Spatial analysis of microgeographic genetic structure in Richardson's ground squirrels

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Abstract: Local genetic structure has a sound theoretical basis, yet empirical demonstration in animal species has proved elusive, even in apparently ideal candidate species. Techniques based on the distribution of individual genotypes may offer a more complete picture of population structure than traditional measures focusing on isolation by distance and dispersal behavior. We used spatial autocorrelation and contiguous clustering to identify structure in a population of Richardson's ground squirrel (*Spermophilus richardsonii*) for which deviation from Hardy–Weinberg expectations indicated population subdivision. Nonrandom aggregates of genotypes were detected at five of six enzyme loci examined and selection at one locus. Genetic structuring was highly sex-dependent, being prominent only among females. Isolation by distance cannot account for the patterns of gene diversity observed, but Mantel matrix procedures of inter-individual distance based on demographic–behavioral characteristics and geographic distance were significantly associated. Social and breeding systems of *S. richardsonii* lead to significant local substructure. While philopatry alone may not account for fine-scale genetic structure in small mammals with sex-biased dispersal, nonrandom aggregates will be detected if appropriate social models and rigorous sampling criteria are adopted. Identification of such localized structure remains fundamental to understanding evolutionary models of population genetic structure and sociality.

Résumé : La structure génétique de populations locales repose sur des bases théoriques solides, mais la démonstration empirique d'une structure génétique à l'échelle spécifique est toujours incertaine, même chez des espèces qui sont apparemment idéales pour un tel exercice. Les techniques basées sur la répartition de génotypes individuels offrent probablement une vue d'ensemble plus complète de la structure d'une population que les mesures traditionnelles qui tiennent surtout compte de l'isolement en distance et du comportement de dispersion. Nous avons utilisé des autocorrélations spatiales et des analyses de groupements contigus pour reconnaître la structure d'une population de Spermophiles de Richardson (*Spermophilus richardsonii*) qui différait du modèle Hardy–Weinberg et laissait soupçonner l'existence de sub-divisions. Des regroupements aléatoires de génotypes ont été détectés à cinq des six locus examinés et un locus s'est avéré un siège de sélection. La structure génétique est fortement liée au sexe, un phénomène évident seulement chez les femelles. L'isolement lié à la distance ne peut expliquer les patterns de diversité génétique observés, mais les procédures qui servent à établir la distance entre individus dans une matrice de Mantel et qui sont basées sur les caractéristiques démographiques–comportementales et celles qui sont basées sur les distances géographiques sont reliées significativement. Les systèmes social et reproducteur de *S. richardsonii* mettent en place une sous-structure locale importante. Alors que la philopatrie ne peut à elle seule expliquer la structure génétique fine chez des petits mammifères où la dispersion est l'apanage de l'un des sexes, des regroupements non aléatoires seront détectés à l'utilisation de modèles sociaux appropriés et de critères d'échantillonnage rigoureux. L'identification d'une telle structure localisée reste un atout fondamental à la compréhension de modèles évolutifs de la structure génétique et sociale des populations.
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Introduction

Exploration of the interactions underlying evolutionary models of population genetic structure and sociality (Hamilton 1964a, 1964b; Wilson et al. 1975; Baker and Marler 1980) demands unambiguous description of genetic structure on a microgeographic scale. This has proved elusive, and empirical studies have frequently failed to detect local structure in animals, even in apparently ideal candidate species such as fossorial mammals with sex-biased dispersal and extreme philopatry for one sex (Gaines and Krebs 1971; Daly 1981; Waser and Elliott 1991). In most of these studies, expectations are based on an isolation by distance model focusing exclusively on the effect of dispersal behaviors (Wright 1943). However, theoretical "social" models indicate that dispersal may be less

significant than breeding tactics in genetically structuring populations (Chesser 1991*a*) and that expectations from classical models cannot be applied to local genetic structure (Chesser 1991*b*). Moreover, traditional measures of genetic differentiation such as fixation indices lack a spatial dimension, and a more complete picture of population structure may be obtained from spatial autocorrelation and contiguous clustering (Chesser and Van Den Bussche 1988), which are based on the spatial distribution of individuals (Epperson and Allard 1989; Argyres and Schmitt 1991; White and Svendsen 1992).

