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# Differences in Male and Female Macaque Dispersal Lead to Contrasting Distributions of Nuclear and Mitochondrial DNA Variation

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*Male macaques typically leave their natal group before sexual maturity, while females remain for life. Thus genes flow between groups and populations almost solely through male transfer. This asymmetrical dispersal pattern affects the distribution of variation in the nuclear and mitochondrial genomes differently. Nuclear genetic variation, measured by allozyme polymorphisms, is relatively evenly distributed throughout the populations of a macaque species, provided there are no major geographical barriers. Conversely, the distribution of maternally inherited mitochondrial DNA (mtDNA) diversity is characterized by local homogeneity and large interpopulational differences. Because of differences in inheritance, dispersal, and population structure, the information contained in nuclear and mitochondrial genomes is best used to address different types of behavioral, genetic, and conservation questions.*

**KEY WORDS:** allozymes; mitochondrial DNA; population structure; social organization; macaques.

## INTRODUCTION

Among mammals, the male of a species is commonly the dispersing sex (Greenwood, 1980). This generalization is a probabilistic one, implying that while both males and females disperse, males are much more likely

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to leave their natal area. However, in certain cercopithecine monkeys this form of gender-biased dispersal is taken to an extreme (Clutton-Brock, 1989). In these cases, virtually all males leave the social group into which they are born, while females remain in their natal group throughout their lives (Sade, 1972). There are exceptions to this pattern (Moore, 1984), but in general, it holds (Pusey and Packer, 1987).

Over the past decade there has been considerable debate over the ultimate cause or evolutionary basis for this type of gender-specific asymmetrical dispersal (Moore, 1984; Pusey and Packer, 1987), including suggestions of inbreeding avoidance and resource competition (Moore and Ali, 1984; Clutton-Brock, 1989). While much effort has been put into resolving this issue, it is doubtful that any single explanation will hold as a general rule. Nevertheless, our examination of the effects of primate social organization on population genetic structure requires no such resolution, only an acknowledgment of the existing behavioral patterns as a contingent fact of cercopithecine population dynamics.

Given the extreme asymmetry in dispersal among certain primates, it is reasonable to expect the distribution of genetic variation to reflect these patterns. That is, variation in the nuclear genome, transmitted by both sexes and recombined in succeeding generations, should be fairly homogeneously distributed due to extensive male migration. On the other hand, variation in the mitochondrial genome, transmitted solely by the female parent to the offspring, should be geographically restricted and exhibit marked interlocality heterogeneity. Indeed, this hypothesis of contrasting population structures not only follows from the sex differences seen in dispersal and inheritance but also should stand as a test of the ubiquity of female sedentism, now and in the past, in any species examined. That is, if mtDNA haplotypes were locally heterogeneous and similar between localities, it would suggest that female sedentism is a relatively recent phenomenon.

To test the hypothesis outlined here, we compared the population structure of genetic variation in the nuclear and mitochondrial genomes of the rhesus monkey (*Macaca mulatta*). The rhesus monkey, one of the most widely distributed primate species (Wolfheim, 1983), occupies habitats from sea level to over 3000 m and from semidesert scrub to moist temperate evergreen forest (Richard *et al.*, 1990). Despite this unusually large and ecologically diverse distribution, rhesus monkeys exhibit little morphological variation across their range (Napier and Napier, 1967), suggesting overall genetic similarity throughout the species.

In analyzing the population genetic structure of rhesus macaques and other closely related species, we hope (1) to examine the effects of multimale/multifemale cercopithecine social organization on the distribution of variation in both the nuclear and mitochondrial genome, (2) to determine

exactly how different the two population genetic structures are from one another, and (3) to delineate the uses to which variation in each genome can be put in evolutionary studies of macaques and other similarly organized species.

## MATERIALS AND METHODS

### The Nuclear Genome

In this study, an array of serum protein and erythrocytic enzyme loci is used to examine the structure of nuclear genetic variation. The shortcomings of this approach lie primarily in the unknown action of natural selection on these loci, which may result in broad similarities between populations that do not regularly exchange genes (Ehrlich and Raven, 1969). However, we have shown that the distribution of polymorphism and heterozygosity at these loci do not reflect the action of selection (Melnick, 1988). Therefore, the distribution of variation at these effectively neutral loci is primarily the product of gene flow, accurately reflecting the effects of dispersal on nuclear genetic structure.

