GENETIC CORRELATIONS AND MATRILINEAL STRUCTURE IN A POPULATION OF *SPERMOPHILUS RICHARDSONII*

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We analyzed nine matrilines within a single population of Richardson's ground squirrels (*Spermophilus richardsonii*) from southern Alberta, Canada, for genetic variability at six allozymic loci. Significant genetic differentiation was found among matrilines. The matrix of genetic distance between each pair of individuals was randomly associated with geographic distance, but matrices of genetic distance and coancestry, as well as coancestry and geographic distance, were significantly negatively correlated. Neighboring females tended to be more related than would be expected due to chance, not only within the entire population, but within individual matrilines as well. Correlation of coancestry and genetic distance values indicates that the predictability of kinship from genotypic data alone is unreliable. Female philopatry gives rise to non-random spatial and genetic associations of related individuals. This is the first documented genetic difference between matrilines for a sciurid species with a relatively low level of social complexity.

Key words: population genetics, genetic substructure, *Spermophilus richardsonii*, Richardson's ground squirrel, philopatry, Canada

The dispersal of animals from their natal areas classically was considered to be a random process (Wright, 1940) both in terms of sex and distance. However, observations of a variety of natural populations have documented sexual differences in dispersal tendencies (Cheney and Seyfarth, 1983; Chesser, 1983; Daly, 1981). Such sexual differences in dispersal affect the genetical structure of the population (Chesser, 1991*a*, 1991*b*; Chesser et al., 1993*a*; Prout, 1981), the dispersing sex being responsible for potential gene flow and increasing genetic homogeneity, whereas the philopatric sex enhances stability and genetic discontinuity in the population. Few empirical studies have considered the consequences of dispersal and philopatry for intra-populational genetic structure (but see Waser and Elliott, 1991).

Because philopatry promotes correlation of genes between individuals, genetic similarity over short distances should be high. Geographic proximity of closely related individuals (i.e., those in which the coefficient of relationship $r \geq 0.5$) has been identified in populations of both *Microtus pennsylvanicus* (Sheridan and Tamarin, 1986) and *Marmota flaviventris* (Armitage, 1988). Significant genetic differentiation between social subgroups has been demonstrated for a variety of animals including humans (Neel and Ward, 1972), rhesus monkeys (*Macaca mulatta*—Melnick et al., 1984), black-tailed prairie dogs (*Cynomys ludovicianus*—Chesser, 1983), and yellow-bellied marmots (*M. flaviventris*—Schwartz and Armitage, 1980). However the associated paucity of heterozygotes within groups

most frequently has been interpreted as evidence of outbreeding rather than an effect of social structure (Chesser, 1991*b*).

Extensive behavioral and ecological studies of Richardson's ground squirrel (*Spermophilus richardsonii*) indicate that dispersal by males, philopatry by females, and the retention of social bonds between female kin result in a social system that is matrilineal and matrifocal (Davis, 1984; Michener, 1983*a*). Previous genetic studies of this species primarily were concerned with determining systematic relationships (but see Michener and Michener, 1977). Eleven polymorphic loci have been reported in various phylogenetic studies (Nadler et al., 1982; Serov et al., 1974) using small samples from diverse populations, but the level of genetic variance and the partitioning of this variance in natural populations are unknown.

We investigated the geographic and genetic affinities of matrilineages within a single population of *S. richardsonii,* the null hypothesis being that females are randomly dispersed in the population. Specifically, we aimed to determine whether readily identifiable matrilines exist within the geography of the population and whether this social structure is reflected also in a genetic structuring of the population. We also attempted to discriminate between isolation by distance and behavior as possible determinants of population structure.

Study Area and Methods

Population site and history.—The 18.5-ha study site, located 8 km E Picture Butte, Alberta, Canada (49°59′N, 112°40′W, elev. 870 m), was bounded by a paved highway, cultivated fields, a cattle feed lot, and residences such that it was separated by several kilometers from other large areas of habitat for ground squirrels. The site was flat with a few depressions that temporarily accumulated water from melting snow or heavy rain. Richardson's ground squirrels were known to have inhabited the site since the late 1800s when the district was homesteaded. The land was cultivated for cereals, sugar beets, and alfalfa from 1906 to 1965 when it was seeded to pasture and stocked each spring with domestic cattle. Squirrels reinvaded the site after cultivation ceased. Sporadic poisoning of squirrels before 1979 and removal of some litters from 1979 to 1981 kept population density low. Thereafter, the density of ground squirrels increased from 6.7 adults/ha in 1982 to 12.8 adults/ha in 1984 and to 37.0 adults/ha in 1986 (Michener, 1989). The population was not homogeneously distributed on the site; in 1986, local densities ranged from 11 to 54 adults/ha.