This study focuses on local genetic structure within a single population of Richardson's ground squirrel (*Spermophilus richardsonii*) in southern Alberta, Canada. The social structure of this predominantly herbivorous species has been characterized as "single-family kin cluster" and ranked relatively low in comparison with those of other ground-dwelling sciurids (Armitage 1981; Michener 1983*a*). The species is common on short-grass prairie in the northern United States and Canada, where it now occurs in discrete populations separated by expanses of agricultural activity. The sex ratio among adult *S. richardsonii* is significantly biased toward females, regardless of calendar year, geographical location, size of study site, and population density (Michener 1989). This female bias is generated by lower interyear survival of males, whose greater mobility increases their vulnerability to predation, and from more intense mate competition among males (Michener 1989).

Richardson's ground squirrels in the study population had been monitored for over 6 years (e.g., Michener 1983*b*; Michener 1990; Michener and Locklear 1990). Detailed spatial information on known individuals and the wealth of demographic data for animals in the study population provided an opportunity to identify the structure and determinants of spatial genetic variation in a single population. First we evaluate the likelihood of panmixia versus the existence of genetic subdivision at the level of the entire sample by testing for adherance to Hardy–Weinberg equilibrium. We then analyze the distribution of individual genotypes within the spatial confines of the population and interpret this with regard to the sciurid social and breeding system. Genetic distances among individuals are examined for correlation with geographic distances and with demographic and behavioral characteristics. Finally, contrasting approaches to the investigation of genetic structure are evaluated on the basis of these findings.

Materials and methods

Population history and genetics

The population of *S. richardsonii* inhabited 18.5 ha of cattle pasture located 8 km east of Picture Butte, Alberta, Canada (49°52′N, 112°40′W; elevation 870 m). The site, which was nearly flat and homogeneous, had not been cultivated since 1966. Squirrels had inhabited the area for at least the last 90 years, and population density increased after cessation of cultivation and poisoning. In particular, population density increased 5.5-fold from 1982 to 1986 (6.7–37.0 adults/ha; Michener 1989). Squirrels were not uniformly distributed throughout the site; local densities in 1986 ranged from 11 to 54 adults/ha.

The behavioral ecology of *S. richardsonii* on the site was studied (e.g., Michener 1983*b*; Michener and Locklear 1990) from 1978 to

1986, when a change in land-management practice by the owner forced destruction of the population. In March 1986, when females were in the final trimester of pregnancy, virtually the entire population was removed by livetrapping. Tissue samples (liver, heart, kidney, muscle) were obtained from 494 adult females and 68 adult males. Detailed information on population history, trapping and killing methods, and electrophoretic procedures appear in Michener (1984, 1985, 1989), Dobson and Michener (1995), and van Staaden et al. (1994).

Fifty-five loci were examined, of which 6 were variable and consistently scorable; these were glucose-6-phosphate dehydrogenase (*Gd*), 6-phosphogluconate dehydrogenase (*6-Pgd*), sorbitol dehydrogenase (*Sordh*), esterase (*Est*), transferrin (*Tfn*), and an unidentified locus detected with general protein staining (*Pro-1*). Loci were biallelic except for *6-Pgd* and *Pro-1*, which had three alleles each. Twenty-three of 24 possible genotypes were found, 21 common to both sexes and 1 unique to each sex.

To test for adherance to Hardy–Weinberg equilibrium and thus distinguish between panmixia and subdivision at the level of the entire sample we employed a χ^2 test. For all subsequent analyses the general approach used was analysis of individual genotypes rather than of population allele frequencies.

Spatial analyses of genetic characteristics

Spatial dispersion patterns of individuals within the study area (500 × 250 m) were determined from burrow usage. The study site was inspected daily for the emergence of new animals from hibernation from 2 February 1986 onwards and newly emerged animals were livetrapped immediately, usually within 24 h after first coming above ground. The geographic location of each adult (≥ 1 year old) squirrel on this first capture after emergence was used in spatial analyses. Location was recorded to the nearest 1 m with reference to a 15-m grid on the western 14.0 ha of the site. On the more sparsely populated eastern 4.5 ha, where 11.5% of squirrels emerged, locations were recorded to ±30 m with reference to a 60-m grid.