The data used in this analysis come from a detailed study of one specific rhesus population ((Melnick *et al.,* 1984, 1986), and several other studies of broadly sampled regions (Darga, 1975; Nozawa *et al.,* 1977; Shotake 1979; Melnick, unpublished). The specific allele frequencies at the 25 loci used are described elsewhere (Melnick, 1988), as is the application of Nei's (1973) gene diversity analysis to these data.

### The Mitochondrial Genome

The mitochondrial genomes of 18 rhesus monkeys from 5 regions (Pakistan, India, Burma, Southwest China, Southeast China) were surveyed by restriction enzyme analysis, using 15 restriction endonucleases (*Ava*I, *Bam*HI, *Bgl*II, *Bst*eII, *Cla*I, *Dra*I, *Eco*RI, *Eco*RV, *Hae*II, *Hin*cII, *Hin*dIII, *Kpn*I, *Pst*I, *Sst*I, and *Xba*I). The specific conditions of DNA extraction, restriction enzyme digestion, electrophoresis, and DNA transfer and visualization are detailed elsewhere (Melnick *et al.,* 1991a). Ten unique multienzyme haplotypes were identified, each comprised of 40 to 47 restriction fragments. The restriction sites demarcating each fragment were mapped using single and double digestions and the logic of parsimony (Dowling, 1990).

Restriction site data were used to estimate within-population diversity and between-population differences employing the methods of Nei and Ta-

jima (1983) and the computer program MAXLIKE, which was supplied by M. Nei and L. Jin. The gene diversity analysis developed for mtDNA data is analogous to the methods previously described for nuclear genetic variation and, thus, can be directly compared (Nei, 1982).

### Other Species

Published data from other studies of allozyme variation (Melnick, 1988) were used to estimate population structures of nuclear genetic variation in other species of macaques. Similarly, published and unpublished data on mtDNA variation from several other species of macaques (Hayasaka *et al.,* 1988; Harihara *et al.,* 1988; Williams *et al.,* 1991) were used to shed light on the degree to which the distribution of mtDNA variation in the rhesus monkey can be found in other species with similar dispersal patterns.

## RESULTS

### The Nuclear Genome

#### *Rhesus Monkeys*

As reported elsewhere (Melnick, 1988), the distribution of nuclear genetic variation in the rhesus monkey, at all levels of population subdivision, is extremely homogeneous (Fig. 1). Nearly 96% of the nuclear gene diversity found in the Dunga Gali local population of rhesus monkeys can be found in any one of its constituent social groups. Approximately 99% of the Pakistan region's diversity could be found in either of the local populations surveyed. Furthermore, across the entire species range, only 9% of the total species diversity could be apportioned to interregional differences.

#### *Other Species*

Broad similarities exist at several levels of subdivision in other macaque species that are organized in multimale/multifemale societies with nearly complete male dispersal and female philopatry (Melnick, 1988). Within local populations, three other species (*M. fascicularis*, *M. fuscata*, *M. sinica*) exhibit levels of homogeneity roughly equal to those of the rhesus monkey. The proportion of local population diversity found in any one social group ranged from 92 to 97%. At the regional level results were also quite similar, with estimates of 90 to 93% of a region's diversity appor-