Trapping and ear-tagging of Richardson's ground squirrels began on portions of the study site in 1979, and squirrels were intensively monitored from 1982 to 1986 (Michener, 1983*b*, 1984, 1989; Michener and Locklear, 1990). Both males and females were sexually mature on emergence from their first hibernation at 44–50 weeks of age. Maternity of juveniles, determined at first emergence from the natal burrow, was based on the known identity of the female occupying the burrow system. Paternity was not known for the majority of juveniles. From 1982 to 1985, all litters reared within a focal site of 1.4 ha were trapped at natal emergence, and maternity assigned (89 young in 11 litters in 1982, 141 in 19 litters in 1983, 186 in 32 litters in 1984, and 256 in 37 litters in 1985). Maternity also was assigned to 406 young in 56 litters reared on an additional 17 ha surrounding the focal site in 1982, to 511 young in 71 litters on 17 ha in 1983, and to 382 young in 56 litters on 11 ha in 1984. In 1985, synchronous emergence of litters (67% of litters emerged in a 4-day period), combined with proximity of litters due to the high population density, limited correct assignment of maternity to litters on the focal site and to an additional 38 young in five litters adjacent to this site.

The study was terminated in March 1986 at the request of the landowner by removing the entire population. Of 570 females and 115 males on the 18.5-ha site in the mating season, 505 females and 70 males were still resident at the time of removal. Four lactating females were not collected, and seven females and two males were released elsewhere; the remaining 562 (494 females, 68 males) squirrels were killed by inhalation of carbon dioxide or ether after initial injection of an anesthetic. Tissue (liver, heart, kidney, and skeletal muscle) samples were collected and transferred frozen to Texas Tech University for genetic analyses. With the exception of 94 animals used in a study of bo
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was sired by a single male, and that

of 94 animals used in a study of body composition, skeletal material from the remaining specimens was lodged at the Provincial Museum of Alberta in Edmonton.

Genealogy.—In 1986, virtually all females (92% of 89) resident on the focal site and the majority of females (58% of 59) on the immediately adjacent 1.3 ha were of known maternal history. Maternal identity was known for an additional 88 females elsewhere on the site.

Pedigrees were constructed for all females with known maternal history. The majority (83% of 204) of these females were members of nine matrilines traceable to two females first captured as adults in 1978, two captured as adults in 1979, three females born in 1979, one female captured as an adult in 1980, and one captured as an adult in 1981. These nine matrilines had memberships of five to 34 known descendants in 1986. For four matrilines (founded by females 46, 76, 79, and 3092) localized in the focal site, virtually all descendants were identifiable in 1986. For four matrilines (founded by females 29, 80, 112, and 3093) adjacent to the focal site, all descendants ≥2 years old were identifiable in 1986, but some (matrilines 29 and 3093) or most (matrilines 80 and 112) yearlings were not identifiable because maternal identity had not been assigned to them as juveniles. In one matriline (founded by female 164) remote from the focal site, descendants ≥3 years old were identifiable in 1986, but most 2-year-olds and all yearlings were not identifiable.

Genealogical information facilitated the development of matrilineal pedigrees and the calculation of measures of genetic relationship. Here, we report coancestry, a value that indicates the expected correlation of genes between two individuals due to common ancestry. If those individuals are not inbred, coancestry equals one-half the coefficient of relationship. Coancestry was calculated using the equation:

$$\Phi_{ab} = \frac{1}{4}(\Phi_{F_aF_b} + \Phi_{F_aM_b} + \Phi_{M_aF_b} + \Phi_{M_aM_b}) \quad (1)$$

(Jacquard, 1974), in which Φ represents the expected correlation of genes between individuals a and b due to common ancestry (Cockerham, 1969), and subscripts F and M refer to the father and mother of the respective individuals. We assumed that inbreeding was zero, that each litter was sired by a single male, and that the founding females for each matriline, and all males, were unrelated. Thus, for this study, the coancestry of females within a matrilineage was estimated as:

$$\Phi_{ab} = \frac{1}{4}(\Phi_{M_aM_b}) \quad (2)$$

and the value of $\Phi_{M_aM_b}$ for each pair of females was determined from the pedigree (cf. Jacquard, 1974). While we recognize that these assumptions do not hold absolutely, the extent to which they are violated is unassessable. Spatial dispersion patterns of individuals within the study area were determined by usage of burrows. Geographic location in subsequent analyses is that of the burrow at which the animal was first captured following emergence from hibernation.

