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GENETIC CONSEQUENCES OF MAMMALIAN SOCIAL STRUCTURE

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Populations of social mammals are characterized by several demographic features that may increase the magnitude of genetic drift relative to other evolutionary forces. In particular, polygynous mating and socially mediated constraints on gene flow have been proposed to foster random genetic differentiation among social groups, thereby accelerating rates of evolutionary change. To evaluate this hypothesized link between sociality and genetic subdivision, I examined results of published studies of mammalian populations in which genetic structuring was assessed at the level of social groups. Population genetic data from a taxonomically diverse array of social mammals revealed low to moderately high levels of genetic differentiation among social groups (F_{ST} = 0.006–0.227), coupled with consistently high levels of within-group heterozygosity indicated by negative F_{IS}-values. Relatively higher levels of genetic structuring were observed in populations in which sampling effects associated with polygynous mating were reinforced by female philopatry. The degree of genetic subdivision observed in several taxa, most notably black-tailed prairie dogs (*Cynomys ludovicianus*) and red howler monkeys (*Alouatta seniculus*), indicated that social organization can have a profound impact on population genetic structure. However, in most cases, social barriers to gene flow are likely insufficient to promote the degree of genetic subdivision and inbreeding envisioned by models of rapid drift-induced speciation. It appears that social mammals generally are characterized by a dynamic non-equilibrium mode of population structure in which local demes are characterized simultaneously by small variance effective sizes and large inbreeding effective sizes.

Key words: dispersal, effective population size, genetic subdivision, inbreeding, mating system, social-group fission

Populations of many mammalian species are subdivided into behaviorally segregated breeding groups maintained by sex-biased philopatry and territorial exclusion of immigrants (Chepko-Sade and Shields, 1987; Clutton-Brock, 1989*a*; Dobson, 1982; Greenwood, 1980; Pusey, 1987; Pusey and Packer, 1987*a*). These socially mediated constraints on gene flow, in combination with polygynous mating, are expected to reduce effective sizes (N_e) of local demes (Chesser et al., 1993; Nunney, 1993; Sugg and Chesser, 1994). This mode of socially defined population structure has the general effect of increasing the importance of genetic drift relative to other evolutionary forces and has been cited as a causal explanation for the apparently accelerated rates of chromosomal evolution and speciation in social mammals (Bush, 1975; Bush et al., 1977; Wilson et al., 1975). According to the Bush-Wilson hypothesis, joint effects of drift and inbreeding in socially structured populations facilitate fixation of underdominant chromosomal rearrangements, thereby establishing a postmating isolating mechanism that promotes stasipatric speciation (Bush, 1981; Coyne, 1993; Sites and Moritz, 1987; White, 1978). In this model, reproductive isolation is enforced by reduced fecundity of chromosomal heterozygotes due to meiotic malassortment and impaired gametogenesis. Although the actual degree of negative heterosis associated with chromosomal rearrangements remains controversial (Patton and Sherwood, 1983; Searle, 1993), the importance of small N_es for the fixation of underdominant gene variants is

well supported by analytical and simulation studies (Barton and Rouhani, 1991; Bengtsson and Bodmer, 1976; Chesser and Baker, 1986; Hedrick, 1981; Hedrick and Levin, 1984; Lande, 1979, 1984, 1985; Slatkin, 1981; Walsh, 1982; Wright, 1940, 1941). Because newly arisen chromosomal mutations will be present initially in the heterozygous state, such variants will persist and drift to fixation in subdivisions of a population only if local N_es are sufficiently small to override the effects of underdominant selection. Inbreeding can assist in this regard by speeding the transition of the rearrangement to the homozygous state (Hedrick, 1981).

Although it may prove difficult to test this model directly, it is possible to test a central prediction of the model; namely, that the social structuring of mammalian populations promotes genetic subdivision and inbreeding. The same features of population structure that have been proposed to accelerate rates of chromosomal divergence and speciation also should accelerate rates of change in frequencies of (pre-existing) neutral alleles across generations. Evolutionary consequences of social structure envisioned by the Bush-Wilson hypothesis thus provide explicit and testable predictions about gene dynamics in contemporary time. Specifically, the hypothesis predicts that the diversifying force of genetic drift, operating independently within behaviorally segregated breeding groups, is of sufficient magnitude to overpower the homogenizing influence of gene flow. Therefore, a significant fraction of the total genetic variance should be partitioned among social groups, even in the absence of differentiation at more inclusive levels of population subdivision.

The magnitude of genetic differentiation among social groups is determined by the combination of forces acting on them when they initially are formed and forces acting on them between their initial establishment and their eventual dissolution (Rogers, 1988). Thus, the overall degree of genetic subdivision in socially structured populations is determined by the net effects of sampling and mixing associated with three distinct but interrelated behavioral events: mating, dispersal, and formation of new social groups. Following the initial founding event, social dynamics determine population genetic structure through the interplay of gene flow (mediated by natal dispersal and intergroup exchange of breeding adults) and genetic drift (due to the sampling effects of reproduction). To assess the role of social structure in driving microevolutionary change, it is necessary to determine the independent and joint effects of each of these different behavioral factors on population genetic structure.

