

Genetic population structure of the white sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, southwest Madagascar (1992–2001)

RICHARD R. LAWLER,* ALISON F. RICHARD* and MARGARET A. RILEY†

*Department of Anthropology, Yale University, New Haven CT 06511, †Department of Ecology and Evolutionary Biology, Yale University, New Haven CT 06511, USA

Abstract

Gene flow within and between social groups is contingent on behaviourally mediated patterns of mating and dispersal. To understand how these patterns affect the genetic structure of primate populations, long-term data are required. In this study, we analyse 10 years of demographic and genetic data from a wild lemur population (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, southwest Madagascar. Our goal is to specify how patterns of mating and dispersal determine kinship and genetic diversity among animals in the population. Specifically, we use microsatellite, parentage, and census data to obtain estimates of genetic subdivision (F_{ST}), within group homozygosity (F_{IS}), and relatedness (r) within and among social groups in the population. We analyse different classes of individuals (i.e. adults, offspring, males, females) separately in order to discern which classes most strongly influence aspects of population structure. Microsatellite data reveal that, across years, offspring are consistently more heterozygous than expected within social groups (F_{IS} mean = -0.068) while adults show both positive and negative deviations from expected genotypic frequencies within groups (F_{IS} mean = 0.003). Offspring cohorts are more genetically subdivided than adults (F_{ST} mean = 0.108 vs. 0.052) and adult females are more genetically subdivided than adult males (F_{ST} mean = 0.098 vs. 0.046). As the proportion of females in social groups increases, the proportion of offspring sired by resident males decreases. Offspring are characterized by a heterozygote excess as resident males (vs. nonresident males) sire the majority of offspring within groups. We link these genetic data to patterns of female philopatry, male dispersal, exogamy, and offspring sex-ratio. Overall, these data reveal how mating and dispersal tactics influence the genetic population structure in this species.

Keywords: F -statistics, lemur, mating system, population structure, *Propithecus verreauxi*

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Introduction

Natural populations typically have some amount of genetic subdivision that can be arranged hierarchically (Wright 1978). Depending on the population size and range, the degree to which the population subunits will genetically differentiate is contingent on a variety of factors including gene flow, mutation, regional adaptation and drift. Although modelling the interplay among all these factors is complex, it is possible to gain insight into population structure by

focusing solely on how genetic variation is apportioned among population levels under localized panmictic mating and drift (Wright 1969). Wright developed several F -statistics that measure the genotypic deviations from panmictic proportions among population levels. In order to increase their generality, F -statistics were derived within the framework of an idealized population (Wright 1921). F -statistics have been widely used to study geographical population structure (cf. Wright 1978). However, as many researchers have noted, F -statistics do not take into account several behavioural and demographic features that are typical of socially structured populations (e.g. Sugg *et al.* 1996; Balloux *et al.* 1998). These factors include sex-specific dispersal and

Correspondence: Richard R. Lawler.

E-mail: richard.lawler@yale.edu

philopatry, socially stratified reproductive opportunities, and the presence of reproductive and nonreproductive members within social units. Chesser (1991a, 1991b) derived explicit formulations of gene dynamics for socially structured populations that determined the transitional and asymptotic values of genetic variation among different population levels. Chesser's work made clear two issues that were implicit in early studies of socially structured populations (e.g. Melnick *et al.* 1984; Long 1986). First, care must be taken in defining geographical or demic population levels so as not to overlook hidden reproductive structure within demes. Second, significant gene correlations can accrue from sex-biased dispersal and polygyny without needing to invoke inbreeding.

Although derived for any type of socially structured species, the genetic consequences of social structure are often studied in mammalian species (cf. Dobson 1998; Storz 1999). Storz (1999) has noted that mammal populations were previously assumed to be organized into small, semi-isolated, panmictic social units that retain high levels of inbreeding because of limited dispersal (e.g. Bush *et al.* 1977; White 1978; Chepko-Sade & Shields 1987). These assumptions were based precisely on the issues Chesser sought to rectify: inbreeding, subpopulation divergence, and coancestry are not always causally linked. More recent mammalian studies have applied F -statistics at the level of social group – the lowest level at which random mating may prevail – and reveal a different partitioning of genetic variation within the population (e.g. Pope 1992, 1996, 1998; Dobson *et al.* 1997; Dobson 1998; Storz 1999; Storz *et al.* 2001; Richardson *et al.* 2002). These values are more credibly interpreted with respect to the sociodemographic factors mediating gene flow and reproduction within and among breeding groups rather than invoking drift, restricted dispersal, and random mating (Chesser 1991a; 1991b; Sugg *et al.* 1996; Storz 1999). Examining the relationship between social and genetic structure has become known as the 'social structure' view of population genetics (cf. Sugg *et al.* 1996; Balloux *et al.* 1998).