Nominal spatial autocorrelation of genotypes (Sokal and Oden 1978; Cliff and Ord 1981) was performed separately for adult males and adult females at six variable loci to identify specific distances over which nonrandom associations of genotypes occur. Spatial autocorrelation analysis tests whether the observed value of a variable at one locality is significantly correlated with the values at neighboring localities. Here we assumed a continuous population, and used join-count statistics to determine the separation distances over which spatial distribution of individual genotypes was nonrandom. Results are presented as correlograms in which standard normal deviates (SND) are plotted over a range of separation distances. SND values in excess of +1.96 and −1.96 indicate a significant ($\alpha = 0.05$) nonrandom correlation of individuals, identifying a greater or lesser number of homotypic pairs than expected, respectively. Preliminary tests ranging from 5 to 50 m identified units of 30 m as the most informative resolution for separation distance. Spatial distribution of the sexes was also examined by autocorrelation.

Contiguous clustering (Chesser and Van Den Bussche 1988) was then used to identify the precise spatial location of nonrandom aggregates of genotypes. This method compares the distribution of characters in a spatially contiguous subgroup with that of the entire population using χ^2 cross-entropy values (binomial distribution). Contiguous clustering was performed separately for adult males and females at all six loci.

To facilitate comparison of different loci, only females for which data for all six loci were available were used ($n = 328$). Although these comprised a random subset of the original sample, two-thirds of the 166 excluded females were located in the eastern section of the population. Because sample sizes for males were

smaller, none were excluded; sample sizes for different loci varied from 26 to 61.

Analyses of correlated factors

The importance of spatial separation (i.e., isolation by distance) and life-history features for inter-individual genotypic differences was probed by a pairwise set of Mantel's matrix procedures (Mantel 1967; Smouse et al. 1986). The matrix of inter-individual genetic distances was calculated according to Rogers (1972) for all females for which complete genetic data were available. Geographic distance was the straight-line distance between pairs of individuals at emergence from hibernation. Inter-individual differences in life history for females ($n = 328$) resident in 1986 were characterized as the Euclidean distance of age (in years), emergence date, emergence mass (recorded to nearest 5 g), litter size (from embryo counts and litters born in captivity), and number of estrous periods (one or two; procedure SIMILARITIES; SPSSx Inc. 1988). These characteristics encompassed the complex of life-history traits of burrowing sciurids (Armitage 1981), primarily reflecting breeding tactics. The matrix of composite distance measures was related to geographic and genetic distance measures.

Results

Hardy–Weinberg equilibrium

Though it says nothing about spatial clustering within the sample area, the χ^2 test is a direct and sufficiently powerful test of panmixia versus subdivision in the study population as a whole, owing to the large sample size and low number of alleles. All loci deviated significantly ($P \leq 0.001$) from expected proportions: Pro-1 ($n = 543$, 3 df, $\chi^2 = 55.858$); Sordh ($n = 469$, 1 df, $\chi^2 = 77.074$); Est ($n = 535$, 1 df, $\chi^2 = 91.717$); Gd ($n = 409$, 1 df, $\chi^2 = 52.564$); 6-Pgd ($n = 516$, 3 df, $\chi^2 = 265.189$); and Tfn ($n = 486$, 1 df, $\chi^2 = 101.618$). All loci displayed a paucity of heterozygotes, except for Pro-1, which had an excess.

Spatial autocorrelation

Significant spatial autocorrelation was detected for 86% of the 23 genotypes examined. The most informative analyses, and the least susceptible to random fluctuations, are typically those for like-homozygotes of the most common allele at each locus (Fig. 1). For males and females, 6 and 20 out of 90 possible SND values, respectively, were significantly different from null expectations. Correlograms with highly significant test statistics over several distances indicated local genetic structure in females (Fig. 1A), whereas males were not structured (Fig. 1B). With the exception of the Pro-1 locus, the tendency in females is for negative correlations at short distances and positive correlations at greater distances. Because it is rare that many enzyme polymorphisms track the same environmental agent, we follow Sokal and Oden (1991) in attributing these common patterns to migration. In contrast, the single Pro-1 correlogram, representing a unique pattern, is interpreted to indicate selection on this locus.