My objective was to evaluate the hypothesis that mammalian social structure promotes genetic subdivision and inbreeding. I compiled the results of published studies of mammalian populations in which genetic structuring was assessed at the level of social groups. A comparison of these results across a diverse array of species should provide insights into the general relationship between mammalian sociality and population genetic structure. Of primary interest was if particular features of the social system of a given species had any necessary or consistent relationship with the observed degree of genetic subdivision. Thus, where relevant behavioral and demographic data were available, I evaluated the relative importance of mating, dispersal, and formation of new social groups in determining the observed apportionment of genetic variance. I evaluated models that describe the influence of population genetic structure on different mechanisms of evolutionary diversification (Bush et al., 1977; Templeton, 1980, 1981; Wilson et al., 1975; Wright, 1980).

Materials and Methods

In the studies examined, genetic consequences of social structure were evaluated using a hierarchical genetic analysis in which social groups were treated as the fundamental level of popu-

lation subdivision (i.e., the least inclusive spatial scale at which genetic exchange occurs). I considered only those studies in which the sampling design distinguished between socially and geographically defined levels of population subdivision. In each study, the partitioning of genetic variance was assessed for a network of adjacent social units inhabiting a geographically contiguous area. Thus, interpretation of the degree of genetic subdivision attributable to social structure was minimally affected by the potentially confounding effects of extrinsic barriers to gene flow such as geographic distance or habitat fragmentation. In each case considered, social groups constituted an identifiable and distinct hierarchical level of population structure. Although demographic conditions that restrict gene flow and minimize N_e are not necessarily limited to taxa characterized by group-living sociality, I restricted the analysis to populations that were organized into distinct groups to make meaningful comparisons among studies. I considered only those studies in which among-group genetic variance was assessed at three or more polymorphic loci for three or more adjacent social units.

The partitioning of genetic variance within and among social groups was assessed in terms of hierarchical F-statistics (Wright, 1951, 1965) as applied to socially defined levels of population structure. Accordingly, F_{ST} provides a measure of the fraction of genetic variance partitioned among social groups, F_{IS} provides a measure of the allelic correlations within individuals relative to the social group, and F_{IT} provides a measure of the corresponding allelic correlations relative to the entire collection of social groups composing the local population. The value of F_{ST} can attain a theoretical minimum of zero, indicating complete panmixia, and a theoretical maximum of 1.0, indicating the reciprocal fixation of alternative alleles (Wright, 1951). The estimated values for F_{IS} and F_{IT} indicate the extent to which genotypic frequencies deviate from Hardy-Weinberg proportions within social groups and within the total collection of social groups, respectively. Values of F_{IS} and F_{IT} can each attain a theoretical minimum of -1.0 and a maximum of 1.0. If random mating prevails within the identified social units, positive values indicate positive allelic correlations between uniting gametes (excess homozygosity) due to close-pedigree inbreeding (F_{IS}), or due to the combined effects of close-pedigree inbreeding and the indirect inbreeding that accumulates in the extended pedigree of the total population (F_{IT}). In each study examined, population structure was assessed in terms of allozymic variation, except the studies of Girman et al. (1997) and Petit et al. (1997) in which variation at microsatellite loci was assayed. Although different marker loci and different numbers of loci were assayed in each study, the degree of genetic subdivision was estimated using a standardized index of allelic frequency variance, F_{ST}, that served as a useful statistic for comparisons among taxa with regard to the evolutionary implications of population structure (Hartl and Clark, 1997; Neel and Ward, 1972; Wright, 1978). A theoretical framework for the interpretation of F-statistics and effective sizes in socially structured populations (Sugg et al., 1996) was developed by Chesser (1991*a*, 1991*b*), Chesser et al. (1993), and Sugg and Chesser (1994).

Results

Population genetic data on differentiation among adjacent social groups were available from independent studies of 18 species of non-human mammals, representing five orders: Rodentia (n = 3), Carnivora (n = 1), Chiroptera (n = 3), Primates (n = 9), and Artiodactyla (n = 2; Table 1). The majority of F_{ST} values were <0.05, indicating relatively low levels of genetic structuring. With the exceptions of black-tailed prairie dogs (*Cynomys ludovicianus*—Chesser, 1983; Dobson et al., 1997, 1998), red howler monkeys (*Alouatta seniculus*—Pope, 1992, 1998), and white-tailed deer (*Odocoileus virginianus*—Mathews and Porter, 1993), each species was characterized by a population structure wherein >88% of the total genetic variance was contained within any single social group in the local population. No consistent patterns were apparent with respect to taxonomy. Populations of different primate species, for example, spanned the range of observed F_{ST} values, with red howler monkeys at the high end (F_{ST} = 0.225—Pope, 1992) and various macaque species (*Macaca*) at the low end (F_{ST}