Primate species would appear to be ideal taxa with which to test the predictions of the social structure view of population genetics. Relative to other mammalian orders, primate social systems are very well-studied (cf. Richard 1985a; Strier 2000). Furthermore, most primate species are gregarious and characterized by female philopatry, male dispersal, and different degrees of mating competition (cf. Smuts *et al.* 1987; Lee 1999; Kappeler 2000). However, despite their well-characterized social systems, there are few available data sets that contain reproductive information on an entire primate population; therefore, the apportionment of genetic diversity in primate populations is not well understood. Out of logistical necessity, many long-term primate studies focus on one or a few social groups instead of an entire population (but see, for example, Altmann *et al.*

1996; Keane *et al.* 1997; Sauther *et al.* 1999). The population-levels parameters determining gene dynamics in the population are determined by intra- and intergroup membership and mating. In order to understand how gene correlations change through time as a function of group membership and mating, longitudinal data collected from numerous social groups are required. Here, we analyse the genetic structure of a wild population of lemur, the white sifaka (*Propithecus verreauxi verreauxi*) using longitudinal genetic and demographic data sets. Sifaka live in spatially and socially cohesive groups that contain from two to 14 animals (mean = 6.5). Females are generally philopatric, although females born into groups with several older females may disperse (unpublished data). In contrast, all males disperse from their natal group usually around the age of 5 years (Richard *et al.* 1993). However, unlike many anthropoid primates, sifaka have a restricted breeding season that lasts about 6–8 weeks. The mating season disrupts the spatial and social cohesion of some groups in the population (Richard 1992; Brockman 1999). Observations during the mating season indicate that some sifaka males make forays into neighbouring groups to seek reproductive opportunities. An analysis of paternity on this population confirmed these observations. Across several groups, males sired offspring in social groups other than their own (Lawler 2003).

The objective of this study is to test several predictions of the social-structure view of population genetics. First, under the conditions of sex-biased dispersal, the degree of among-group genetic variation in adults should be proportional to the relatedness of the philopatric sex within groups; for sifaka, female relatedness within groups should be positively related to adult F_{ST} (Chesser 1991a). Second, when breeding groups are properly defined, offspring should have negative F_{IS} values; therefore, if the sifaka social group corresponds to a reproductive unit, offspring cohorts within groups should show negative F_{IS} values (Cockerham 1969; Chesser 1991a). Third, reproductive skew within social groups is expected to increase F_{ST} values and decrease F_{IS} values in offspring. We approximate reproductive skew as the proportion of resident males siring offspring. We expect that when a single resident male, or several related resident males, sire the majority of offspring within groups, offspring cohorts will be characterized by increasingly negative F_{IS} values (Chesser 1991b). Fourth, under female philopatry and polygyny, offspring cohorts are expected to have F_{ST} values that are relatively equal to adults, because female offspring cohorts – united by a subset of paternal alleles – are recruited into their natal group (Chesser 1991a; Storz *et al.* 2001). We estimate F_{IS} and F_{ST} values at the level of the social group and interpret them with respect to mating and dispersal patterns in this population. We analyse offspring and adult cohorts separately. This separation is the most effective way to operationalize

expectations from theoretical models using genetic data (Spielman *et al.* 1977; Storz *et al.* 2001).

The motivation for this study is straightforward: how genetic variation is apportioned within a population determines the distribution of kinship ties. Relatedness among individuals is one condition that can foster the evolution of altruism and cooperation (cf. Trivers 1985). In this regard, demographic factors that affect gene correlations among individuals could have potentially important consequences for how cooperative and agonistic behaviours are manifested in different lemur species. This is the first of a series of studies that examines the relationship between demography, behaviour and genetic structure. Here, we take a broad approach by using mean values to capture population structure across space and through time. Future studies will examine the spatial (e.g. isolation by distance) and temporal (e.g. individual and group variation in reproductive success) aspects of population structure in more detail.

Materials and methods

The study population

The present study analyses data gathered over the last 10 years from a continuing long-term study of white sifaka at Beza Mahafaly Special Reserve in southwest Madagascar. The population has been the focus of numerous studies including analyses of sifaka life history (Richard *et al.* 2000, 2002), demography (Richard *et al.* 1991, 1993), reproductive endocrinology (Brockman *et al.* 1998) and behaviour (Brockman 1994; Kubzdela 1997). Beginning in 1984, wild *P. v. verreauxi* were captured, measured, and marked (using colour-coded collars and numbered tags) in order to determine their long-term demographic movements (Richard *et al.* 1991). During the capture procedure, 33 morphometric measurements, dental casts, hair and tissue samples, and a range of qualitative data are gathered from each animal. Yearly and monthly census data yield information on population size, number of social groups, group composition (sex and age), transfers of individuals, disappearances, deaths and births. The study population lies within the protected sector of the Beza Mahafaly Reserve, but animals may disperse and move back and forth freely between the reserve and surrounding unprotected forest. Data used in this study come from 10 to 28 core social groups censused since 1992. This is not an exhaustive set of social groups, there are 'buffer zone' groups whose home ranges lie partially within the reserve (cf. Richard *et al.* 2002). The demographically important features of core groups are the following: (1) the home range of each core group lies entirely within the protected reserve; (2) core groups contain individually marked animals; (3) core groups have been censused monthly since 1992; and (4) more animals

Table 1 Yearly population data used in this study

Year	<i>n</i> total	Adult females	Adult males	<i>n</i> groups	Sex ratio (F/M)
1992	77	31	37	13	0.84
1993	79	28	28	10	1.00
1994	93	30	39	12	0.77
1995	147	57	81	22	0.70
1996	122	49	62	27	0.79
1997	105	40	58	21	0.69
1998	178	63	109	27	0.58
1999	191	77	106	28	0.73
2000	148	51	52	25	0.96
2001	131	48	48	22	1.00

F, females; M, males.

are born into, or transfer between, core social groups than migrate into these groups from outside the protected sector (Richard *et al.* 2002; unpublished data). In this study, all analyses are conducted on groups of four or more animals. Table 1 gives the yearly data on number of females and males, number of groups, and average population sex ratio.