Contiguous clustering for genotypes

Significant clustering of genotypes was found for both males and females at all loci (Table 1). Females demonstrated a higher degree of genetic substructure than males (Fig. 2), forming an average of 75 clusters per locus (range 60–101). Of the 450 clusters identified, 99 contiguous clusters were significant at $P \leq 0.001$ and 351 at $P \leq 0.01$. Average cluster length was 84.7 ± 16.6 m (range 56.4–160.5 m). All individuals were included in more than one significant cluster. The percentage of individuals clustered per locus varied from 61.2 to 83.5% (Table 1), with 77% of females clustered at $P \leq 0.001$. In contrast, within the male populace only a total of 33 contiguous clusters was found over the six loci, with an average of 5.5 significant clusters per locus (range 1–9). Average cluster length (maximum separation distance) was 99.2 ± 8.0 m (range 69.3–124.7 m). Twenty of 61 males (32.8%) were not included in any significant cluster, whereas 32 individuals (78% of those clustered) were included in more than one cluster, and 33% of males clustered at $P \leq 0.001$. Clusters unique at this significance level are shown in Fig. 2C. Considering male clusters at both levels of significance, it is evident that Est and Gd formed few and relatively small clusters compared with the other loci examined (Table 1). There were few differences among loci except in mean separation distance, the average of all possible distances between individuals in a cluster, which ranged from 63.5 m in 6-Pgd to 124.7 m in Gd. An interesting arrangement of genotypes was noted for Pro-1, with homozygous clusters located on the periphery of the population and heterozygous clusters located toward the center.

Genetics, geography, and individual characteristics

The matrix of life-history measures for females was based on five variables with the following descriptive statistics (mean ± SD, with the range in parentheses): age (years) 1.9 ± 0.7 (1–5); litter size 6.9 ± 2.0 (0–14); emergence date 7–8 March ± 3.7 days (26 February – 19 March); emergence mass (g) 227 ± 35 (150–330); number of estrous periods 1.0 ± 0.2 (1–2).

Mantel matrix regression indicated that genetic distance was not significantly related to geographic ($R = -0.028$) or life-history distance matrices ($R = 0.002$), indicating that isolation by distance and individual differences were not significant factors in the genetic structuring of this population. However, as matrices of geographic and life-history distance were related ($R = 0.136$, $P \leq 0.001$), geographically closer individuals were more similar in terms of life-history characteristics than those more widely separated.

Spatial autocorrelation of sex showed only two significant associations. Significantly fewer females ($0.05 < P < 0.01$), but more males ($P < 0.001$) than expected, were separated by a distance of 150 m.

Discussion

Overall, our data indicate that Richardson's ground squirrels within this single population are not genetically panmictic, but rather are significantly clustered. Despite the potential for individual movement over areas larger than the entire study site, behavioral or historical factors have resulted in insufficient genetic exchange to homogenize the distribution of genotypes throughout the population. This is consistent with findings of local genetic structure in other social mammals, including black-tailed prairie dogs (Chesser 1983), eastern chipmunks (White and Svendsen 1992), humans (Neel and Ward 1972), and red howler monkeys (Pope 1992).