= 0.067–0.006; de Ruiter, 1994; Kawamoto, 1996; Kawamoto et al., 1982; Melnick et al., 1984*b*; Nozawa et al., 1982; Shotake et al., 1991). F_{ST} values for black-tailed prairie dogs (Chesser, 1983; Dobson et al., 1997, 1998) and red howler monkeys (Pope, 1992) fell within the range (0.15–0.25) indicative of "moderately great genetic differentiation" according to the qualitative guidelines of Wright (1978: 85). According to the equilibrium expectations of Wright's (1951) island model, maximal F_{ST} values reported for populations of these two species (0.225 for troops of *A. seniculus*—Pope, 1992; 0.227 for coteries of *C. ludovicianus*—Chesser, 1983) indicated that levels of gene flow were too low to counteract genetic differentiation of social groups via drift. Although it is not clear to what extent socially structured populations might contravene one or more of the assumptions of the island model, these results implicate social barriers to gene flow as an important determinant of population genetic structure.

A relatively consistent pattern was apparent in the reported F_{IS} values (Table 1). With three exceptions, black-tailed prairie dogs (Chesser, 1983), long-tailed macaques (*Macaca fascicularis*—de Ruiter, 1994; Kawamoto et al., 1982), and hamadryas baboons (*Papio hamadryas*—Rogers, 1989), all F_{IS} values were negative, indicating excess levels of heterozygosity within social groups relative to Hardy-Weinberg proportions. As expected, F_{IT} was either close to zero, or small but positive in cases in which moderately high levels of genetic subdivision were recorded.

Discussion

The negative F_{IS} values (Table 1) suggest that high levels of heterozygosity within social groups may be a common feature of mammalian populations. Despite the apparent generality of high within-group variance (as measured by F_{IS}), there is no clear indication of a necessary or consistent relationship between social structure and among-group variance (as measured by F_{ST}). This agrees with the view of Lidicker and Patton (1987) that, in small-bodied rodents at least, genetic subdivision is not an inevitable outcome of social structure or spatially heterogeneous dispersion. However, despite the lack of any clear and consistent trends with respect to among-group variance, the relatively high F_{ST} values reported for some taxa, most notably black-tailed prairie dogs and red howler monkeys, indicate that social organization can have a profound impact on population genetic structure. A similar pattern of local heterogeneity in allelic frequencies coupled with relatively high levels of individual heterozygosity has been documented in pocket gophers (*Thomomys bottae*—Daly and Patton, 1990; Patton and Feder, 1981) and several other rodents (Lidicker and Patton, 1987). Thus, even in taxa characterized by more continuously distributed populations and lesser degrees of social cohesion, demographic conditions that promote skewed sex ratios, intrasexual variance in reproductive success, natal philopatry, and territoriality can produce the same genetic effects as those associated with group-living sociality. The potential evolutionary importance of microspatial population structure in mammals is exemplified by the fact that the level of genetic differentiation among adjacent social groups or spatially defined breeding units can exceed in some cases that between more inclusive, geographically defined subdivisions of a population. This disparity between local and regional levels of genetic divergence has been documented in black-tailed prairie dogs (Chesser, 1983; Dobson et al., 1997), California voles (*Microtus californicus*—Bowen, 1982), vervet monkeys (*Cercopithecus aethiops*—Dracopoli et al., 1983), rhesus macaques (*Macaca mulatta*—Melnick et al., 1984*a*, 1986), and red howler monkeys (Pope, 1992), and indicates that local genetic differentiation may be an important evolutionary force in mammalian populations.

The majority of mammalian species exhibit a social system characterized by po-

lygynous mating and female philopatry (Clutton-Brock, 1989*a*, 1989*b*; Greenwood, 1980). In the absence of close-pedigree inbreeding, this mode of social organization is expected to maximize genetic subdivision (Chesser, 1991*a*, 1991*b*; Nunney, 1993). Additionally, the shorter persistence times of social groups relative to more inclusive levels of population subdivision suggest that unstable local dynamics may play an important role in driving microevolutionary change. Studies of group-living mammals that combined behavioral and genetic data permit an assessment of specific ways in which mating, dispersal, and formation of new social groups influence population genetic structure.

Mating and dispersal.—Polygynous mating involves sampling a small nonrandom fraction of the gene pool of adult males in each generation. The ability of individual males to monopolize reproductive access to groups of females results in high levels of relatedness within the cohort of offspring in each group. Specifically, if a single male inseminates all breeding females in a group, progeny of different females will be related as paternal half-siblings ($R = 0.25$). Likewise, if litter size is greater than one, progeny of the same female will be full siblings ($R = 0.50$).