Analysis of population structure and parentage

Seven polymorphic microsatellite loci were isolated and screened on this population in order to determine parentage and population structure. Details of genomic DNA preparation from tissue, microsatellite isolation and screening, primer sequences, and polymerase chain reaction (PCR) conditions for locus amplification can be found in Lawler *et al.* (2001). The number of alleles at these seven loci ranged from 6 to 11 and heterozygosity ranged from 0.62 to 0.75 with a mean heterozygosity of 0.70 across all loci. The probability of these seven loci to exclude a random individual from parentage when one parent is known is 99% (Lawler *et al.* 2001).

Tests for deviations from Hardy–Weinberg equilibrium among the loci were determined within each yearly population using an exact test (Raymond & Rousset 1995). Tests for gametic phase disequilibrium among the loci were determined using the permutation tests. Using a *G*-test, we tested for differences in allele frequencies between males and females in the population. To measure genetic variation within and between groups, we used two *F*-statistics: F_{IS} represents the correlation of alleles in individuals relative to the breeding group and F_{ST} represents the correlation of alleles in breeding groups relative to the total population. *F*-statistics for adults and offspring each year were estimated using FSTAT 2.8 (Goudet 1995). This program calculates Weir & Cockerham's (1984) estimators of genetic variance ($f = F_{IS}$, $\theta = F_{ST}$) and each subgroup is weighted by sample size. Despite overlapping generations, a year-by-year

analysis is appropriate as animals enter and leave groups each year through birth, death, immigration and emigration. R_{ST} values were not used in the analysis as not all of our microsatellite markers followed a stepwise mutational pattern and furthermore, F -statistics are not generally contingent on mutation rates when applied at small spatial scales (Rousset 2001). Significance tests were determined using randomization procedures that calculated significant departures away from zero. F -statistics from offspring cohorts were calculated by pooling offspring into groups spanning 4-year intervals. This interval maximizes the sample size of the offspring cohort but precludes those female offspring coming into reproductive maturity (at age 5) within the social group. In this sense, *offspring cohort* is synonymous with *sibship*. All offspring cohorts contain infants born over the last 4 years; for example, the 1992 offspring cohort contains infants born in 1989, 1990, 1991 and 1992. Because offspring cohorts have adjacent (i.e. nonindependent values) for each year, a Durbin–Watson test was used to test for first-order autocorrelation. Under Model I regression, this test determines whether adjacent values have correlated errors through time (Chatfield 1975).

Average relatedness (r) of adult females to each other within a group, relative to the total population, was estimated using the coefficient of relatedness derived by Queller & Goodnight (1989). Relatedness was calculated using the program RELATEDNESS 5.08, correcting for bias within groups (Goodnight & Queller 1999). This same definition of relatedness was used to characterize adult males and offspring. Associations between variables were tested using parametric and nonparametric tests. Because both were significant, we only present nonparametric results. Parentage was determined using the program CERVUS 2.0 (Marshall *et al.* 1998). Confidence in parentage was determined at the 80% and 95% levels. Additional information was available for determining parentage, this included age

and location of the animal during the time of potential siring or conception. Further details of the parentage analysis are presented in Lawler *et al.* (2001) and Lawler (2003). Here, only data pertaining to whether the offspring within a group are sired by resident males (i.e. males who live in the same group as their offspring) or sired by nonresident males are presented (i.e. males who reside in groups other than the group into which they have sired an offspring).

Results

Hardy–Weinberg, gametic phase disequilibrium and F-statistics

Deviations of genotypic proportions from Hardy–Weinberg equilibrium were assessed for the population. When the entire sample of genotypes was pooled across years, one locus (Locus 4) deviated from Hardy–Weinberg (Lawler *et al.* 2001). However, an exact test (with $P = 0.05$) of expected genotypic proportions within the population for each year revealed no significant deviations. For each year in our analysis, a test of gametic phase disequilibrium was performed. Using a resampling test with 3000 permutations, these tests detected no significant gametic phase disequilibrium (with $P < 0.01$) between all pairwise combinations of loci. There were no significant differences in allele frequencies between males and females at each locus (P -values ranged from $P = 0.17$ to $P = 0.28$).