Fig. 1. Spatial autocorrelation analysis for like-homozygotes of the most common allele at six loci for adult female ($n = 328$) (A) and adult male ($n = 60$) *Spermophilus richardsonii* (B) as a function of geographic distance. Ordinate indicates standard normal deviates (SND) and the abscissa indicates separation distances. Asterisks indicate SND values that are significant at $\alpha = 0.05$.
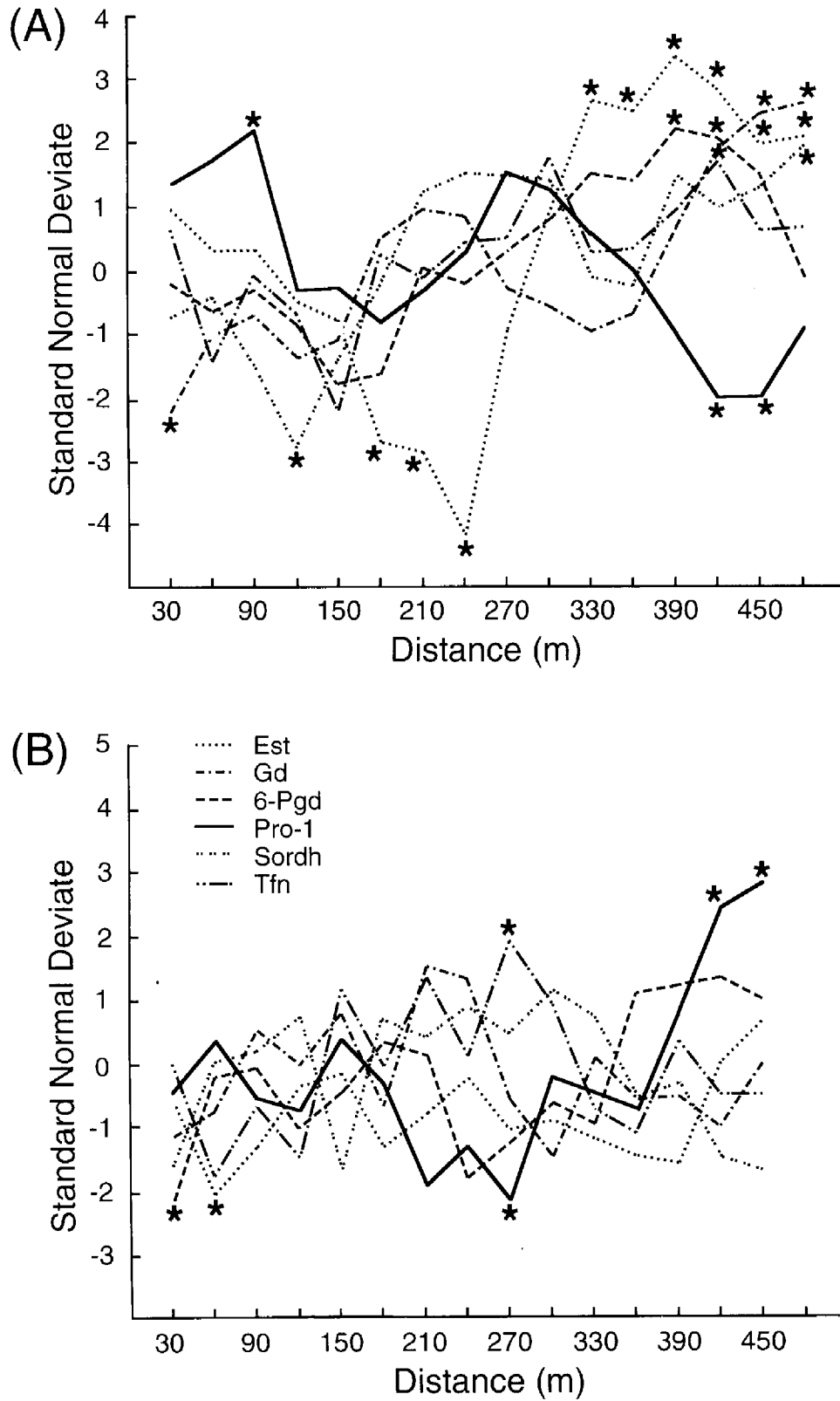
Table 1. Contiguous clustering (Chesser and Van Den Bussche 1988) by genotype for adult female (*n* = 328) and male *Spermophilus richardsonii*.

Locus	No. of clusters at: P ≤ 0.001	P ≤ 0.01	% individuals clustered: once	>once	Mean no. of individuals per cluster	Mean proportion of clusters with tested genotype	Mean separation distance (m)	Mean max. separation distance (m)
Females								
Pro-1	17	45	82.3	52.3	10.8 (4.56)	0.84 (0.05)	32.8 (4.82)	58.9 (12.46)
Sordh	10	58	78.6	71.0	34.8 (10.46)	0.77 (0.07)	51.8 (6.34)	101.1 (16.87)
Est	28	73	79.8	76.2	62.9 (8.68)	0.86 (0.04)	73.6 (6.21)	160.5 (17.13)
Gd	17	43	61.2	41.9	18.3 (6.34)	0.81 (0.07)	39.6 (5.39)	69.5 (13.15)
6-Pgd	16	60	83.5	58.7	10.4 (4.86)	0.87 (0.05)	37.0 (4.81)	62.3 (13.91)
Tfn	11	72	70.3	46.8	9.1 (2.68)	0.92 (0.03)	31.6 (4.25)	56.4 (9.55)
Males								
Pro-1 (n = 61)	5	4	44.3	6.6	4.6 (1.30)	0.91 (0.11)	87.4 (19.49)	123.4 (32.53)
Sordh (n = 43)	1	5	37.2	9.3	3.3 (0.99)	1.00 (1.00)	81.8 (25.47)	112.9 (21.04)
Est (n = 60)	0	3	10.0	0.0	2.0 (0.00)	1.00 (0.00)	75.3 (91.67)	75.3 (91.67)
Gd (n = 26)	0	1	7.7	0.0	2.0 (0.00)	1.00 (0.00)	124.7 (0.00)	124.7 (0.00)
6-Pgd (n = 57)	2	7	28.0	7.0	2.6 (0.59)	0.94 (0.09)	63.5 (11.75)	85.3 (21.95)
Tfn (n = 52)	0	5	21.2	3.9	3.2 (0.33)	1.00 (0.00)	46.8 (16.89)	69.3 (29.81)