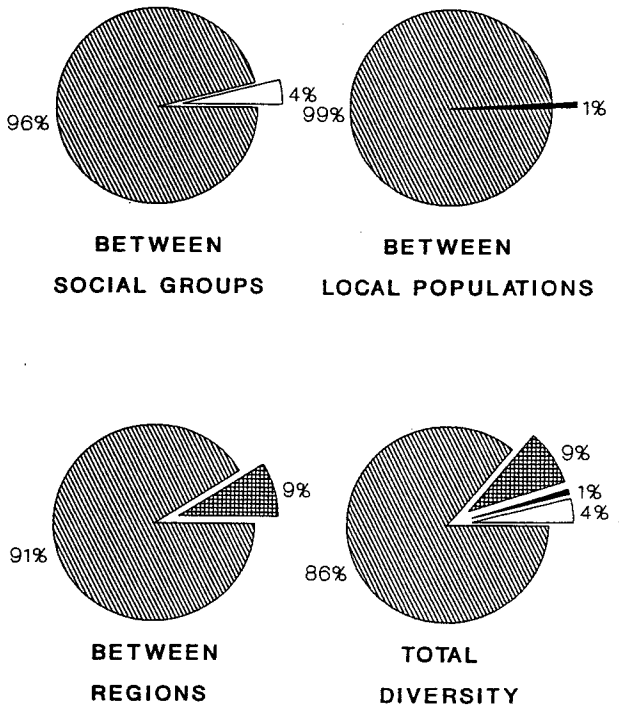


**Fig. 1.** A diagrammatic representation of the distribution of genetic diversity at different levels of rhesus monkey organization. In each instance the smaller wedge represents the portion of total local population (upper left), total region (upper right), and total species (lower left) diversity that can be attributed to differences between the subunits designated below the respective pie charts. The pie on the lower right is a depiction of the apportionment of total species diversity to variation within social groups (Large shaded portion) and to differences between social groups (white wedge), local populations (black wedge), and regions (cross-hatched wedge). See the text for further discussion of these results and Melnick (1988) for a more detailed presentation of the data and their analysis.

tioned to differences between individuals in the same local population. Major differences, however, were identified at the species level (Fig. 2). Here species whose geographic ranges were fragmented by water exhibited much more structure to their genetic variation, with as little as 67% of the species diversity found in the regional populations of *M. fascicularis*. However, the proportion of species diversity found in regional populations of other species with continuous geographic ranges was similar to that of the rhesus monkey, exceeding 90% (Melnick, 1988). Thus, in the absence of any sig-

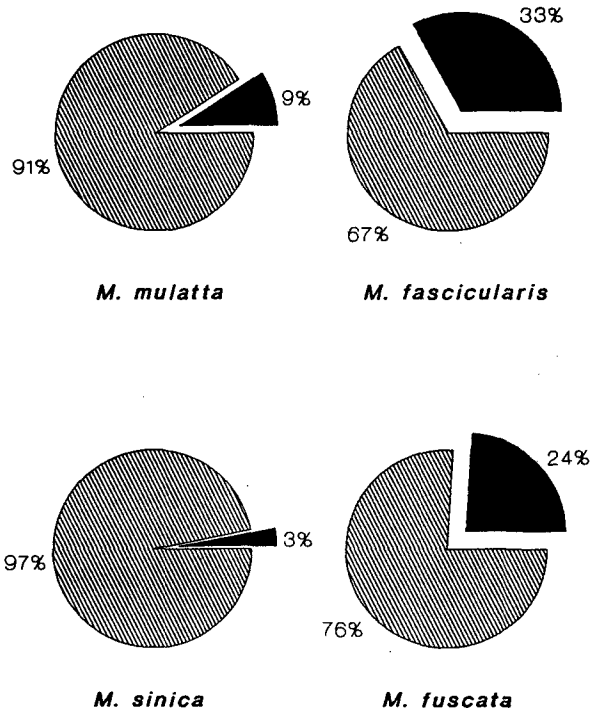


**Fig. 2.** A diagrammatic representation of the portion of total species diversity that can be attributed to variation within a geographic region (shaded) and to differences between regions (black wedge). Note that the geographic distributions of *M. fascicularis* and *M. fuscata* are fragmented by water, contributing to the comparatively large interregional differences.

nificant geographic barrier, nuclear genes appear to flow freely across the range of most macaque species. The population structure described here for the macaques was also found in other cercopithecine species (*Cercopithecus aethiops*, *Papio anubis*), which exhibit the same type of social organization (Melnick, 1988).

## The Mitochondrial Genome

### *Rhesus Monkeys*

Estimated mtDNA sequence divergence (0.2–4.5%) among rhesus monkeys (Melnick *et al.*, 1991a) is much higher than that found in most

species of primates (Melnick *et al.,* 1992) or other mammals (Wilson *et al.,* 1985). Apportioning this diversity to within- and between-population differences reveals two characteristics of mtDNA population structure that are antithetical to our findings in the nuclear genome. First, their is very little sequence variation within any regional population (0.23%). Second, the sequence differences between populations (2.45%) are an order of magnitude larger than those found within them. Hence, diversity analysis (Nei, 1982) indicates that roughly 9% of the total species diversity can be apportioned to within population differences, while a full 91% of the species diversity consists of between population differences. These statistics are the exact opposite of what one finds in the nuclear genome (Fig. 3).