The values of f and θ for adults and offspring cohorts are listed in Table 2. Figure 1 shows θ -values for adults vs. offspring and adult females vs. adult males. Overall, the results in Table 2 indicate that for each year included in the study, offspring show a greater degree of heterozygote excess and a greater degree of between-group differentiation than do adults. The mean θ across years for adults was 0.052 (range 0.024–0.075) and for offspring it was 0.108 (range 0.074–0.130). Adult female values of θ were consistently larger

Table 2 θ and f -values for parents and offspring by year

Year	θ Adults	θ Offspr.	θ Adult F	θ Adult M	f Adults	f Offspr.
1992	0.055*	0.092*	0.062*	0.025*	0.047	-0.020
1993	0.045*	0.104*	0.056*	0.023	0.017	-0.026
1994	0.044*	0.110*	0.082*	0.047*	0.013	-0.051
1995	0.041*	0.090*	0.068*	0.057*	0.005	-0.051
1996	0.024*	0.074*	0.093*	0.043*	0.019	-0.038
1997	0.057*	0.102*	0.112*	0.034*	-0.025	-0.064
1998	0.050*	0.126*	0.109*	0.049*	0.013	-0.091*
1999	0.055*	0.127*	0.110*	0.031*	-0.001	-0.097*
2000	0.075*	0.126*	0.145*	0.077*	-0.040	-0.116*
2001	0.075*	0.130*	0.147*	0.071*	-0.011	-0.130*

Offspr., offspring; F, females; M, males.

* $P < 0.05$.

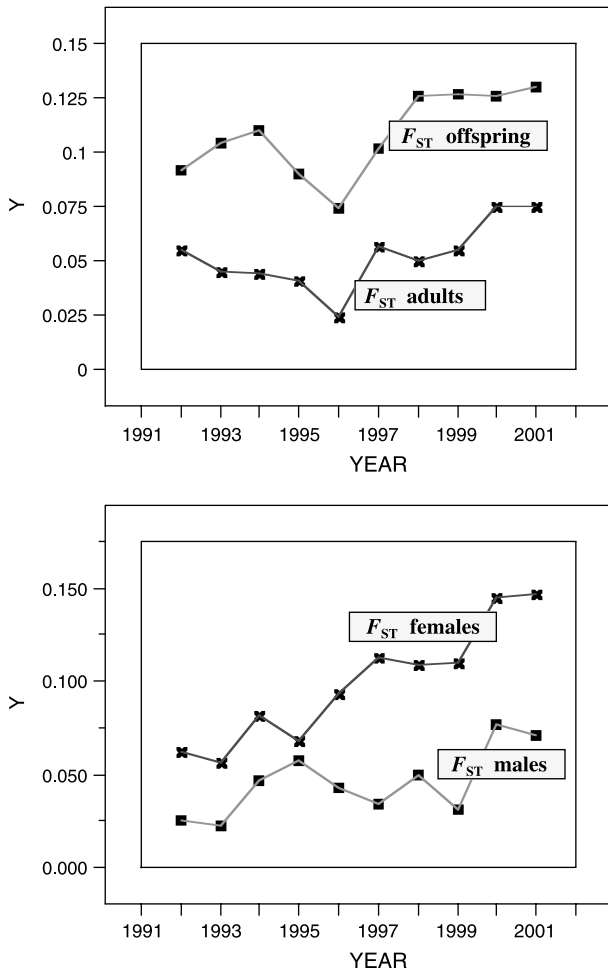


Fig. 1 Values of $F_{ST}(\theta)$ for adults and offspring (top) and adult females and adult males (bottom) by year. Y-axis is F_{ST} value (see Table 2).

than those for adult males. The mean value of θ for adult females was 0.098 (range 0.056–0.147) whereas for adult males it was 0.046 (range 0.023–0.077). The mean degree of deviations from expected heterozygosity (f) across years

for adults was 0.003 (range –0.04 to 0.047) and for offspring was –0.068 (range –0.13 to –0.02).

Relatedness and siring patterns

Relatedness (r) and siring patterns within the population by year are presented in Table 3. Offspring had a higher level of relatedness within a group than did adults (mean adults: 0.098, range: 0.04–0.14; mean offspring: 0.2063, range: 0.14–0.24). Similarly, females were more related to each other than males within groups (mean females: 0.186 range: 0.100–0.27; mean males: 0.086 range: 0.04–0.14). Using parentage data, Table 3 also presents data on whether offspring within a group were sired by resident or nonresident males. The percentages refer to the proportion of offspring born into groups that were sired by resident males of that group (vs. males from another group) each year. In all years but one, a majority of offspring (> 50%) were sired by resident males within groups. The lowest percentage of infants sired within a group by resident males is 35% (1993), one year after there was a major drought at Beza Mahafaly that reduced the population size and altered the population structure (see Discussion in Richard *et al.* 2002). The highest percentage of resident-sirings was in 1998, with 83% of all infants born into groups sired by resident males. Based on yearling censuses, the majority of offspring born in the population were males. Across years, the average percentage of male offspring born into the population is 61% (range 17–78%).

Interactions between variables

There is a significant negative relationship between adult θ -values and offspring f -values (Fig. 2A) (Spearman Rho = –0.648, $P = 0.0426$). This indicates that as adults among social groups become more genetically differentiated, offspring cohorts show a greater degree of heterozygote excess (f). Genetic differentiation of adults among social groups (θ)

Table 3 Relatedness (r) of individuals and siring patterns by year

Year	(r) females	(r) males	(r) adults	(r) offspring	% of infants sired by resident males	n offspring	n male offspring
1992	0.11	0.04	0.10	0.17	44.0	9	7
1993	0.10	0.04	0.08	0.19	35.0	23	13
1994	0.15	0.08	0.08	0.20	46.0	24	16
1995	0.12	0.10	0.07	0.17	66.0	9	7
1996	0.17	0.08	0.04	0.14	63.0	11	6
1997	0.21	0.06	0.11	0.19	71.0	7	5
1998	0.20	0.09	0.09	0.24	83.0	6	1
1999	0.20	0.05	0.10	0.24	75.0	8	5
2000	0.27	0.14	0.14	n.d.	n.d.	n.d.	n.d.
2001	0.27	0.13	0.14	n.d.	n.d.	n.d.	n.d.

n.d. (no data): offspring captured in 2000 and 2001 were not analysed.