Electrophoretic methods.—Tissue samples obtained from 142 adult females with known matrilineal affiliations were analyzed. Tissues were homogenized in a grinding solution (Tris-EDTA, pH 6.8), and the homogenate was stored in an ultra-cold freezer at −80°C.

Fifty-four loci were resolved using standard horizontal starch-gel electrophoresis. Staining procedures essentially followed those of Harris and Hopkinson (1976). The following 49 loci were monomorphic or inconsistently scorable (associated Enzyme Commission number in parentheses): acid phosphatase (3.1.3.2); aconitase (4.2.1.3); adenosine deaminase (3.5.4.4); adenylate kinase (2.7.1.20); albumin; alcohol dehydrogenase (1.1.1.1); aldehyde oxidase (1.2.3.1); aldehyde reductase (1.1.1.2); aldolase (4.1.2.13); alkaline phosphatase (3.1.3.1); aspartate aminotransferase (2.6.1.1); catalase (1.11.1.6); creatine kinase (2.7.3.2); NADH diaphorase (1.6.2.2); fumarase (4.2.1.2); β-galactosidase (3.2.1.23); glucokinase (2.7.1.2); glucose dehydrogenase (1.1.1.47); glucose-6-phosphate isomerase (5.3.1.9); α-glucosidase (3.2.1.20); β-glucosidase (3.2.1.21); glutamate dehydrogenase (1.4.1.2); glutamate pyruvic transaminase (2.6.1.2); glutathione reductase (1.6.4.2); glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12); glyceric dehydrogenase (1.1.1.29); glycerol-3-phosphate dehydrogenase (1.1.1.8); guanine deaminase (3.5.4.3); hexokinase (2.7.1.1); hexosaminidase (3.2.1.52); inorganic pyrophosphatase (3.6.1.1); isocitrate dehydrogenase (1.1.1.42); lactate dehydrogenase (1.1.1.27); leucine aminopeptidase (3.4.11.1); malate dehydrogenase (1.1.1.37); malic enzyme (1.1.1.40); mannose-6-phosphate isomerase

(5.3.1.8); α-mannosidase (3.2.1.24); peptidase 1, 2, 3, and 4 (3.4.11.−); phosphoglucomutase (2.7.5.1); phosphogluconate dehydrogenase (1.1.1.46); phosphoglycerate kinase (2.7.2.3); purine-nucleoside phosphorylase (2.4.2.1); pyruvic kinase (2.7.1.40); shikimic kinase (2.7.1.71); succinate dehydrogenase (1.3.99.1); superoxide dismutase (1.15.1.1); triose-phosphate isomerase (5.3.1.1); xanthine dehydrogenase (1.2.1.37).

Five loci (abbreviation and associated Enzyme Commission number in parentheses) were polymorphic and consistently scorable: esterase (EST, 3.1.1.1); glucose-6-phosphate dehydrogenase (GD, 1.1.1.49); 6-phosphogluconate dehydrogenase (6-PGD, 1.1.1.44); sorbitol dehydrogenase (SORDH, 1.1.1.14); transferrin (TFN). In addition, a single variable locus, protein-1 (PRO-1), which was further unidentified, was resolved on vertical slab polyacrylamide-gel electrophoresis (7% gel with a tris-HCl pH 8.5 buffer) with upper and lower tank electrode buffers tris-HCl (pH 7.3) and tris-glycine (pH 8.8), respectively. Tissue samples were diluted 1:1 with bromophenol blue-sucrose loading buffer prior to electrophoresis (5°C, 38 mA, 5 h). Gels were stained overnight with Coomassie Brilliant Blue R250 and destained in 11% acetic acid, and the mobilities of PRO-1 bands were scored relative to a known standard.