### *Other Species*

Data on mtDNA variation in other cercopithecine primate species are limited. Nevertheless, the data that exist corroborate our findings in the rhesus monkey. Among populations of *M. fuscata*, no intrapopulational sequence diversity was found, while interpopulational sequence differences averaged 1.74% [data from Hayasaka *et al.* (1988), reanalyzed by Melnick *et al.* (1991a]. Similarly, the average sequence divergence between populations of *M. fascicularis* was between three and four times that of the differences within populations (Harihara *et al.,* 1988). Again, the same was generally true of *M. nemestrina* (Williams *et al.,* 1991).

In more detailed studies of individual local populations, either we found no variation at all (*M. mulatta* in Dunga Gali) or the differences

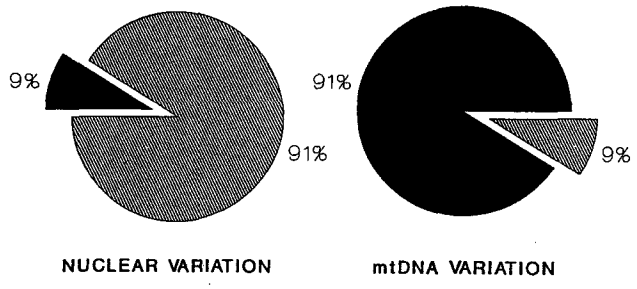


**Fig. 3.** A diagrammatic representation of the portion of total rhesus macaque species diversity in the nuclear and mitochondrial genomes that can be attributed to variation within a geographic region (shaded) and to differences between regions (black). Note that the distributions depicted are the mirror images of one another, in large measure due to the gender-biased dispersal patterns in macaques (see text).

that were found (*M. sinica* in Polonnaruwa) were distributed solely as between-social group differences (Melnick *et al.,* 1991a; Hoelzer *et al.,* 1991b). Hence, members of any social group were monotonously uniform in their mtDNA haplotypes, and all intrapopulational differences were distributed as between group differences. Again, this is the exact opposite of what one finds in the nuclear genome for these populations.

## DISCUSSION

### The Nuclear Genome

The ubiquity of species nuclear gene diversity throughout the rhesus range indicates very high rates of nuclear gene flow (Melnick, 1988). Empirically, we have observed exceptionally high rates of male migration at the local population level in Dunga Gali, resulting in rhesus monkey social groups that are slightly outbred (Melnick *et al.,* 1984b) and genetically very similar to one another (Melnick *et al.,* 1984a). Nearly identical patterns of migration have been noted in other populations of rhesus (Lindburg, 1969; Sade, 1972) and other macaque species (Dittus, 1975). Hence, even though migration is essentially limited to one sex, half the genes contributed to any new cohort are migrant genes, more than enough to inhibit the development of large nuclear genetic differences between populations (Wright, 1951).

Despite this general picture of genetic homogeneity, the small genetic differences that exist between the Dunga Gali social groups are statistically significant (Melnick *et al.,* 1984a). That is, the collection of genes found in each social group is not simply a random assortment of the genetic material available in the population. However, there is some reason to believe that the asymmetrical patterns of dispersal will create a complex of random and nonrandom components in any group's gene pool.

Using multiple randomization tests, we found that the adolescent/adult male portion of any social group was essentially a random genetic sample of the entire population's male gene pool, while the adult female/offspring portion was not a random sample of its age–sex-specific gene pool (Melnick *et al.,* 1991b). These results parallel what we know of the dispersal of rhesus monkeys, in which the adolescent/adult male portion of a social group is primarily a random collection of individuals in that age–sex class and the adolescent/adult female portion represents the descendants of females that have remained in the group generation after generation. Thus, we find (1) a general background of broad genetic homogeneity, due largely to high rates of male migration and gene flow, against which we also find (2) small statistically significant genetic differences between groups, which are the

product primarily of differences between each group's nonrandom genetic component, that contributed by the adult females and their offspring.

## The Mitochondrial Genome

If in the face of overwhelming male-limited gene flow, macaque female sedentism has had a significant effect on nuclear population genetic structure, then we should expect maternally inherited genetic variation to be more highly differentiated between groups and populations. This is precisely what we have found. In a species for which nuclear genetic variation is homogeneously spread across a geographically continuous range, we find exceptionally large interpopulational differences (i.e., levels of sequence divergence) in mtDNA. This combination of a continuous geographic distribution of individuals and geographic discontinuity of mtDNA haplotypes conforms to category II of Avise and co-workers (1987) mtDNA population structure classification. They argue that this pattern, rarely seen among the mammalian species studied thus far, is the outcome of recent secondary contact between populations that were separated for a long time. However, empirical evidence (Melnick *et al.,* 1991a) and computer simulations (Hoelzer *et al.,* 1991a) both suggest that "large" interpopulational macaque mtDNA distances can develop in the absence of geographic barriers. Instead, this divergence reflects the fact that the unusually high degree of female philopatry found in macaques greatly limits the dispersal of any new mtDNA mutation, effectively causing social groups to be isolated by distance (Wright, 1943) instead of by geographic barriers.