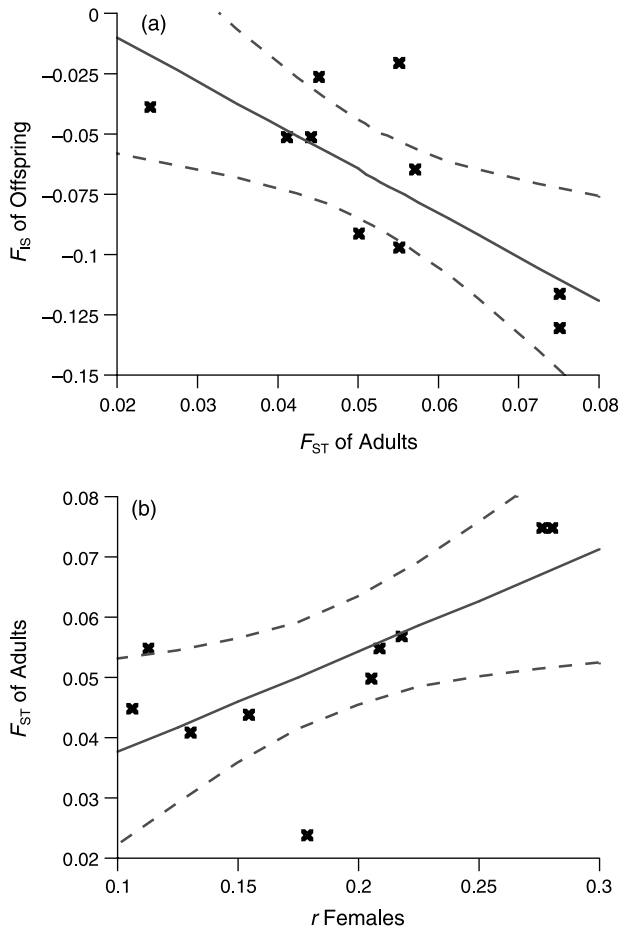


Fig. 2 The relationship between adult F_{ST} (θ) and offspring F_{IS} (f) (a) and the relationship between adult F_{ST} (θ) and relatedness (r) of females within groups (b). Regression lines and confidence intervals are calculated from a least-squares regression; however, non-parametric results are presented in the text.

shows a positive association with relatedness of females (r) within groups (Fig. 2B) (Spearman $Rho = 0.701$, $P = 0.0239$). The relationship between male relatedness and adult group differentiation did not show a significant relationship. Relatedness of adult females and males within a group is significantly associated with offspring heterozygosity. As relatedness of females within a group increases, offspring have increasingly negative f -values (Fig. 3A) (Spearman $Rho = -0.898$, $P = 0.0004$). This relationship does not have significant autocorrelation ($P = 0.322$). A similar negative relationship obtained for males and offspring f -values but the association was not as strong (Fig. 3B) (Spearman $Rho = -0.687$, $P = 0.0282$). However, this relationship has significant positive autocorrelation ($P = 0.022$).

Patterns of siring by resident and nonresident males influence genetic variation within offspring cohorts (Fig. 4A). There is a negative relationship between heterozygote excess in offspring cohorts and the percentage of