Statistical analysis.—Genetic differentiation of ground squirrels was analyzed using Wright's (1965) *F*-statistics as modified by Nei (1977), reflecting the degree of genetic divergence between the matrilines (F_{ST}), and the divergence from random mating within (F_{IS}) and among (F_{IT}) the matrilineages. Significance of differences in gene frequency was tested for each locus by the chi-square test, $\chi^2 = 2nF_{ST}(k - 1)$ with $(k - 1)(s - 1)$ degrees of freedom, where n is the total sample size, k is the number of alleles for the locus, and s is the number of matrilines (Workman and Niswander, 1970). The F_{ST}-values were corrected for the binomial sampling variance as $F_{ST} = F_{ST} - (1/2n)$ (Workman and Niswander, 1970), and all *F*-values were calculated using weighted means and variances of allelic frequencies. Statistical analyses were performed on a VAX 8650 computer using FORTRAN-77 programs. Significance was considered when the probability of obtaining the observed result by chance alone was <5% (α = 0.05).

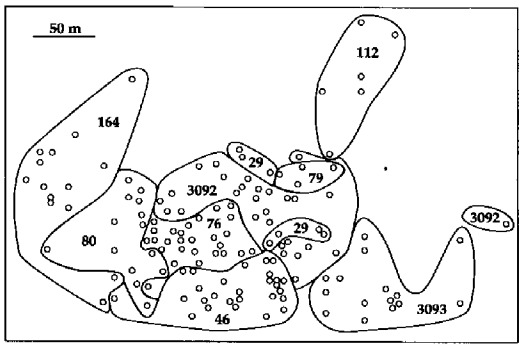

FIG. 1.—Spatial distribution of female *Spermophilus richardsonii* from nine matrilines resident at the time of removal in 1986. Location is based on the burrow site at which each squirrel was first captured following emergence from hibernation. Solid lines enclose members of a lineage. Numbers refer to the lineage "founder."

Genetic distance, a measure summarizing the degree to which individuals differ in the genetic characteristics assayed, was calculated according to Rogers (1972) using all individuals for which some electrophoretic data were available. Because data were incomplete for some individuals at some loci, genetic distance was calculated relative to the number of loci common to the individuals compared. Geographic distance was the straight line distance between each pair of individuals at emergence in spring of 1986. Coancestry values were calculated from pedigrees as previously described. Mantel matrix correlations (Mantel, 1967) were employed to investigate the relationship between parametric (Φ) and directly sampled (D) genetic distance measures (Rogers, 1972) and geographic distance.

RESULTS

Kin clusters and coancestry.—Because female Richardson's ground squirrels rarely dispersed, kin tended to remain spatially clustered as adults (Fig. 1). Females settled near their kin both in years when population density was low (<8 females/ha in 1982 and 1983) and high (>25 females/ha in 1985 and 1986). Dispersal occasionally occurred, providing the potential for a matriline to split into several clusters. For example, two cousins in matriline 29

independently moved ca. 85 and
2-year-olds in 1985, such that the
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from matriline 3092. These fem
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were recorded for two yearling
but neither had surviving desc
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venile in 1985 that disappeared
after emergence in 1986; new
did not develop as a result of the
movements. Between emergence
in 1986 and removal of squirre
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potential founders of split matril
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(Fig. 1).

Pedigrees showing the genea
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spring 1986 in the four larges
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(0.002–0.250) for matriline
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independently moved ca. 85 and 120 m as 2-year-olds in 1985, such that they were remote from close kin and adjacent to females from matriline 3092. These females and a daughter born to each of them in 1985 remained resident at the new location in 1986, thus establishing a focus for another kin cluster. A split arose in matriline 3092 in 1985 when two yearling sisters dispersed ca. 120 and 165 m, independently establishing residence in an area of low density. Because these females were then outside the monitored area, their offspring were not captured in 1985 and only the one surviving disperser could be identified in the new locale in 1986. Movements of >120 m also were recorded for two yearlings in 1982, but neither had surviving descendants in 1983, one juvenile in 1984 that was removed from the site in 1985 and one juvenile in 1985 that disappeared <1 week after emergence in 1986; new kin clusters did not develop as a result of these dispersal movements. Between emergence of females in 1986 and removal of squirrels 3 weeks later, a yearling and a 2-year-old moved >120 m and, therefore, would have been potential founders of split matrilines. However, such dispersal by females was rare, and some dispersers did not succeed in founding new kin clusters; therefore, most related adult females lived within a single kin cluster derived from a single matriarch (Fig. 1).

