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# GENETIC STRUCTURE IN STRIPED SKUNKS (*MEPHITIS MEPHITIS*) ON THE SOUTHERN HIGH PLAINS OF TEXAS

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ABSTRACT.—Genetic variation within populations reflects population-level social and demographic processes and influences how a population behaves as an evolutionary unit. We examined partitioning of genetic variation in striped skunks (*Mephitis mephitis*) from the Southern High Plains of Texas during 1994–1995. Sixty-nine male and 35 female skunks were sampled on four 12.8-km$^2$ study plots. Plot centers ranged from 17.6 to 61.6 km apart. We used multi-locus DNA fingerprinting with 2 probes, pV47 and CTTxAGG, to test 3 hypotheses: (1) females are more genetically similar to other females than males are to other males on the same plot (indicating greater female philopatry than male philopatry), (2) genetic similarity is greater within plots than among plots (indicating partitioning of genetic variation in space), and (3) genetic similarity of males decreases as the distance separating males increases (indicating geographic distance affects rates of gene flow). In general, males on a plot had lower average genetic similarity than females. Genetic similarity within plots was not different from genetic similarity among plots for males or for females. Genetic similarity of males did not decrease with increasing distance among plots. The lack of geographical genetic structure in striped skunks suggests at the scale of this study (<60 km) that gene flow of biparentally inherited genes is not distance-mediated. However, the higher similarity values for females than for males on the same plot supports an effect of male-biased dispersal and female philopatry on partitioning of genetic variation between sexes.

*Key words: DNA fingerprinting, genetic structure,* Mephitis mephitis, *population genetics, striped skunks.*

The genetic structure of a population is determined by the demographic processes of the population (birth, death, and dispersal), by behavior (social organization), and by genetic processes such as selection, recombination, and mutation (Slatkin 1994). Knowledge of the genetic structure of a population may allow inferences about the levels and patterns of gene flow (Hastings and Harrison 1994, Slatkin 1994). Gene flow is important because it determines the extent to which each local population is an independent evolutionary unit (Slatkin 1994).

Spatial variation in genetic structure among populations is common (Chesser and Baker 1996). Estimates of gene dynamics must take spatial genetic structure into consideration. Avise (1995) proposed a general verbal model predicting geographic genetic structure in animal populations as a function of gender-specific dispersal patterns and gene-flow regimes. For markers in autosomal genes, his model predicts observable geographical genetic structuring only under conditions of low male and low female dispersal. However, Avise (1995) did not provide guidance on what constitutes low dispersal. Chesser and Baker (1996) modeled the effects of various types of social organization on changes in gene diversity; they found that with a "typical" mammalian social organization (polygyny, female philopatry, and male-biased dispersal), the greatest amount of variance would be in maternally inherited genes. High male dispersal rates reduce the variation in paternally and biparentally inherited genes.

We investigated the genetic structure of striped skunks (*Mephitis mephitis*) within and among four 12.8-km$^2$ study plots in the Southern High Plains of Texas in 1994 and 1995 using multi-locus DNA fingerprinting (Lynch 1990, 1991). Striped skunks appear to fit Chesser and Baker's (1996) model of "typical" mammalian social organization, with polygyny and high rates of dispersal (Bjorge et al. 1981, Sargeant et al. 1982). However, the geographic scale at which genetic variation is mediated by dispersal is not known. Multi-locus DNA

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fingerprints are a primarily biparentally inherited and effectively neutral nuclear genetic marker with high variability among individuals (Lynch 1991). We used average numbers of scorable bands per individual, similarity indices, and an index of between-plot similarity adjusted for within-plot similarity to examine partitioning of genetic variation in striped skunks between sexes and among study plots (Gill et al. 1985, Lynch 1991, Degnan 1993, Rave et al. 1994, Scribner et al. 1994, Sundt et al. 1994). We tested 3 hypotheses concerning striped skunk genetic structure: (1) females are more genetically similar to other females than males are to other males on the same plot (indicating greater female philopatry than male philopatry), (2) genetic similarity is greater within plots than among plots (indicating partitioning of genetic variation in space), and (3) genetic similarity of males decreases as the distance separating males increases (indicating geographic distance affects rates of gene flow).