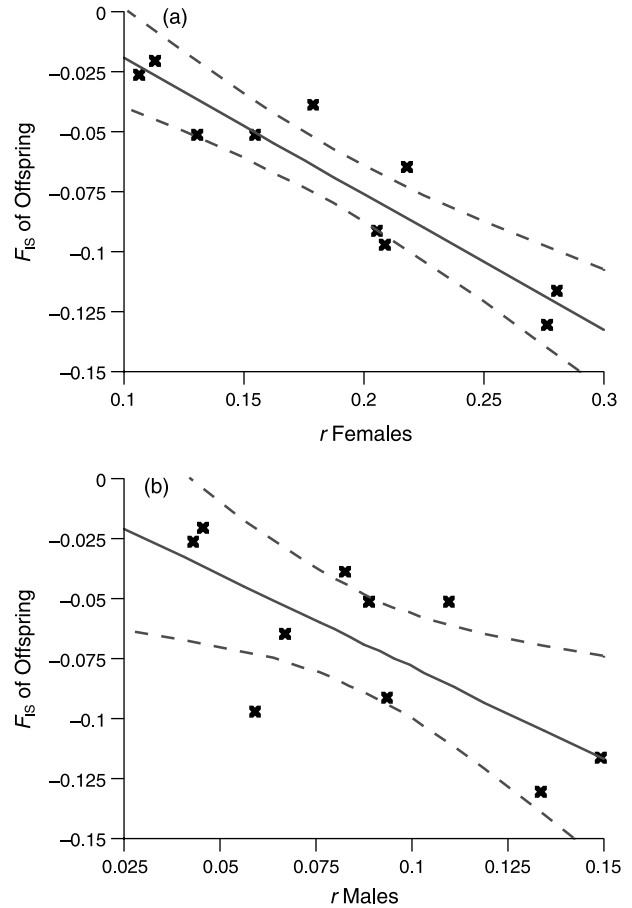


Fig. 3 The relationship between relatedness (r) of females within groups and offspring F_{IS} (f) (a) and the relationship between relatedness (r) of males within groups and offspring F_{IS} (f) (b). Regression lines and confidence intervals are calculated from a least-squares regression; however, non-parametric results are presented in the text.

offspring sired by resident males (Spearman $Rho = -0.910$, $P = 0.0017$); there is a significant amount of positive autocorrelation for this relationship ($P = 0.041$). However, there is no significant relationship between percentage of infants sired by resident males and adult group genetic differentiation (θ). There is a significant negative association between adult sex-ratio within a group and the percentage of offspring sired by resident males (Fig. 4B). As the number of females within a group increases (sex ratio > 1), the number of offspring sired by resident males decreases (Spearman $Rho = -0.905$, $P = 0.0020$).

Discussion

Philopatry, dispersal and heterozygosity

Across all years, there is a negative relationship between adult social group differentiation (θ) and offspring

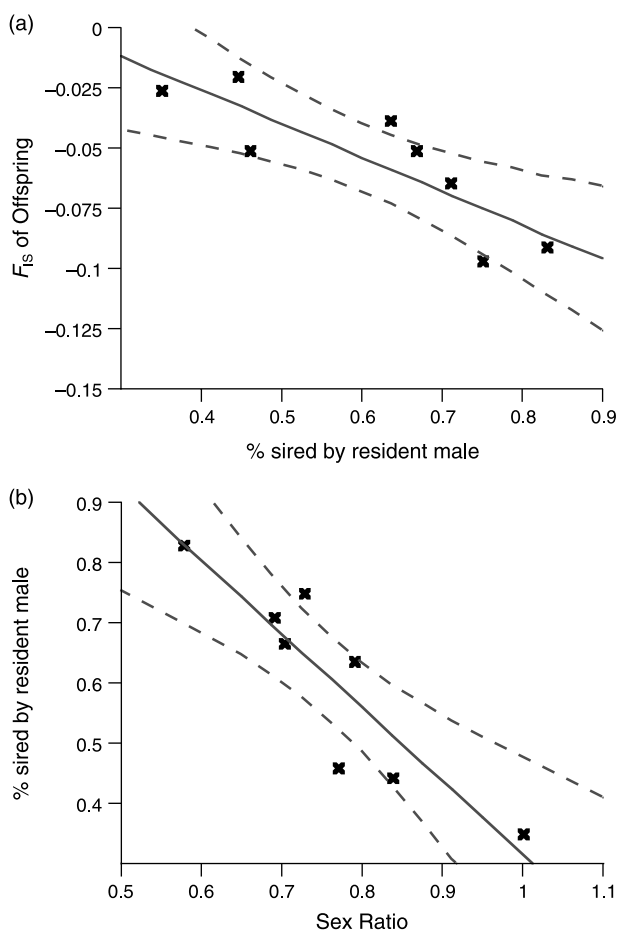


Fig. 4 The relationship between the percentage of offspring sired by resident males of a group and offspring F_{IS} (a) and the relationship between the percentage of offspring sired by resident males of a group and the adult sex ratio (females / males) in the population (b). Regression lines and confidence intervals are calculated from a least-squares regression; however, non-parametric results are presented in the text.

within-group heterozygosity (f). We attribute this excess heterozygosity in offspring cohorts to differences in dispersal in adult males and females. Each year, a minority of the offspring are female and there is considerable female philopatry such that daughters are recruited into their natal social groups (Richard *et al.* 1993; Kubzdela 1997). As daughters reach sexual maturity and join the adult breeding pool, this creates the opportunity for gene correlations to build up among female sifaka within groups. As Table 3 shows, females are more related to each other within groups than are males. Through time, each matriline becomes genetically distinct due to factors such as drift and mutation. Figure 2(B) shows that as female relatedness (r) within groups increases, so does the genetic subdivision among adult social groups. Relatedness (r) can be linked to population

structure through the equation $r = 2F_{ST}/(1 + F_{IT})$ (Hamilton 1971), and because r is proportional to F_{ST} , it is evident that female relatedness within groups drives the genetic differentiation of adult social groups. Vitalis (2002) has derived equations to calculate the sex-specific dispersal rates using pre- and post-reproductive values of θ . In our population, adult female θ -values were consistently larger than adult male θ -values — a pattern consistent with female philopatry and male dispersal. Male relatedness within groups is lower than that of females. It does not show a significant relationship with adult group subdivision. Therefore, female philopatry and the coancestry that builds up within matriline strongly influences the degree of genetic structure in adult sifaka groups.