Note: Numbers in parentheses are 95% confidence intervals. For an explanation of locus abbreviations see the text. Significant clusters formed at $0.001 < P \leq 0.01$ and $P \leq 0.001$ are mutually exclusive. Descriptive information about clustering refers to both significance levels combined. Clustering is based on the spatial arrangement of genotypes compared with the entire population, therefore clusters significant for the tested genotype may also include a proportion of alternative genotypes. Mean separation distance is the average distance between every possible pair of animals in the cluster.

Spatial patterns and processes

Our spatial autocorrelation findings are concordant with three expectations for neutral loci in genetically structured populations with low to moderate dispersal. First, the development of single homozygote genotype patches are a dominant feature of the correlograms (Turner et al. 1982; Sokal and Wartenburg 1983) of females, fulfilling Epperson's (1993) "strong hypothesis test" for neutral loci in natural populations. Second, statistics for join-counts between like-homozygotes estimate patch size (Epperson 1995) for females to be, on average, 135 m (range 40–210 m). This corresponds suggestively to the average diameter of a female social group (138 m; van Staaden et al. 1994), although the true nature of the relationship between patch size, social group, and neighborhood size is unknown (Epperson 1993). Subsequent crossings of the *x* axis by the correlograms at longer distances are interpreted to indicate that patch distribution is regular, and may also reflect the high sensitivity of join-counts between homozygotes to changes in dispersal for relatively small neighborhood sizes (Epperson 1995). Finally, although genetic correlation is expected to be a

decreasing function of distance under fairly general conditions, both theoretical (Cockerham 1973; Chesser 1991a) and empirical studies (Pope 1992; van Staaden et al. 1994) demonstrate a negative correlation of genes within individuals relative to those within the lineage in socially structured populations. Such excess heterozygosity within social lineages reverses traditional expectations of autocorrelation analysis (Heywood 1991), and with the exception of the selected *Pro-1* locus, females in the present study display negative autocorrelation at small distances and positive autocorrelation at greater distances for like-homozygotes.

Selection at the *Pro-1* locus resulting in a circular gradient was supported by the unique pattern of spatial autocorrelation (Sokal and Oden 1991), by contiguous clustering (peripheral homozygotes surrounding central heterozygote clusters), and by the fact that F_{IS} values were negative at all loci except *Pro-1* (van Staaden et al. 1994).

Dispersal and breeding tactics

In *S. richardsonii*, as in theoretical studies (Chesser 1991b), breeding tactics appear more important in the development of