## STUDY AREA

We conducted this study in northeastern Lamb County, Hale County, and southern Swisher County, Texas. This area has a dry, steppe climate with mild winters (USDA Soil Conservation Service 1974). Average annual precipitation is 44 cm, and approximately 79% of this amount falls from May through October. Thunderstorms are common during May through June. The area is a nearly level to sloping, treeless prairie, dissected by a few intermittent streams and sloping basins around playa lakes. Land use is primarily agricultural, with the main crops being corn, cotton, and grain sorghum. Primary mortality factors for striped skunk in this area are human-caused traumas, including shooting and roadkill (Hansen 1997).

## METHODS

We selected four 12.8-km$^2$ plots based on cover type similarity, distance among plots, and landowner consent. Each plot had 20–30% Conservation Reserve Program lands and 2 to 4 playa lake basins. The majority of the remaining land was in irrigated crop production, intermingled with some homesteads and farm buildings.

We captured striped skunks using box traps (80 × 22 × 22-cm, double-door, folding traps, Tomahawk Live Trap Co., Tomahawk, WI) on each study plot for 7 nights each month in March through July 1994 and 1995. Trapping was conducted during the breeding and kit-rearing period, and all animals used in the study were potentially breeding adults. Skunks were immobilized with a 4:1 mixture of ketamine hydrochloride and xylazine hydrochloride (100 mg · mL$^{-1}$ concentration of ketamine, 10 mg · mL$^{-1}$ concentration of xylazine, average dosage of 0.17 mL · kg$^{-1}$; Rosatte and Hobson 1983). At first capture, we amputated approximately 2.5 cm (2–3 g) from the end of each skunk's tail to provide a tissue sample for genetic analysis. Tissue samples, consisting of fur, flesh, and some bone, were stored at –80°C until analyses could be done. Wounds caused by this procedure were disinfected with betadine, and recaptured skunks were examined for chronic injury from infection. For 32 striped skunks recaptured within a field season, examinations found no evidence of chronic injury from the tail wound. For 7 skunks captured in both years of the study, we could not detect the tail wound with a physical examination during the 2nd year because fur had grown from the wound location at the end of the tail.

DNA was isolated from the tissue samples using Maltbie's (1992) procedures. We selected the enzyme/probe combinations of *Hae*III/pV47 (Longmire et al. 1990) and *Hae*III/CTTxAGG (Longmire et al. 1993) for the DNA fingerprint analyses from 4 enzymes and 3 probes tested because they had the greatest variability among individual fingerprints. Genomic DNA (10 μg) was digested with *Hae*III using the supplier's recommended buffer and endonuclease concentrations. Digested samples were electrophoresed in a 20-lane 0.8% agarose gel in 1 X TAE buffer (Maltbie 1992). Restriction fragments in gels were transferred to a nylon membrane (Ampersham) using the procedure of Southern (1975). Probes were radioactively labeled with $P^{32}$ and hybridized to single-stranded DNA on the nylon membrane. The probe pV47 was hybridized using the procedure Westneat et al. (1988) developed for M13. The probe CTTxAGG was hybridized using the procedure of Longmire et al. (1993).

Each gel contained a standardized marker (*Hind*III-digested lambda DNA) in the 1st, 7th, 13th, and 19th lanes. DNA from 1 skunk (#295) was run in 2 lanes on every gel, and DNA from another animal (different for each

gel) was also run in 2 lanes on each gel. Skunk #295 was chosen as a control because we had a relatively large quantity of DNA from that skunk. We scored autoradiograms using the program NSCA GelReader (National Center for Supercomputing Applications, Champaign, IL), which compared fingerprint bands to the 4 lanes of standardized marker to estimate the molecular weight of each band. We compared the molecular weights of bands for control animals to determine variability in estimation of molecular weights of individual bands among autoradiograms. We could not reliably separate all bands on different autoradiograms. Therefore, to score fingerprints, we constructed floating bins which bracketed sets of bands that were indistinguishable between autoradiograms (Balazs et al. 1989, Timms et al. 1993). Bins were scored by comparing the number of bands within a bin between individuals. For example, if bin 1 in individual 1 had 1 band, and bin 1 in individual 2 had 2 bands, the pair was scored for bin 1 as having 1 shared band. The numbers of shared bands within bins were summed across all bins to determine the total number of shared bands for the pair. Bin boundaries were established at 5.20, 6.15, 6.50, 7.10, 7.60, 7.88, 8.46, 8.80, 9.20, 10.23, 11.23, 11.90, 13.20, 13.79, and 15.65 kb for scoring pV47 fingerprints, and at 4.50, 4.84, 5.00, 5.63, 5.80, 6.15, 6.40, 6.65, 7.10, 7.55. and 7.95 kb for scoring CTTxAGG fingerprints.