Female philopatry results in social groups that represent a reduced nonrandom fraction of the gene pool of adult females. Replacement of breeding females by their female progeny results in genetic differentiation among groups due to matrilineal allelic correlations that accrue independently within each social lineage. Levels of relatedness among breeding females within a group will be much higher than those between random females from different groups. Consequently, relatedness among members of a given cohort of offspring is enhanced by the collective inheritance of a correlated sample of maternally contributed alleles. If the degree of polygyny is high, this maternal coancestry within a cohort of offspring augments relatedness attributable to shared paternity. Thus, genetic homogeneity of a single group's cohort of offspring and the concomitant among-group variance at the population level are maximized by a high degree of polygyny coupled with a high degree of female philopatry. Studies of greater spear-nosed bats (*Phyllostomus hastatus*) and red howler monkeys illustrate the different ways in which the interplay between mating and dispersal can influence population genetic structure.

In Trinidad, West Indies, cave-roosting colonies of greater spear-nosed bats are subdivided into compact roosting clusters containing an average of 18 reproductive females (range = 10–25) and a single adult male (McCracken and Bradbury, 1977, 1981). These harems are highly stable, and female roostmates form long-term behavioral associations. Paternity-exclusion tests revealed that harem males sire 60–90% of the progeny in each harem's cohort of offspring and several males retained their harem-breeding status through a minimum of three reproductive periods (McCracken and Bradbury, 1981). This degree of polygyny indicates that individual harem males have a highly disproportionate impact on the genetic composition of succeeding generations. The most successful harem males may father ≥50 offspring during their reproductive lifespan, while the overwhelming majority of males who reach adulthood never acquire a harem and consequently fail to reproduce (McCracken and Bradbury, 1981). Clearly, a minute fraction of the total gene pool of adult males is sampled each generation. However, genetic structuring of cohorts of harem offspring is not incorporated into the gene pool of adults because juveniles of both sexes disperse from their natal harems, thereby randomizing the distribution of genetic variation within the total population ($F_{ST} = 0.031$—McCracken, 1987; McCracken and Bradbury, 1977, 1981).

In the central llanos of Venezuela, troops of red howler monkeys also are characterized by a harem polygynous mating system

TABLE 1.—*Partitioning of genetic variance within and among social units in local populations of group-living mammals.*

Taxon	Social units	Number of loci	F_{ST}	F_{IS}	F_{IT}	References
Rodentia						
Yellow-bellied marmot *Marmota flaviventris*	Colonies within a locality[a]	8	0.07	−0.09	−0.07	Schwartz and Armitage, 1980, 1981
Black-tailed prairie dog *Cynomys ludovicianus*						
New Mexico	Coteries within wards	7	0.227	0.112	0.307	Chesser, 1983
South Dakota	Coteries within wards	4	0.166	−0.218	−0.014	Dobson et al., 1997, 1998
Richardson's ground squirrel *Spermophilus richardsonii*	Matrilines within a locality	6	0.045	−0.397	−0.336	van Staaden et al., 1994
Carnivora						
African wild dog *Lycaon pictus*	Packs within a locality	14[c]		−0.021		Girman et al., 1997
Chiroptera						
Greater spear-nosed bat *Phyllostomus hastatus*	Harems within cave colonies	3	0.031			McCracken and Bradbury, 1977, 1981; McCracken, 1987
White-lined bat *Saccopteryx bilineata*						
Females	Roosting colonies within a locality	3	0.013			McCracken, 1984, 1987
Males	Roosting colonies within a locality	3	0.104			McCracken, 1984, 1987
Common vampire bat *Desmodus rotundus*	Multi-male/multi-female groups within a locality	7	0.049			Wilkinson, 1985
Primates						
Vervet monkey *Cercopithecus aethiops*						
Ethiopia	Troops within a locality	4	0.062			Turner, 1981
Kenya	Troops within a locality	4	0.08			Dracopoli et al., 1983

TABLE 1.—*Continued.*

Taxon	Social units	Number of loci	F_{ST}	F_{IS}	F_{IT}	References
Long-tailed macaque *Macaca fasciculatis*						
Sumatra	Troops[b] within a locality	10	0.045	0.016	0.060	de Ruiter, 1994
Lesser Sunda Islands	Troops[b] within a locality	4	0.022	0.086	0.106	Kawamoto et al., 1982
Moor macaque *Macaca maura*	Troops within a locality	7	0.067			Kawamoto, 1996
Japanese macaque *Macaca fuscata*	Troops within a locality	8	0.006			Nozawa et al. 1982
Rhesus macaque *Macaca mulatta*	Troops within a locality	5	0.040	−0.085	−0.049	Melnick et al., 1984*a*, 1984*b*
Toque macaque *Macaca sinica*	Troops within a locality	11	0.037			Shotake et al., 1991
Hamadryas baboon *Papio hamadryas*	Troops within a locality	4	0.053	0.073	0.123	Rogers, 1989
Gelada baboon *Theropithecus gelada*	Herds[b] within a locality	3	0.036			Shotake and Nozawa, 1984
Red howler monkey *Alouatta seniculus*						
Mata	Troops within a locality	9	0.225	−0.161	0.100	Pope, 1992, 1998
Gallery	Troops within a locality	8	0.142	−0.064	0.087	Pope, 1992, 1998
Piñero	Troops within a locality	6	0.09	−0.37	−0.24	Pope, 1998
El Frío	Troops within a locality	6	0.12	−0.27	−0.12	Pope, 1998
Artiodactyla						
White-tailed deer *Odocoileus virginianus*	Sociospatial groups within a locality	7	0.12	−0.25	0.10	Mathews and Porter, 1993
Mediterranean mouflon *Ovis gmelini*	Sociospatial groups within a locality	6[c]	0.043	−0.048		Petit et al., 1997