Computer simulations have also shown that macaque female philopatry, differential reproductive success, and social group fission lead to a rapid loss of matrilines in any finite population (Hoelzer *et al.,* 1991a). Thus, within a relatively short time all social groups within a local population trace their matrilineal ancestry to a single female "foundress." This process of lineage sorting (Avise *et al.,* 1984), coupled with very low levels of mtDNA gene flow and high mtDNA mutation rates (Brown *et al.,* 1979), should result in a highly structured, heterogeneous species with low levels of within population mtDNA diversity and large between population differences. Again, this is precisely what we find.

## Contrasting Population Structures

It is clear from our analysis of rhesus monkeys and other macaque species (*M. fascicularis*, *M. nemestrina*, *M. sinica*) that the population struc-

tures of nuclear and mitochondrial genetic variation are very different. With the exception of major water barriers, nuclear genetic variation in all macaques studied is quite uniformly distributed throughout a species range. Thus, most of the rhesus species diversity can be found in any single regional subdivision and the differences between rhesus populations are surprisingly low, given the distances that separate populations in this widely distributed species. Other continuously distributed cercopithecine species exhibit virtually identical nuclear genetic population structures.

The distribution of mitochondrial genetic variation is the mirror image of nuclear genetic structure. Almost all of a species diversity is distributed as between-population differences and there is relatively little within-group or within-population mtDNA diversity. In the rhesus, within- and between-population diversities in the two genomes are the exact opposite (Fig. 3). Hence, depending upon which genome one used to characterize the rhesus, one gets completely different pictures of population genetic structure.

For some time it has been clear that the mitochondrial genome is a rich, easily interpreted source of genetic variation for population genetic analysis (Advise, 1986; Avise *et al.*, 1987). Because the mitochondrial genome evolves at a rate 5 to 10 times faster than the nuclear genome (Brown *et al.*, 1979), one generally finds much more variation, and thus genetic information, when comparing closely related populations or species. Additionally, its clonal inheritance, lack of recombination, and economical organization (Brown, 1983; Honeycutt and Wheeler, 1989) simplify the quantitative analysis of mtDNA data relative to their nuclear counterparts. Thus, if the population structures of the two genomes were congruent, mtDNA would provide a simpler and perhaps more abundant source of data with which to analyze the population genetics of macaques.

This congruence was not indicated by our results. The population structure of mitochondrial genetic variation is not only a poor reflection of nuclear population genetic structure but also a misleading one. Large mtDNA differences between populations could, in general, be associated with either large or small nuclear genetic differences. In rhesus monkeys and other macaques, the latter case is most prevalent. While the population genetics of mtDNA are intrinsically interesting (Avise, 1986), the mitochondrial genome represents such a small fraction of an organism's overall genetic makeup and its population genetic structure in macaques is so different from the nuclear genome that it tells us virtually nothing about the overall genetic similarities or differences within and between macaque populations.

## What Are Nuclear and Mitochondrial Genetic Data Good for?

Among their many uses, genetic data have been employed in the study of primates (1) to assess the population genetic consequences of demographic and behavioral phenomena, (2) to determine the phylogenetic relationships of populations and species, and (3) to examine the degree to which populations of a species differ and to use this information as part of a wildlife management strategy to conserve the greatest possible amount of the species genetic diversity. For each of these uses we can assess the relative utility of the two genomes to meet a specific goal.

### *Population Genetics*

As we have already stated, the distribution of mtDNA variation in macaque species is an unreliable reflection of the "true" population genetic structure. In this sense mtDNA is a poor population genetic marker. The nuclear genome is a direct source of population genetic data, and if neutral or nearly neutral loci are used, an accurate picture of population structure and its relationship to sociodemographic processes can be obtained.