Female philopatry is often associated with male dispersal (Smale *et al.* 1997) and a 7-year study of dispersal and transfer found that all male sifaka disperse from their natal groups ($n = 191$ cases of transfer) (Richard *et al.* 1993). Males tend to transfer into neighbouring groups; for example, in a 5-year census period, all males transferred no more than two home ranges away from their natal group ($n = 19$). The pattern of adjacent (and secondary) transfers among core social groups causes some groups to have related males (Table 3), resulting in a 'neighbourhood-like' social organization (Richard 1985b; Richard *et al.* 1993). Within social groups, breeding females represent a subset of the total female gene pool. When these females mate with a subset of adult males, a Wahlund-effect occurs (cf. Pope 1992; Storz *et al.* 2001). We interpret the heterozygote excess in offspring to be a consequence of consolidating gene pools that are from different maternal lineages (Chesser 1991a). Effectively, so long as males eventually transfer into unrelated matriline, the differences in allelic combinations that characterize breeding males and females will produce a heterozygote excess in the first filial generation (cf. Cockerham 1973; Long 1986).

The pattern of female philopatry and male dispersal observed in this population is similar to that seen in other mammalian species. As predicted from theoretical studies by Prout (1981) and Chesser (1991a, 1991b), female relatedness within breeding groups is proportional to adult θ . This finding has been recorded in diverse taxa such as howling monkeys (Pope 1992), white tailed-deer (Mathews *et al.* 1997), soay sheep (Coltman *et al.* 2003), Indian fruit bats (Storz *et al.* 2001), black-tailed prairie dogs (Dobson *et al.* 1997), rabbits (Richardson *et al.* 2002), and Alpine marmots (Goosens *et al.* 2001). Furthermore, many of these studies found different degrees of heterozygote excess within the reproductively delineated sampling units (e.g. breeding group, coterie, etc.). The negative correlation of uniting gametes results from parents derived from different maternal lineages within the population and it is enhanced by reproductive skew (cf. de Jong *et al.* 1994; Storz *et al.* 2001).

Male reproduction in social groups and inbreeding

Sifaka are seasonal breeders and have a mating season that lasts for about 6–8 weeks. Social group boundaries tend to break down during the mating season, and some males will make forays into neighbouring groups, possibly to assess the reproductive status of neighbouring females (Richard 1985b). Male–male interactions within and between groups can be quite aggressive during the mating season (Richard 1992; Brockman *et al.* 1998). Females exhibit oestrous asynchrony within the breeding season and show positive mate choice toward resident and nonresident males (Brockman & Whitten 1996). Both male mate competition and female mate choice can lead to high variance in male reproductive success. This skew in male reproduction will further contribute to heterozygote excess in offspring because only a small portion of the total paternal gene pool is used to start the next generation. Polygyny enhances sampling error of adult gametes leading to deviations from random mating. The consequences of related males reproducing in social groups leads to a similar phenomenon of complete polygyny: only a subset of male alleles are represented in the offspring generation. As discussed above, the pattern of transfers among adult males results in some groups containing related males. When related males (or a single male) sire the offspring in groups, this causes a heterozygote excess in offspring cohorts because of sampling error. We interpret the relationship in Fig. 4(A) to be the result of either a single resident or related resident males siring the majority of offspring in groups. As additional males contribute to the progeny gene pool, the variance in alleles donated from adult males decreases, resulting in smaller departures from panmictic expectations in offspring genotypes (Fig. 4A). However, increased offspring subdivision may result from offspring united by maternal alleles, independent of the degree of polygyny (Chesser 1991a, 1991b; Balloux *et al.* 1998). We are currently investigating the variance in paternity and maternity on a finer spatial scale. Within groups, we expect that as the proportion of offspring sharing the same father increases, offspring subdivision (θ) will also increase. Behaviourally, the potential for reproductive skew can be approximated by adult sex ratios within groups. In Fig. 4(B), we divide the number of adult females by number of adult males within groups. As expected, the percentage of offspring sired by resident males decreases when the number of adult females in a group increases (cf. Andelmann 1986; Altmann 1990). We note that this longitudinal, intra-specific data – which measures the reproductive outcome of male dispersion and not just a mating opportunity – supports the general pattern found using interspecific data sets: as the number of females within a group increases, males apart from resident males are also able to mate (cf. Mitani *et al.* 1996).

Avoidance of inbreeding within these groups increases the heterozygote excess in offspring cohorts. Median tenure length of males in sifaka groups is about 3 years and this is shorter than the average age of reproductive maturity of female sifaka. This suggests that breeding males will disperse (or be evicted by adult females; cf. Richard *et al.* 1993) prior to the age that their female offspring reach sexual maturity. Such conditions would decrease the probability of father–daughter matings (Clutton-Brock 1989; Richard *et al.* 1993; also see Pereira & Weiss 1991). Thus, in sifaka offspring cohorts, significant heterozygote excess is related to sex-biased dispersal and is also probably enhanced by the timing of adult male dispersal. This dispersal reduces the chances for close consanguineous matings and keeps homozygosity among offspring to a minimum. However, it is important to note that considerable amounts of inbreeding may occur before a heterozygote deficit will be observed (cf. Pope 1992).