[a] For the sampling schemes employed in each study, locality denotes a geographically contiguous area circumscribed by the spatial extent of sampling effort.
[b] Social units likely constitute amalgamations of two or more functionally independent reproductive units.
[c] Variation was assessed at microsatellite loci.

(Pope, 1990, 1992). Troops of red howler monkeys typically consist of two to four adult females and at least one breeding male. Paternity-exclusion tests revealed that a single male, even in multi-male troops, generally sires all or most progeny (Pope, 1990). As with greater spear-nosed bats, adult females seldom transfer among troops. The periodic replacement of breeding males, which occurs every 7.5 years (0.67 female generations) on average, is the only source of gene flow into established troops. Juvenile males disperse from their natal troop before reaching breeding age, but unlike the case with greater spear-nosed bats, ca. 33% of female offspring are recruited into their natal troops; the remainder form new troops. In greater spear-nosed bats, sampling effects engendered by an extremely high variance in male reproductive success are counterbalanced by the mixing effects of natal dispersal. In contrast, genetic structuring of cohorts of offspring of red howler monkeys due to polygynous mating is reinforced by a moderate degree of female philopatry, resulting in high levels of genetic differentiation among adjacent troops (F_{ST} = 0.142–0.225—Pope, 1992).

Contrasting outcomes in this interplay between polygynous mating and female philopatry also have been observed in two species of highly social ground squirrels, the yellow-bellied marmot (*Marmota flaviventris*) and the black-tailed prairie dog. In the subalpine of Colorado, populations of yellow-bellied marmots are subdivided into discrete colonies, each containing a single territorial male and one to five adult females (Armitage, 1984, 1986, 1991; Schwartz and Armitage, 1981). Within each group, paternity apparently is restricted to the resident male (Armitage, 1986; Schwartz and Armitage, 1980). About one-half of the female offspring are recruited into their natal colony, whereas nearly all males disperse before reaching sexual maturity (Armitage, 1984; Schwartz and Armitage, 1980). As a result, levels of gene flow among colonies are sufficient to prevent substantial genetic structuring (F_{ST} = 0.07—Schwartz and Armitage, 1980, 1981). In South Dakota, local populations of black-tailed prairie dogs are subdivided into discrete wards, each of which is further subdivided into coteries that typically contain a single territorial male and two to three females (Hoogland, 1995). With few exceptions, paternity within coteries is restricted to the resident male and variance in lifetime reproductive success is substantially higher for males relative to females (Hoogland, 1995). In contrast to marmots, natal dispersal is almost exclusively limited to males (Dobson et al., 1997, 1998; Hoogland, 1995). Consequently, populations of black-tailed prairie dogs exhibit a substantial degree of genetic differentiation among coteries (F_{ST} = 0.166—Dobson et al., 1997, 1998). Chesser (1983) reported even higher levels of genetic divergence among coteries for this same species in New Mexico (F_{ST} = 0.227).

Inbreeding also can enhance genetic structuring of social groups. When females are philopatric, the potential for inbreeding depends on the frequency with which breeding tenure of males overlaps the onset of sexual maturity of their female progeny and the frequency with which juvenile males attain breeding status within their natal group (either as a result of non-dispersal or dispersal followed by a return to the natal group after one or more intergroup transfers). Thus, when females are philopatric, the potential level of inbreeding will be determined by the rate at which males transfer among groups.

Inbreeding may be minimized in populations of social mammals either as a direct result of behaviors that promote the active avoidance of incestuous matings or as an indirect outcome of sex-biased dispersal (Clutton-Brock, 1989*a*; Dobson, 1982; Moore, 1993; Pusey, 1987; Pusey and Wolf, 1996; Smith, 1993). Either way, levels of inbreeding within populations of social mammals are unlikely to conform to expec-