Pedigrees showing the genealogical relationships among adult females present in spring 1986 in the four largest matrilines are given in Fig. 2. Average expected genetic correlation (coancestry) values between individuals within matrilines ranged from 0.036 to 0.175 with five averaging below 0.0625 (first cousins). Average coancestry (minimum and maximum in parentheses) for matrilines where virtually all descendants were identifiable were: 0.036 (0.001–0.250) for matriline 46; 0.037 (0.002–0.250) for matriline 76; 0.175 (0.016–0.250) for matriline 79; 0.052 (0.001–0.250) for matriline 3092. For matrilines where some descendants were unidentified, these values were 0.073 (0.008–0.250) for matriline 29; 0.057 (0.016–0.250) for matriline 80; 0.088 (0.004–0.250) for matriline 112; 0.041 (0.004–0.250) for matriline 164; 0.102 (0.002–0.250) for matriline 3093.

Fixation indices.—For females in the nine matrilines, allelic frequencies were: 0.663, 0.284 and 0.053 for PRO-1 (n = 141); 0.842 and 0.158 for SORDH (n = 120); 0.913 and 0.087 for EST (n = 138); 0.692 and 0.308 for GD (n = 112); 0.761, 0.151, and 0.088 for 6-PGD (n = 136); 0.600 and 0.400 for TFN (n = 130). Results of analysis of the standardized variance of allelic frequencies (F_{ST}'s; Table 1) indicated significant differentiation among matrilines at two of the six variable loci examined. Differentiation of allelic frequencies also was significant when data from all loci were combined. For individual matrilines, F_{IS}-values were negative for all loci except PRO-1 for which a paucity of heterozygotes was indicated. The negative F_{IS}-value indicated that, on average, heterozygous animals exceeded that expected within each matriline. Similarly, negative F_{IT}-values indicated fewer homozygous individuals than expected for five of six loci and when data are pooled across all matrilines. This concordance of F_{IS}- and F_{IT}-values indicates that there is no Wahlund effect, i.e., that subdivisions of the population have been accurately defined. On average, ca. 5% of the total variance of allelic frequencies was due to the genetic differences of squirrels among the matrilines ($\bar{F}_{ST}$ = 0.045); that is, ca. 95% ($1 - \bar{F}_{ST}$) of the total gene diversity is found within any given matriline.

Mantel matrix comparisons.—Mantel matrix-correlation procedures (Table 2) demonstrated a significant negative correlation between matrices of interindividual coancestry and geographic distance in three of the four largest matrilines as well as across all matrilines combined, indicating that females with high coancestry lived in greater proximity than those with low coan-