Genetic subdivision in adults and offspring

Offspring cohorts consistently show more genetic variation between groups than adult cohorts. Up to 13% of the genetic variation is found between groups of offspring cohorts, whereas this value is only about 8% for adults. This pattern can be illuminated by considering variation in reproduction and yearling sex-ratio. A long-term analysis of fecundity and mortality shows that within the sifaka population there is a yearling sex ratio bias towards males (Richard *et al.* 1991, 2002). This sex ratio bias may be related to adult female competition for breeding opportunities within groups; selection may favour male offspring, which – unlike females – do not have to compete for breeding opportunities in their natal group (Richard *et al.* 2002). Cohorts of young males outnumber cohorts of young females, and male yearlings make up a greater proportion of the offspring cohort every year in this study except for one (cf. Richard *et al.* 2002).

Average offspring relatedness in groups is high, approaching the half-sib value of 0.25 in some years. However, birth rates in sifaka groups are low, with no more than two surviving infants per group, per year (Richard *et al.* 2002). To increase the sample size, offspring cohorts were pooled such that each yearly sample could contain offspring born across 4 years (i.e. offspring cohorts are sibships; see Materials and methods section). High relatedness among offspring cohorts (which can contain individuals born in sequential years) suggests offspring are united by subsets of paternal (and maternal) alleles. By definition, closely related offspring cohorts are likely to share alleles identical-by-descent from only a subset of individuals in the total parental gene pool. If there is high reproductive variance across numerous social groups then such non-random sampling of the adult gamete pool will increase the rate that certain alleles are differentially lost between

groups. These conditions will enhance the genetic differentiation of offspring cohorts among groups.

Female philopatry and male natal dispersal breaks up the average relatedness of offspring cohorts. As sifaka primary and secondary sex ratios are skewed towards males, a majority of the related offspring cohorts — young males — transfer out of their natal group. Approximately 35% of all young males transfer each year and there are no clear patterns of kin-based immigration (Richard *et al.* 1993). Although dispersing males generally transfer into a neighbouring group, a single group range boundary in this population can overlap with up to six other groups. Distantly related adult males (i.e. a pairwise relationship of 0.10 or less) may end up in the same group together (as discussed above); however, pairs of males from the same offspring cohort have never been observed to transfer together (Richard *et al.* 1993). These data suggest that the genetic structure of the offspring cohort is rearranged — via male dispersal — prior to recruitment into adult social groups. Thus, offspring cohorts united by maternal and paternal alleles, as well as sex-ratios biased towards males within groups accounts for why genetic structure of offspring cohorts exceeds that of adults each year: cohorts of young males within groups disperse randomly into adult breeding groups. This may explain why our results differ from the predictions of Chesser (1991a). 'Breeding group' models assume a female-biased adult sex ratio within lineages and equal sex ratios among progeny (Chesser 1991a, 1991b).

Relevance for the study of social behaviour in primates

Linking demographic and reproductive factors to the distribution of gene correlations within and between social groups has implications for kin selection. Simply knowing if there is a continuity (due to natal recruitment) or disjunction (due to natal dispersal) between the genetic structure of offspring cohorts and the genetic structure of adults can assist in understanding whether kin-selected social behaviours are likely to evolve (Storz *et al.* 2001). For example, among many group-living primates, same-sex related animals are characterized by dominance hierarchies that appear to mediate disputes over resources; this is particularly true of matrilineal societies in macaque species (Gouzoules & Gouzoules 1987). Here, female coancestry provides the impetus for one mechanism through which dominance hierarchies can evolve. This mechanism pertains to maternal investment in future reproductive value. In establishing dominance ranks, mothers often intervene in daughter conflicts on behalf of the youngest daughter. Implicitly, this is a maximization of inclusive fitness for the mother because she is supporting the daughter most likely to have the highest expected future reproduction (Chapais & Schulman 1980; but see Horrocks & Hunt 1983). This behavioural mechanism is more likely to evolve in female

philopatric societies because the opportunity for selection to maximize inclusive fitness is prolonged if daughters remain in the same group as their mothers; that is, if matrilineal lines are not randomized by female dispersal.

Recognizing such patterns may help to explain divergent systems of agonistic behaviour in lemur species (e.g. between *Lemur catta* and *Eulemur fulvus rufus*; cf. Pereira & Kappeler 1997). It is illuminating to consider how genetic correlations of same-sexed offspring cohorts relate to the genetic structure of adults in social groups. With regard to the ontogenetic development of adult social behaviours (Pereira 1995), genetic correlations in offspring cohorts that are preserved into adulthood could facilitate the evolution of complex kin-based social behaviours in adults. However, if both sexes of offspring disperse, then adult social groups may not retain evolutionary significant genetic correlations and kin-selected behaviours may not be favoured by selection (cf. Pope 2000; Storz *et al.* 2001). In specifying the relationship between demographic and genetic structure in adults and offspring, the analyses presented above help identify when such conditions are likely to be met.

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Richard R. Lawler is a PhD candidate in the Department of Anthropology at Yale University. His dissertation research focuses on the population genetics and mating system of the white sifaka. Alison F. Richard's research focuses on the evolution, ecology and social dynamics of primate populations, notably the white sifaka of Madagascar. Margaret A. Riley's research investigates the ecology and evolution of microbial defense systems.