tations of traditional demic models of population genetics (Chesser 1991*a*, 1991*b*; Sugg et al., 1996). When mate choice and recruitment into breeding groups are determined by complex behavioral associations or discrimination of kin, patterns of mating are probably highly nonrandom (Sugg et al., 1996). For example, in a harem-polygynous social system characterized by male dispersal and female philopatry, all or most matings occur between an immigrant male derived from one matriline and multiple females composing a divergent matriline. This results in positive allelic correlations among female gametes within a group, but negative allelic correlations between female gametes and those of the immigrant male. This negative correlation between uniting gametes within social groups results in a disproportionately high level of heterozygosity within the first generation offspring. The extent to which this excess of heterozygotes departs from Hardy-Weinberg equilibrium (measured by F_{IS}) is directly proportional to the genetic variance between matrilines (Chesser, 1991*a*; Prout, 1981). Therefore, genetic differentiation among social groups and heterozygosity within them will be maximized when single males mate exclusively within the same female matrilines across multiple generations (Chesser, 1991*a*, 1991*b*). This relationship between intergroup divergence and heterozygote excess runs counter to predictions of genetic models designed for geographic demes (Kimura and Weiss, 1964; Wright, 1978), in which restricted gene flow leads to the gradual loss of genetic variation and increased correlations between uniting gametes as a result of indirect inbreeding.

The negative F_{IS}-values (Table 1) most likely reflect the consequences of male dispersal and female philopatry. With the exception of African wild dogs (*Lycaon pictus*—Girman et al., 1997), a pattern of male-biased dispersal characterizes each of the species for which negative F_{IS}-values were reported (Table 1), and appears to be the prevailing mode of intergroup transfer in mammals in general (Clutton-Brock, 1989*a*; Dobson, 1982; Greenwood, 1980; Pusey and Packer, 1987*a*; Smith, 1993). Taken at face value, these negative F_{IS}-values support the suggestion that mammalian social groups generally are not characterized by substantial levels of inbreeding (Ralls et al., 1986). However, identification of causes underlying a particular value of F_{IS} is problematic as several different features of population structure can cause genotypic proportions to depart from Hardy-Weinberg equilibrium, thereby potentially masking or enhancing effects of inbreeding (Neel and Ward, 1972). In populations of social mammals, where mates are often drawn from genetically differentiated social lineages, a substantial degree of inbreeding may be required to register a positive F_{IS}. In villages of the Yanomama tribe (*Homo sapiens*), for example, Neel and Ward (1972) reported an F_{IS} value of -0.012 despite relatively high levels of observed inbreeding in the form of first-cousin matings (MacCluer et al., 1971; Neel, 1978).

Positive F_{IS} values in black-tailed prairie dogs (Chesser, 1983), long-tailed macaques (*Macaca fascicularis*—de Ruiter, 1994; Kawamoto et al., 1982), and hamadryas baboons (*Papio hamadryas*—Rogers, 1989) are not necessarily indicative of inbreeding and may be explained by non-random mating within the social units sampled. For example, troops of long-tailed macaques in the lowland rainforest of Sumatra are composed of 8–50 individuals of both sexes (de Ruiter, 1994; de Ruiter and Geffen, 1998; de Ruiter et al., 1994). Although each troop represents a discrete social unit, reproductive dominance relationships among both males and females results in considerable reproductive substructuring. Paternity-exclusion tests revealed that the α-male generally sires 50–90% of the progeny within a given cohort of offspring and mates preferentially with closely related females that have high social ranks. The β-male sires the remaining 10–50% of the troop's progeny and mates with females of lower-ranking

matrilines (de Ruiter and Geffen, 1998; de Ruiter et al., 1994). The resultant genotypic variance between the progeny of high- and low-ranking matrilines should then result in a disproportionate number of homozygotes relative to Hardy-Weinberg expectations for the troop as a whole. The magnitude of homozygote excess relative to Hardy-Weinberg equilibrium (measured by F_{IS}) is proportional to the genetic variance between the two reproductive subgroups (Wahlund, 1928).

Formation of new social groups.—Formation of a new social group involves the sampling of alleles from one or more parent groups. The degree of randomness in this sampling will determine levels of genetic variance within newly-formed groups and consequently, the level of among-group variance at the population level. If founders of a new group are drawn randomly from an array of genetically distinct parent groups, genetic correlations within the nascent group will be low. This mode of group formation conforms to Slatkin's (1977) migrant-pool model of colonization and may either enhance or diminish genetic subdivision, depending on the nature of the founding event (Wade and McCauley, 1988; Whitlock and McCauley, 1990). By contrast, if new groups form by the fissioning of formerly cohesive social groups, genetic correlations within daughter groups may be relatively high. This mode of group formation conforms to Slatkin's (1977) propagule-pool model of colonization and may significantly enhance levels of genetic variance among groups (Wade and McCauley, 1988; Whitlock and McCauley, 1990). As discussed above, the degree of polygyny and female philopatry jointly determine the extent to which groups (or age cohorts within groups) are oriented along lines of patrilineal or matrilineal descent. If fissioning occurs along such lines of kinship, the resulting daughter groups will be much more genetically distinct from one another, and other groups in the population, than would be the case if fissioning were random (Smouse et al., 1981; Whitlock and McCauley, 1990). The migrant-pool and propagule-pool models of colonization represent extreme ends of a continuum that varies according to the probability of common origin among founders of new groups (Whitlock and McCauley, 1990). For fissioning of social groups to enhance genetic subdivision in the total population, genetic variance among newly formed groups must be greater than that among pre-existing groups at genetic equilibrium (Whitlock and McCauley, 1990). Genetic variance among newly founded groups is determined by size of the founding group, probability of common origin among the founders, and degree of randomness in group fission with respect to kinship (Fix, 1978; Rogers, 1987, 1988; Rogers and Harpending, 1986; Wade and McCauley, 1988; Whitlock and McCauley, 1990).