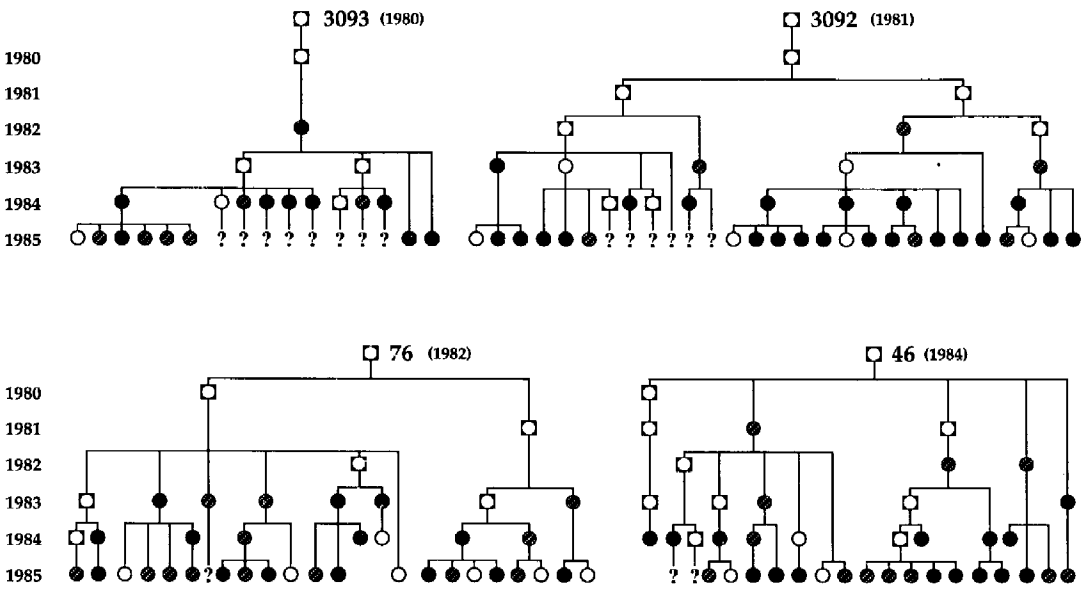

FIG. 2.—Matrilineal pedigrees for descendant adult female *Spermophilus richardsonii* alive in 1986 from the four largest lineages (17, 30, 34, and 34 known descendants for matrilines 3093, 46, 76, and 3092, respectively) sampled in a population in southern Alberta. The identification number for the "founder" female is given at the top of each pedigree; the year in which the founder was last alive is given in parentheses. Descendants are listed in their year of birth. Circles indicate females alive in 1986; solid circles depict females for which complete electrophoretic data were available, striped circles indicate females for which partial electrophoretic data were available, and open circles indicate females for which no electrophoretic data were available as they were not collected, died or disappeared before collection, or were released at a new site. A question mark indicates that yearling descendants from that female may have been present, but were not recognizable because maternal identity was not assigned in 1985. These pedigrees only display connections that resulted in living female descendants in 1986; squares indicate females that were no longer alive in 1986, but were progenitors of the females present in 1986.

cestry. A significant negative relationship was detected between coancestry and genetic distances in two of the four largest matrilines and across all matrilines combined, indicating that, in a general sense, parametric and empirical measures of genetic variation are in agreement. Matrices of genetic and geographic distances were not significantly associated.

DISCUSSION

Female *S. richardsonii* exhibit philopatry or site tenacity, which results in a non-random geographic distribution of matrilineages in which related individuals are spatially contiguous. Significant negative correlation of coancestry and geographic distance indicates that neighboring females tend to be more related than expected by chance, not only in the total population, but also within single matrilines. Results of the present study indicate that there is no isolation by distance effect, but that behavioral factors result in a population that is genetically structured in a non-random manner.

Variance partitioning.—Social organization has a discernible effect on the distribution of genotypes within this single population. The average genetic differentiation between matrilines is ca. 5% (F_{ST} = 0.045), greater than that among social groups of rhesus monkeys (F_{ST} = 0.035—Melnick et al., 1984) or villages of tribal Makiritare (F_{ST} = 0.036—Neel and Ward, 1972), but

TABLE 1.—*F-statistics for six varie rels from nine matrilines within a si Significance of the* F_{ST} *values was de*

Locus	F_{IT}
PRO-1	0.589
SORDH	−0.815
EST	−0.704
GD	−0.425
6-PGD	−0.449
TFN	−0.210
Mean	−0.336

** Significant at $P \leq 0.01$.
*** Significant at $P \leq 0.001$.

lower than that between villages mama (F_{ST} = 0.063—Neel a 1972). It is well within reported local differentiation of other sm rodents ranging from 0.02 (Bowe ford, 1987) to 0.07 (Patton a 1981), is similar to that of house *musculus*) from different farm 0.047—Selander and Kaufman, almost twice that found between different barns (F_{ST} = 0.025—Se Kaufman, 1975). Heterogeneity a trilines of Richardson's ground sc proximates that between wards v ulations of black-tailed prairie d 0.045 to 0.065—Chesser, 1983), stantially less than that amon

TABLE 2.—*Mantel matrix correla and coancestry (Φ) for four matril combined. Sample sizes* n_d *apply to animals for which electrophoretic a adjusted to be the same size. Sampl lation of* $\Phi \times G$.

Matriline	n_d	
46	27	−(
76	27	(
3092	28	−(
3093	15	−(
Combined	142	−(

* Significant matrix correlation at $P \leq 0.0$
** Significant matrix correlation at $P \leq 0.0$

TABLE 1.—*F-statistics for six variable loci, and for combined loci, in Richardson's ground squirrels from nine matrilines within a single population. Locus abbreviations are explained in the text. Significance of the* F_{ST} *values was determined by chi-square.*

Locus	F_{IT}	F_{IS}	F_{ST}	χ^2	*d.f.*
PRO-1	0.589	0.570	0.043	1,169.4***	16
SORDH	−0.815	−0.843	0.015	2.5	8
EST	−0.704	−0.731	0.016	3.1	8
GD	−0.425	−0.616	0.118	18.0**	8
6-PGD	−0.449	−0.511	0.041	16.7	16
TFN	−0.210	−0.254	0.035	5.5	8
Mean	−0.336	−0.397	0.045	1,215.2***	64

** Significant at $P \leq 0.01$.
*** Significant at $P \leq 0.001$.

lower than that between villages of Yonomama (F_{ST} = 0.063—Neel and Ward, 1972). It is well within reported values for local differentiation of other small-bodied rodents ranging from 0.02 (Bowen and Koford, 1987) to 0.07 (Patton and Feder, 1981), is similar to that of house mice (*Mus musculus*) from different farms (F_{ST} = 0.047—Selander and Kaufman, 1975), and almost twice that found between mice from different barns (F_{ST} = 0.025—Selander and Kaufman, 1975). Heterogeneity among matrilines of Richardson's ground squirrels approximates that between wards within populations of black-tailed prairie dogs (F_{ST} = 0.045 to 0.065—Chesser, 1983), but is substantially less than that among coteries within wards (F_{ST} = 0.227—Chesser, 1983).