Similarity indices ($S_{xy}$) were calculated for each pair of individuals for each probe (Lynch 1990, 1991). Errors in assigning bands to bins reduced the similarity indices for individuals compared to themselves from the expected value of 1.00. Because of measurement error, alleles (bands) that fall close to the boundary of a bin may not be consistently placed within the same bin. However, the alleles near a boundary should fall randomly, and therefore frequency values of bins should not be skewed (Budowle et al. 1991).

We used analysis of variance to compare the number of bands per individual among plots (Sokal and Rohlf 1981). We used the formulas provided by Lynch (1991) to calculate average similarity indices ($\overline{S}$) for groups of skunks and an unbiased estimate of variance of $\overline{S}$ within and between plots. We also used formulas provided by Lynch (1990) to calculate indices of between-population similarity adjusted for within-population similarity ($\overline{S}_{ij}$). We constructed 95% confidence intervals for each $\overline{S}_{ij}$ to determine if the value was significantly less than 1.0. Values less than 1.0 indicate partitioning of genetic variation among populations, with greater genetic similarity within populations than between populations.

We used Student's $t$ test to test the hypothesis that similarity index values for pairs of females within plots were greater than similarity index values for pairs of males within plots. We used Pearson's product-moment correlation and the Mantel-Haenszel test for linear association to test the hypothesis that average similarity indices between plots ($\overline{S}$) decreased with increasing distance between plots (Sokal and Rohlf 1981, SPSS Inc. 1994). Males and females were analyzed separately. For all parametric analyses, we examined data for deviations from normality using normal probability plots, and for data used in analysis of variance, we tested for homogeneous variance using Levene's test (Zar 1996).

## RESULTS

We captured 69 male skunks and 35 female skunks. The number of male skunks used in genetic analyses per plot each year ranged from 6 to 14, and the number of females used in genetic analyses per plot each year ranged from 1 to 10 (Table 1). The distribution of captures over time was different for males and females (Hansen 1997). Therefore we suspect that differences in capture probabilities between the sexes as well as numbers of skunks affected our capture results.

### Bin Scoring

The average similarity index ($S_{xy}$) calculated by comparing fingerprints of skunk #295 to itself within and among autoradiograms was 0.977 ($s$ = 0.017) for pV47 fingerprints and 0.917 ($s$ = 0.014) for CTTxAGG fingerprints. The average similarity index ($S_{xy}$) calculated by scoring fingerprints of all skunks that were repeated within and among autoradiograms against themselves was 0.916 ($s$ = 0.069) for pV47 fingerprints ($n$ = 40 comparisons) and 0.895 ($s$ = 0.048) for CTTxAGG fingerprints ($n$ = 18 comparisons). Of the 19 bins used to score DNA fingerprints produced from the probe pV47, 14 contained the same maximum number of bands for males and females and 4

TABLE 1. Number of skunks with scorable DNA fingerprints ($n$), average within-plot similarity indices ($\bar{S}$), and standard error ($s_{\bar{x}}$) calculated from pV47 and CTTxAGG DNA fingerprints for male and female striped skunks from 4 plots on the Southern High Plains, Texas, 1994–1995.