Fissioning of social groups has been reported for black-tailed prairie dogs (Hoogland, 1995), yellow-bellied marmots (Armitage, 1984), white-nosed coatis (*Nasua narica*—Gompper et al., 1997), African lions (*Panthera leo*—Pusey and Packer, 1987*b*), and a variety of cercopithecine primates (Chepko-Sade and Sade, 1979; Dittus, 1988; Melnick and Kidd, 1983; Nash, 1976; Scheffrahn et al., 1993). With respect to population genetic consequences, the phenomenon has been studied most intensively in macaques (Melnick, 1987; Melnick and Hoelzer, 1996). Social groups of rhesus macaques are reported to fission along lines of matrilineal kinship (Chepko-Sade and Sade, 1979; Ober et al., 1984). This mode of new group formation represents an extreme form of Slatkin's (1977) propagule-pool model of colonization, in which founding groups are kin-structured (Whitlock and McCauley, 1990). The potential for matrilineal fission to enhance genetic subdivision is maximized by a high variance in the number of progeny per breeding female and a low degree of polygyny (Melnick, 1987; Melnick and Kidd, 1983). When variance in the number of

progeny per female is high, it is more likely that a small number of matrilines within a group will achieve disproportionate representation in succeeding generations (Melnick, 1987; Melnick and Hoelzer, 1996; Pope, 1996, 1998). The lineal fissioning of groups comprising a small number of well-differentiated matrilines will produce daughter groups that are genetically distinct from one another and other groups in the population. In the free-ranging colony of rhesus macaques in Cayo Santiago, Puerto Rico, for example, matrilineal fission dramatically increases average degree of relatedness within newly formed groups (Chepko-Sade and Olivier, 1979; Chepko-Sade and Sade, 1979; Olivier et al., 1981) and genetic differentiation among groups (Buetnner-Janusch et al., 1983; Cheverud and Dow, 1985; Cheverud et al., 1978; Duggleby, 1977; Ober et al., 1984). In contrast, when variance in the number of progeny per female is low, groups will comprise a relatively greater number of matrilines, each containing relatively fewer individuals. The lineal fissioning of such groups will produce daughter groups that likely contain representatives of multiple matrilines.

The degree of relatedness within each of the newly formed groups will be relatively low and the level of genetic variance between them will be correspondingly reduced. In a wild population of rhesus macaques in Dunga Gali, Pakistan, matrilineal fission produced daughter groups that were no more genetically distinct from one another than would be expected if fissioning were random (Melnick and Kidd, 1983). Contrasting effects of social group fission in the populations of rhesus macaques in Cayo Santiago and Dunga Gali also may be partly explained by the prevailing degree of polygyny (Melnick, 1987; Melnick and Hoelzer, 1996; Melnick and Kidd, 1983). When the degree of polygyny is high, patrilineal relatedness among members of a given age cohort may dilute the genetic impact of matrilineal differentiation when groups split (Altmann, 1979; Melnick and Kidd, 1983). Relative to the situation in Cayo Santiago, paternity within the troops in Dunga Gali is reportedly restricted to a proportionately smaller number of males (Melnick, 1987; Melnick and Hoelzer, 1996). Consequently, genetic divergence between matrilines within a group is constrained by patrilineal relatedness, and matrilineal fission does not appreciably enhance genetic variance between daughter groups beyond that expected by effects of random sampling alone (Melnick and Kidd, 1983).

With regard to population genetic structure, the importance of the formation of new social groups relative to the effects of mating and dispersal depends on the rate at which it occurs. If the mode of formation of new groups enhances the magnitude of genetic drift, the importance of the associated sampling effects relative to those associated with each subsequent reproductive cycle is determined by how long social groups persist. Likewise, if the mode of formation of new groups enhances gene flow, the importance of the associated mixing effects relative to those associated with recurrent intergroup dispersal also is determined by persistence times of social groups. For example, in the populations of red howler monkeys studied by Pope (1992, 1998), new troops are formed by solitary dispersers of both sexes. Matrilineal relatedness accrues within troops from one generation to the next as a result of differential recruitment of the female progeny of a single female. As a result, relatedness is higher within established troops than in newly formed troops. Thus, the mean level of genetic variance among troops is inversely proportional to the rate at which new troops are formed. Pope (1992, 1998) documented how rates of formation of new troops produced a disparity in among-group genetic variance in four study populations in Venezuela that were undergoing different rates of growth. Mixing effects associated with the founding of new troops were especially

pronounced in the more rapidly growing population, resulting in a lower overall degree of genetic subdivision. The opposite pattern is expected when social groups split along lines of kinship. When fissioning of social groups is lineal, relatedness is expected to be highest in newly formed groups. In such cases, population genetic structure is expected to be most pronounced when the rate of formation of new groups is high, as expected during colonization by an expanding population.