Theoretical models by Rothman et al. (1974) and computer simulations by Fix (1978) demonstrated that the splitting of lineages has an inflationary effect on F_{ST}-values, even when the population was effectively a single breeding unit with extensive gene flow. The relatively high F_{ST}-values documented here owe little to the effects of matrilineal fissioning because splitting of matrilines in ground squirrels is relatively rare. Over the 6-year study period, only two (28.5%) of seven documented intrapopulational dispersals (>120 m) with the potential to found matrilines succeeded in doing so, and only one of these contrib-

TABLE 2.—*Mantel matrix correlations of geographic distance* (G)*, Rogers' genetic distance* (D)*, and coancestry* (Φ) *for four matrilines of Richardson's ground squirrels and for nine matrilines combined. Sample sizes* n_d *apply to correlations with genetic distance* (D) *and reflect the number of animals for which electrophoretic data were available; matrix sizes of the dependent matrix were adjusted to be the same size. Sample sizes* n_a *include all animals alive in 1986 and apply to correlation of* $\Phi \times$ G.

		Matrix correlations			
Matriline	n_d	$\Phi \times D$	$G \times D$	$\Phi \times G$	n_a
46	27	−0.019	−0.015	−0.228**	30
76	27	0.013	0.099	−0.073**	34
3092	28	−0.072*	−0.080	−0.242**	34
3093	15	−0.194**	−0.044	−0.142	17
Combined	142	−0.015*	−0.049	−0.146**	170

* Significant matrix correlation at $P \leq 0.05$.
** Significant matrix correlation at $P \leq 0.01$.

uted to the variance partitioning values presented here.

The trend for negative F_{IS}-values (Table 1), indicative of excess heterozygosity within lineages, is concordant with expectations for sex-dependent migration (Prout, 1981) and socially structured populations (Chesser, 1991*a*, 1991*b*; Cockerham, 1969, 1973) in which genetic units have been accurately identified. Overall, the variance partitioning values indicate that limitations to intrapopulational movements, possibly imposed by intraspecific antagonistic interactions, have a significant effect in genetically structuring populations of Richardson's ground squirrels.

Behavior and genetic structure.—Isolation by distance is not a significant factor in genetically structuring the population. The random association of geographic and genetic distance, both overall and in the analyses of four individual matrilines, is expected given the small area occupied by the population and the few variable loci encountered. Males were highly mobile in the mating season and could easily traverse the entire study site, but their freedom to do so was strongly constrained by the aggressiveness of neighboring males. Genetic structure in this population, thus, reflects behavioral restrictions rather than physiographic limitations.

Behavioral observations of *S. richardsonii* provide some indication of social factors contributing to genetic differentiation within the population and support the prediction of theoretical models that philopatry and polygyny are not independently evolved (Chesser, 1991*a*; Chesser et al., 1993*b*). Where there is close kinship through the maternal line, kin groupings can be identified by a greater proximity between the members than between members of the group at large (Michener, 1983*a*). Although greater overlap of home ranges occurs among female kin than non-kin, kin clusters do not appear to develop into cooperative social groupings, and each adult female retains a core area and separate natal burrow (Michener, 1979, 1983*a*). Such behaviors result in a population consisting of small philopatric groups and create genetic discontinuities in the population. Genetic differentiation between matrilines of *S. richardsonii* may be further enhanced by a tendency to non-random mating. Close spatial location of related females as well as the brevity of the mating season and male-male aggression during this time (Michener, 1983*b*) make it likely that a male's mates are localized; thus, his mates are related to each other and localized litters may share a common father, thereby increasing their genetic relatedness.

At least two other behavioral processes are occurring that influence genetic structure by decreasing genetic differentiation. Dispersal by males makes it unlikely that males mate with close female kin, and multiple mating by females results in litters of mixed paternity thereby decreasing their genetic relatedness.