| Fingerprint type – Year | Study plots | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Claytonville | | | Halfway | | | Plainview | | | Olton | | |
| Sex | $n$ | $\bar{S}$ | $s_{\bar{x}}$ | $n$ | $\bar{S}$ | $s_{\bar{x}}$ | $n$ | $\bar{S}$ | $s_{\bar{x}}$ | $n$ | $\bar{S}$ | $s_{\bar{x}}$ |
| pV47 – 1994 | | | | | | | | | | | | |
| Males | 7 | 0.594 | 0.031 | 11 | 0.576 | 0.044 | 6 | 0.646 | 0.050 | 13 | 0.606 | 0.027 |
| Females | 1 | | | 8 | 0.643 | 0.052 | 1 | | | 4 | 0.612 | 0.153 |
| PV47 – 1995 | | | | | | | | | | | | |
| Males | 8 | 0.577 | 0.014 | 10 | 0.627 | 0.041 | 6 | 0.608 | 0.027 | 6 | 0.633 | 0.042 |
| Females | 4 | 0.640 | 0.035 | 9 | 0.656 | 0.051 | 1 | | | 5 | 0.606 | 0.050 |
| CTTxAGG – 1994 | | | | | | | | | | | | |
| Males | 6 | 0.795 | 0.012 | 9 | 0.708 | 0.066 | 6 | 0.744 | 0.046 | 6 | 0.765 | 0.065 |
| Females | 1 | | | 6 | 0.787 | 0.031 | 1 | | | 3 | 0.691 | 0.065 |
| CTTxAGG – 1995 | | | | | | | | | | | | |
| Males | 6 | 0.806 | 0.049 | 9 | 0.673 | 0.063 | 5 | 0.806 | 0.008 | 5 | 0.813 | 0.091 |
| Females | 2 | 0.800 | | 9 | 0.843 | 0.037 | 1 | | | 5 | 0.838 | 0.125 |

did not. Of the bins which differed between males and females, 2 bins had a maximum of 1 band for females and 2 for males, 1 bin had a maximum of 3 bands for females and 2 for males, and 1 bin had a maximum of 4 bands for females and 5 for males. Of the 12 bins used to score CTTxAGG fingerprints, 8 were similar between sexes and 4 were not. Of the 4 bins which differed between sexes, 1 bin had a maximum of 0 bands for females and 1 for males, 1 bin had a maximum of 2 bands for females and 1 band for males, 1 bin had a maximum of 2 bands for females and 3 bands for males, and 1 bin had a maximum of 3 bands for females and 4 bands for males. Numbers of bands per bin may have differed for males and females because of gender-specific bands (Longmire et al. 1993), because of errors in assigning bands to bins for one or a few individuals, or as a function of sampling almost twice as many males as females. We had less success hybridizing CTTxAGG to membranes, and so fewer individuals had scorable fingerprints using this probe.

### Average Similarity of Males and of Females Within Plots

Average similarity indices ($\bar{S}$) within plots for males using pV47 fingerprints ranged from 0.57 to 0.64, and using CTTxAGG fingerprints ranged from 0.69 to 0.81 (Table 1). For females, $\bar{S}$ within plots ranged from 0.61 to 0.66 with pV47 fingerprints, and from 0.69 to 0.84 for CTTxAGG fingerprints. Average values were not calculated for females on the Plainview plot in 1994 and 1995, or for the Claytonville plot for 1994, because only a single female was caught on each of the plots in those years. In 5 of 6 plot-year comparisons using pV47 and 4 of 6 comparisons using CTTxAGG, females had higher average similarity values (Table 1). Pooling data from all plots and years, we found the similarity values for pairs of females within plots were significantly higher than for pairs of males within plots using both the CTTxAGG fingerprints ($t = 1.91$, $P = 0.016$, df = 34, 1-tailed $t$ test) and pV47 fingerprints ($t = 1.07$, $P = 0.073$, df = 37, 1-tailed $t$ test) at the $\alpha = 0.10$ level.

### Average Similarity of Males and of Females Among Plots

We used Lynch's (1991) index of between-population similarity corrected by within-population similarity ($\bar{S}_{ij}$) to determine if there was partitioning of genetic variation among plots. Using pV47 and CTTxAGG fingerprints for both male and female striped skunks, we noted that none of the $\bar{S}_{ij}$ values were significantly $<1.0$, indicating that between-plot genetic variation was similar to within-plot genetic variation for each sex (Table 2).