Fig. 2. Spatial representation of individual adult female (n = 328) and male (n = 26−61) *Spermophilus richardsonii*
for contiguously clustered genotypes at six loci. Because clustering results are complex for females, they are
presented in separately (A and B) for clarity. Significant nonrandom genotypic clusters shown were determined by
the cross-entropy χ^2 method of contiguous clustering (Chesser and Van Den Bussche 1988) at $P \leq 0.001$ and
include 33% of males in 6 clusters (3 for *Pro-1*, 1 for *Sordh*, 2 for *6-Pgd*) and 77% of females in 23 clusters (5 for
Pro-1, 2 for *Sordh*, 3 for *Est*, 4 for *Gd*, 4 for *6-Pgd*, 5 for *Tfn*).
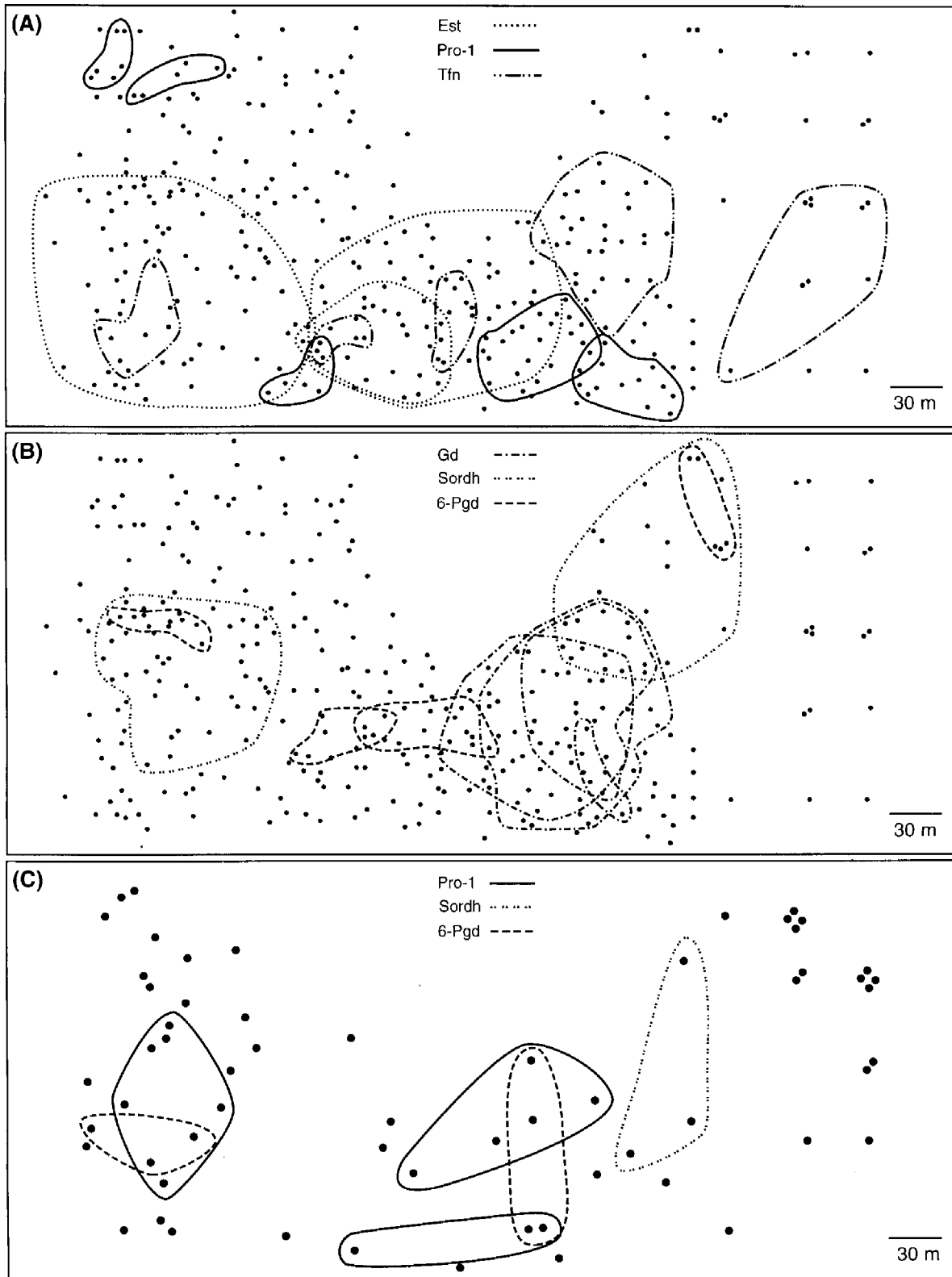
local genetic structure than dispersal characteristics. A similar conclusion is implicit in Lidicker and Patton's (1987) review of four rodent taxa. In the present study, Mantel tests of geographic versus genetic distance matrices suggest that the classical isolation by distance model leading to differentiated regions of the population is inadequate to explain the observed level of local genetic structure. Contrary to isolation by distance model predictions, social models demonstrate that excess heterozygosity occurs in lineages of locally structured populations. This explains the fact that spatial autocorrelations are significant, yet the Mantel test of geographic and genetic distance is not.