In macaques at least, evidence suggests that under certain ecological and demographic conditions, formation of new social groups by lineal fissioning may enhance genetic subdivision. Because kinship appears to play an important role in maintaining behavioral cohesiveness of social groups (Armitage, 1987), fissioning of groups along kin lines may prove to be a common feature of the demography of social mammals. It thus seems likely that group formation in social mammals will often entail sampling effects that significantly enhance genetic subdivision.

Evolution in socially structured populations.—The Bush-Wilson hypothesis (Bush, 1975; Bush et al., 1977; Wilson et al., 1975) of chromosomal evolution and stasipatric speciation envisions populations of social mammals as networks of partially isolated demes characterized by small N_es and relatively high levels of inbreeding. This same mode of population structure is a prerequisite for the operation of phase 1 of the shifting-balance process of evolution (Wright, 1931, 1932, 1940, 1941, 1980). The picture that emerges from the findings reviewed here suggests that social units of mammalian populations do not closely approximate the inbred isolates envisioned by the Bush-Wilson hypothesis. This hypothesis predicts the general occurrence of high F_{ST} (due to the combined effects of small N_es and low rates of intergroup dispersal) and positive F_{IS} values (due to inbreeding within closed social groups). Inbreeding is an important component of the process of chromosomal transilience because an increased level of individual homozygosity is expected to mitigate the effects of underdominant selection by reducing the number of generations during which chromosomal variants segregate in heterozygotes. With the exception of Chesser's (1983) study, high F_{ST} values (0.12–0.225—Dobson et al., 1997, 1998; Mathews and Porter, 1993; Pope, 1992, 1998) were always accompanied by strongly negative F_{IS} values (Table 1), indicating significant levels of heterozygote excess. It thus appears that in populations of many mammalian species, social units are characterized simultaneously by small variance N_es (due to female-biased breeding sex ratios compounded by a high variance in intrasexual reproductive success) and large inbreeding N_es (due to inbreeding avoidance or random mating in combination with sex-biased dispersal). In mammalian populations, it thus appears that inbreeding N_es are not generally small enough to mitigate effects of negative heterosis associated with chromosomal rearrangements, and social barriers to gene flow are typically not strong enough to facilitate the local fixation of such variants. I conclude that mammalian social structure does not generally produce population genetic effects that would facilitate stasipatric speciation through chromosomal transilience (Patton and Sherwood, 1983; Templeton, 1981).

Compared to Wright's (1951) island model, it seems likely that group-living social mammals generally are characterized by a more dynamic, non-equilibrium mode of population structure in which lineal fissioning of social groups plays an important role in determining the spatial and temporal distribution of genetic variation. Relative to the island model, this type of socially defined population structure is much more conducive to founder-induced speciation through genetic transilience (Templeton, 1980). In a socially structured population characterized by high levels of heterozygosity within groups, a founding event po-

tentially can induce a dramatic reduction in the inbreeding N_e. However, if new groups are formed through lineal fissioning, low levels of genetic variance within a given founder group may result in a reduced capacity to respond to the selective bottleneck. This mode of new group formation appears to be common among cercopithecine primates (Melnick, 1987; Melnick and Hoelzer, 1996). In contrast, if new groups are formed by random sampling across the population, the founder event would still induce the necessary reduction in inbreeding N_e, but the level of genetic variance within a given founder group would be augmented by the variance partitioned among groups in the ancestral population (F_{ST}). Thus, formation of new groups that conforms to Slatkin's (1977) migrant-pool model of colonization provides optimal conditions for genetic transilience in socially structured populations (Templeton, 1980). This mode of formation of new groups has been reported in red howler monkeys (Pope, 1992, 1998) and may be common in those taxa in which territorial behavior precludes immigration into established groups. As pointed out by Melnick et al. (1984*a*), social structure alone may not produce the degree of genetic subdivision envisioned by the Bush-Wilson hypothesis, but it may facilitate such subdivision in the event of geographical or ecological isolation. Because newly formed social groups may be more likely to disperse from their original home range and colonize previously unoccupied peripheral environments, sampling effects associated with the formation of new groups may significantly enhance genetic divergence due to habitat fragmentation.

Although the role of social structure in different modes of drift-induced diversification remains uncertain, genetic structuring of social groups likely exerts a powerful influence on the course of microevolutionary change within populations of many mammalian species. Because the genotypic composition of social groups may influence the inclusive fitness of individual group members (Hamilton, 1964*a*, 1964*b*) and the opportunity for interdemic selection (Wade, 1982; Wade and McCauley, 1980, 1984; Wilson, 1975), socially defined population structure has far-reaching implications for a diverse array of evolutionary processes.

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