection and life history on the genetic structure of redfronted lemur, *Eulemur fulvus rufus*, groups. *Anim Behav* 64:557–568.
- Wimmer B, Tautz D, Kappeler PM. 2002. The genetic population structure of the gray mouse lemur (*Microcebus murinus*), a basal primate from Madagascar. *Behav Ecol Sociobiol* 52:166–175.
- Witte SM, Rogers J. 1999. Microsatellite polymorphisms in Bolivian squirrel monkeys (*Saimiri boliviensis*). *Am J Primatol* 47:75–84.
- Wrangham RW. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262–300.
- Wrangham RW, Peterson D. 1996. *Demonic males*. New York: Houghton Mifflin.
- Wright S. 1943. Isolation by distance. *Genetics* 23:114–138.
- Wright S. 1951. The genetical structure of populations. *Ann Eugen* 15:323–353.
- Wright S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. *Evolution* 19:395–420.
- Zane L, Bargelloni L, Patarnello T. 2002. Strategies for microsatellite isolation: a review. *Mol Ecol* 11:1–16.
- Zhang D-X, Hewitt GM. 1996. Nuclear integrations: challenges for mitochondrial DNA markers. *Trends Ecol Evol* 11:247–251.