Matrix correlations indicate that individual differences in life history are related to geographic distance rather than genetic distance. Geographically closer individuals are thus more similar in life-history attributes than are more distant individuals, perhaps as a result of the non-uniform distribution of resources, microhabitat differences, genetically shared characters, and (or) the mutual influences of neighboring females.

Social organization and genetic structure

The local genetic structure of this *S. richardsonii* population is one in which females alone form a framework of somewhat separated genetic subunits, genetic similarity and geographic distance are decoupled, and breeding tactics assume paramount importance. Intersexual differences in gene flow are reflected in behavioral observations indicating that females are philopatric, whereas males disperse widely and most males leave their natal sites (Michener 1989; Michener and Locklear 1990). Female cooperation in subdividing the natal site with daughters, site tenacity, and incomplete turnover of breeding adults resulted in significant genetic clustering. Genetic structure in females was further enhanced by synchronization of emergence and estrus, which promoted a tendency for spatially close females to mate with the same male. In contrast, intermale relations were essentially competitive, between relatively few, unrelated males of high vagility. Although breeding was not confined to isolated demes within the population, the results indicate contiguous areas of highly localized breeding activity, as well as enhanced relatedness among offspring and cohesiveness of the matriline. Occasional dispersal by females (van Staaden et al. 1994) contributed to the disruption of a simple isolation by distance relationship, but was insufficient to disrupt the genetic identity of breeding groups. Local structure in *S. richardsonii* is contingent also on the large variance in male reproductive success associated with dominance, including such tactics as defense of estrous females, wide-ranging movements of males in the mating season, and the fact that males may remain in the same general vicinity in successive breeding seasons (Davis and Murie 1985; Michener and McLean 1996).

Our study population occurred as a dense population occupying a small, geographically isolated patch of habitat. Overlapping generations, longevity, and sharing of vital resources such as burrow systems contribute to a low turnover of matrilines and long-term stability of the population. New matrilines arose only on the rare occasion that a female succeeded in rearing a litter more than 120 m from her natal site (van Staaden et al. 1994). The local system of *S. richard-*

sonii may be adaptive solely in terms of efficient exploitation of environmental resources, but the genetic substructure remains potentially favorable for evolutionary trial and error among local populations as envisaged by Wright's (1931) shifting-balance theory. Whereas average heterozygosity and polymorphism were low ($H = 0.026$, $P = 0.109$), the population retained a high potential for colonization, with the ability to expand population size rapidly. For example, the study population experienced a 5.5-fold increase in size between 1982 and 1986, and 7 adult females and 2 adult males transplanted from the study population to a new site in 1986 gave rise to 255 adults (and at least 4 times as many juveniles) by 1990.

Detecting local structure

The results of this study suggest that it is possible to detect local genetic structure in animal populations by means of autocorrelation methods. Moreover, selective processes, sexual differences in genetic substructure, and estimates of the size and arrangement of genetic units are manifest. Correlograms may thus serve as guides to some of the processes that have generated patterns, as well as to the patterns themselves (Sokal et al. 1989; Sokal and Jacquez 1991). Long-term behavioral data are unnecessary, but minimum requirements are a population close to equilibrium with respect to contemporary population dynamics and sampling over an area expected to contain at least four to nine patches, with at least 10–20 sample points for each patch area (Epperson 1993). In addition, breeding tactics rather than simply dispersal behavior should be the behavioral focus, and genetic expectations ought to be based on social models. Contiguous clustering was unable to discern precise groups at this fine scale. However, it remains unclear whether the high degree of overlap and chaining of clusters is an analytical artifact or a biological reality. The variation in location of clusters for different loci is consistent with previous findings from spatial autocorrelation which show that independently segregating loci may not depict identical population topographies even in highly structured populations (Michod and Anderson 1979). Similar results were found for the highly social black-tailed prairie dog, in which genotypic clusters encompass a number of coteries (Chesser and Van Den Bussche 1988).

Although the genetic structure observed for this population represents a single manifestation of many possible structures, it is patently nonstochastic. Contigent on behavioral factors other than simple dispersal, local genetic structuring in small-mammal populations is likely to be chaotic (sensu stricto), extremely sensitive to initial conditions, and not in equilibrium (May 1976), but nonetheless real. Thus, techniques based on the distribution of individual genotypes can provide a fundamental prerequisite for testing evolutionary models of population genetic structure and sociality.

Acknowledgements

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