There are some population genetic investigations that might be enhanced by using mtDNA. Since mtDNA evolves rapidly, is maternally inherited without recombination, and tends to become locally homogeneous, it should be straightforward to use mtDNA haplotypes, provided sufficient variation exists, both to trace the geographic origin of migrant males and to establish a matrilineal phylogeny of social groups within a population. Combining these two sets of data one should be able to correlate levels of intergroup aggression and natal male exchange with the degree of maternal relatedness among social groups. Further, because females generally do not migrate, one can also use mtDNA markers to determine the direction of gene flow across a hybrid zone between two closely related species. If hybrids of species A and B have species B mtDNA, then nuclear genes are undoubtedly flowing from species A to species B. That is, the only way to have a hybrid with B mtDNA is for B females to have been impregnated by A males. Since philopatric B females are not migrating up into the A species range, A males must be migrating down into B's range. We are currently using mtDNA in all three of these ways, though finding sufficient intrapopulational variation to tag males and to create a finely resolved matrilineal group phylogeny may ultimately require PCR amplification and sequencing of a highly variable region in the mtDNA genome (e.g., the D-loop).

### *Phylogenetics*

The same population dynamics that make mtDNA a poor marker for reconstructing overall population genetic structure make it an excellent phylogenetic marker. Evidence of biogeographical events and instances of intraspecific paraphyly, which have been nearly obliterated in the nuclear genome by subsequent gene flow through male migration and recombination, can be preserved in the mitochondrial genome. For example, the separation of rhesus monkeys in the eastern and western parts of their range, probably due to a glacial barrier in the Bramaputra River Valley during the late Pleistocene (Fooden, 1988), is at once clearly reflected in major mtDNA differences and obscured by general nuclear genetic homogeneity (Melnick *et al.*, 1991a). When the distinctive mtDNA haplotypes of eastern and western rhesus populations were treated as separate taxa in a phylogenetic analysis of the fascicularis species group, it became clear that *M. fuscata* and, probably, *M. cyclopis* were derived from the eastern rhesus population after the initial separation of the two rhesus populations. An additional advantage to using mtDNA in phylogenetic reconstruction is that the rapid nucleotide substitution rate in the mtDNA genome generally results in much more character state data than are is provided by a comparable study of nuclear genetic variation.

### *Conservation Genetics*

Because this field relies heavily on both population genetic and phylogenetic analyses, one must be very cautious when applying mtDNA data to issues of wildlife management. There is little risk of underestimating large nuclear genetic differences when mtDNA differences are small (Ashley *et al.*, 1989), but the opposite is not true. Large mtDNA differences do not necessarily reflect large overall genetic differences and thus should not be used as the sole genetic criterion for wildlife management plans. For example, a management plan based on mtDNA would lead to inappropriate strategies for the maintenance of genetic variation in *M. mulatta* and *M. fascicularis*. Because *M. fascicularis* populations are separated by water and their nuclear genomes are relatively distinct, nearly twice as many regional populations would have to be sampled, relative to *M. mulatta*, to preserve 90% of each species' genetic diversity. Yet if one looked solely at mtDNA one would come to the opposite conclusion because mtDNA sequence divergence is much greater in *M. mulatta*.

As a superior phylogenetic marker, mtDNA has its uses in conservation genetics. However, because most conservation studies must take popu-

lation genetic parameters, as well as phylogenetic considerations into account (see Avise, 1989), mtDNA should not be used without sufficient support from nuclear genetic analysis.

## CONCLUSION

By comparing the distributions of nuclear and mitochondrial genetic variation in macaques we have found that the population structures of each genome are (1) very different from one another, (2) intimately linked to the asymmetrical dispersal patterns of males and females and the maternal inheritance of mtDNA, and (3) variably useful in population genetic, phylogenetic, and conservation biological studies. Since these conclusions are based on our studies of macaque monkey species, we do not suggest that they apply to all taxa. However, it is worth keeping in mind that the patterns of dispersal seen in macaques are an extreme form of what is found in most mammals. We do not know what level of female dispersal will homogenize the distribution of mtDNA variation across a large geographic area. Without this information, there is no a priori reason to believe that the contrasting population structures of nuclear and mitochondrial genetic variation found in macaques will not also be found in other primates and other nonprimate mammals. If this turns out to be true, the cautions we raise with respect to macaques might well apply to many other mammals. Therefore, it seems only prudent to compare the variation in these two genomes in other species before we forge ahead in our use of mtDNA as an all-purpose population genetic tool.

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