Coancestry and genetic distance.—Although significant overall, correlations between coancestry and genetic matrices are relatively weak. Similar weak correlations between kinship and genetic distance were identified by O'Brien (1987) in her study of colonies in a Hutterite population. Our findings confirm her view that gene-frequency data are not reliable sources of information on which to base direct inferences about population structure. Because we can neither assign paternity nor identify relationships between the females prior to 1979, the coancestry values used here are conservative. Females outnumber males, and all females are impregnated; therefore, many males must mate with several females. If a male's mates include females from the same lineage, some offspring will be more related than would be predicted on the basis of the matrilineal pedigree alone. Conversely, if a female mates with several males, multiple paternity decreases relatedness within matrilines because littermates could be either full or half siblings. Some females do mate with several males (Michener, 1984), and there is strong evidence that tw litters of *S. richardsonii* in this had multiple sires (M. J. van Sta obser.). As the level of protein phism in this population is low additional loci probably would resolve genotypic variation; mole yses of highly polymorphic, co and selectively neutral sites are reveal genotypic variation more t

According to Lewontin (197 proportion of populational geneti exists within the small units of tion. Our results indicate that, c genetic differences among mat 5% those of complete differentia 95% of the overall genetic diver population is found within matri result is concordant with the fir number of studies of non-humar where individual social groups found to include >90% of the versity of the local population 1987).

The genetic structuring repor the first documented genetic dif tween social matrilineages for classified as having a relatively l social complexity within the gro ing sciurids. *S. richardsonii* is pl second level of a five-grade s creasing sociality (Michener whereas species previously show it fine-scale genetic structuring, lied marmots (Schwartz and 1980) and black-tailed prairie d ser, 1983), occupy levels 4 and tively. Regardless of whether ge ture per se is of proximate sign individual squirrels, the result o lineal subdivision is a patchwo combinations over relatively sh es. Population structure in this sp corresponds to that required in terdemic selection model of Wr and the trait-group model of se posed by Wilson (1977) and len to the suggestion that genetic

there is strong evidence that two of seven litters of *S. richardsonii* in this population had multiple sires (M. J. van Staaden, pers. obser.). As the level of protein polymorphism in this population is low, sampling additional loci probably would not further resolve genotypic variation; molecular analyses of highly polymorphic, co-dominant, and selectively neutral sites are required to reveal genotypic variation more thoroughly.

According to Lewontin (1972), a large proportion of populational genetic variation exists within the small units of a population. Our results indicate that, on average, genetic differences among matrilines are 5% those of complete differentiation. Thus, 95% of the overall genetic diversity in the population is found within matrilines. This result is concordant with the findings of a number of studies of non-human primates, where individual social groups have been found to include >90% of the genetic diversity of the local population (Melnick, 1987).

The genetic structuring reported here is the first documented genetic difference between social matrilineages for a species classified as having a relatively low level of social complexity within the ground-dwelling sciurids. *S. richardsonii* is placed on the second level of a five-grade scale of increasing sociality (Michener, 1983*a*), whereas species previously shown to exhibit fine-scale genetic structuring, yellow-bellied marmots (Schwartz and Armitage, 1980) and black-tailed prairie dogs (Chesser, 1983), occupy levels 4 and 5, respectively. Regardless of whether genetic structure per se is of proximate significance for individual squirrels, the result of the matrilineal subdivision is a patchwork of gene combinations over relatively short distances. Population structure in this species, thus, corresponds to that required in both the interdemic selection model of Wright (1982) and the trait-group model of selection proposed by Wilson (1977) and lends credence to the suggestion that genetic differences over small distances may be the rule rather than the exception (Smith et al., 1978).

Acknowledgments

F. S. Dobson, M. Beane, and J. Layng helped with collection of squirrels in 1986. L. Haney kindly permitted access to the land. F. S. Dobson, M. R. Gannon, R. Huber, C. Jones, J. K. Jones, Jr., M. K. Rylander, and M. R. Willig offered valuable criticism of previous versions of this manuscript. This project was supported in part by grants from the Council for Scientific and Industrial Research, University of Natal (Durban), Sigma Xi, The American Society of Mammalogists, and the Graduate School of Texas Tech University (to M. J. van Staaden) and from the Natural Sciences and Engineering Research Council of Canada (to G. R. Michener).

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Submitted 19 April 1993. Accepted 27 October 1993.

Associate Editor was Karen McBee.