Another indicator of partitioning of genetic variation among plots is differences in the average number of bands per animal among plots. Males averaged 11.7 bands and females 12.2 bands for pV47 fingerprints; for CTTxAGG fingerprints, the average was 7.6 bands

TABLE 2. Distances between plots and indices of between-population similarity adjusted for within-population similarity ($\bar{S}_{ij}$) for male and female striped skunks using pV47 and CTTxAGG DNA fingerprints on the Southern High Plains, Texas, 1994–1995.

| | | pV47 | | | | CTTxAGG | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Males | | Females | | Males | | Females | |
| Plots compared | Distance (km) | 1994 | 1995 | 1994 | 1995 | 1994 | 1995 | 1994 | 1995 |
| Halfway – Olton | 17.6 | 1.00 | 0.97 | 1.00 | 1.00 | 0.99 | 0.98 | 1.00 | 1.02 |
| Plainview – Claytonville | 24.4 | 1.00 | 1.02 | | | 1.01 | 1.00 | | |
| Plainview – Halfway | 41.2 | 1.00 | 1.00 | | | 1.00 | 0.99 | | |
| Claytonville – Halfway | 47.2 | 1.02 | 1.01 | | 0.99 | 0.99 | 1.00 | | 0.95 |
| Plainview – Olton | 58.4 | 0.98 | 0.99 | | | 1.01 | 0.98 | | |
| Claytonville – Olton | 61.6 | 0.98 | 0.98 | | 1.01 | 1.01 | 1.01 | | 0.93 |

per male and 7.8 bands per female. There was no difference among plots in the number of bands for males or females for either pV47 fingerprints (males $F = 1.40$, $P = 0.253$, df = 3, 57; females $F = 0.08$, $P = 0.971$, df = 3,28) or CTTxAGG fingerprints (males, $F = 1.30$, $P = 0.637$, df = 3,44; females, $F = 1.25$, $P = 0.314$, df = 3,24).

### Relationship Between Genetic Similarity of Males and Geographic Distance

Between-plot similarity ($\bar{S}$) did not decrease as distance between plots increased for males using pV47 (Pearson's product-moment correlation: $r = -0.16$, $P = 0.623$, $n = 12$; Mantel-Haenszel test: $\chi^2 = 0.28$, $P = 0.60$, df = 1; Fig. 1) or CTTxAGG fingerprints (Pearson's product-moment correlation: $r = 0.44$, $P = 0.149$, $n = 12$; Mantel-Haenszel test: $\chi^2 = 2.16$, $P = 0.14$, df = 1; Fig. 1).

## DISCUSSION

Little work has been done on the population genetics of striped skunks. Using allozymes, Bixler (2000) found that striped skunks have levels of heterozygosity and polymorphisms slightly higher than average for terrestrial carnivores. Bixler (2000) found no difference in alleles between populations of striped skunks located 32 km apart in Tennessee, but did find a different allele in skunks from Iowa. Although Bixler (2000) used a very different type of genetic marker than we did, our results agree with her finding that there was little genetic differentiation on a local geographic scale.

Striped skunks appear to be intermediate on the gradient of carnivore sociality. They do not form groups to forage, raise young, or defend against predators, although they may den communally during the winter (Ewer 1973, Gunson and Bjorge 1979, Godin 1982). Neither male nor female striped skunks maintain exclusive home ranges (Hansen 1997, Larivière and Messier 1998, Bixler and Gittleman 2000). Storz (1999), who reviewed studies of genetic structure in highly social mammals, found low to moderately high genetic differentiation among social groups, along with consistently high levels of within-group heterozygosity. He concluded that in most cases social barriers to gene flow are not sufficient to promote high degrees of genetic subdivision and inbreeding. It seems likely that carnivores of intermediate sociality such as striped skunks would demonstrate even less genetic differentiation among local populations. This is consistent with our finding of no spatial effects on partitioning of genetic variation in biparentally inherited genetic markers.

Previous research has suggested that striped skunks are polygynous, probably with male-biased dispersal (Sargeant et al. 1982; but see below). Bjorge et al. (1981) defined juvenile dispersal as any movement between capture locations >4.8 km and found that 23% of juvenile striped skunks captured more than once between July and October had dispersed. Straight-line distances between captures of dispersing juveniles ranged from 5.9 to 10.1 km for 7 males and from 5.6 to 21.7 km for 4 females. Rosatte and Gunson (1984) found no difference between mean dispersal distances of juvenile male and female striped skunks during the period July–December. Dispersal distances ranged from 0.4 to 9.7 km. During our study (which did not follow dispersing animals), adult male skunks on our study area commonly moved straight-line distances ≥3 km

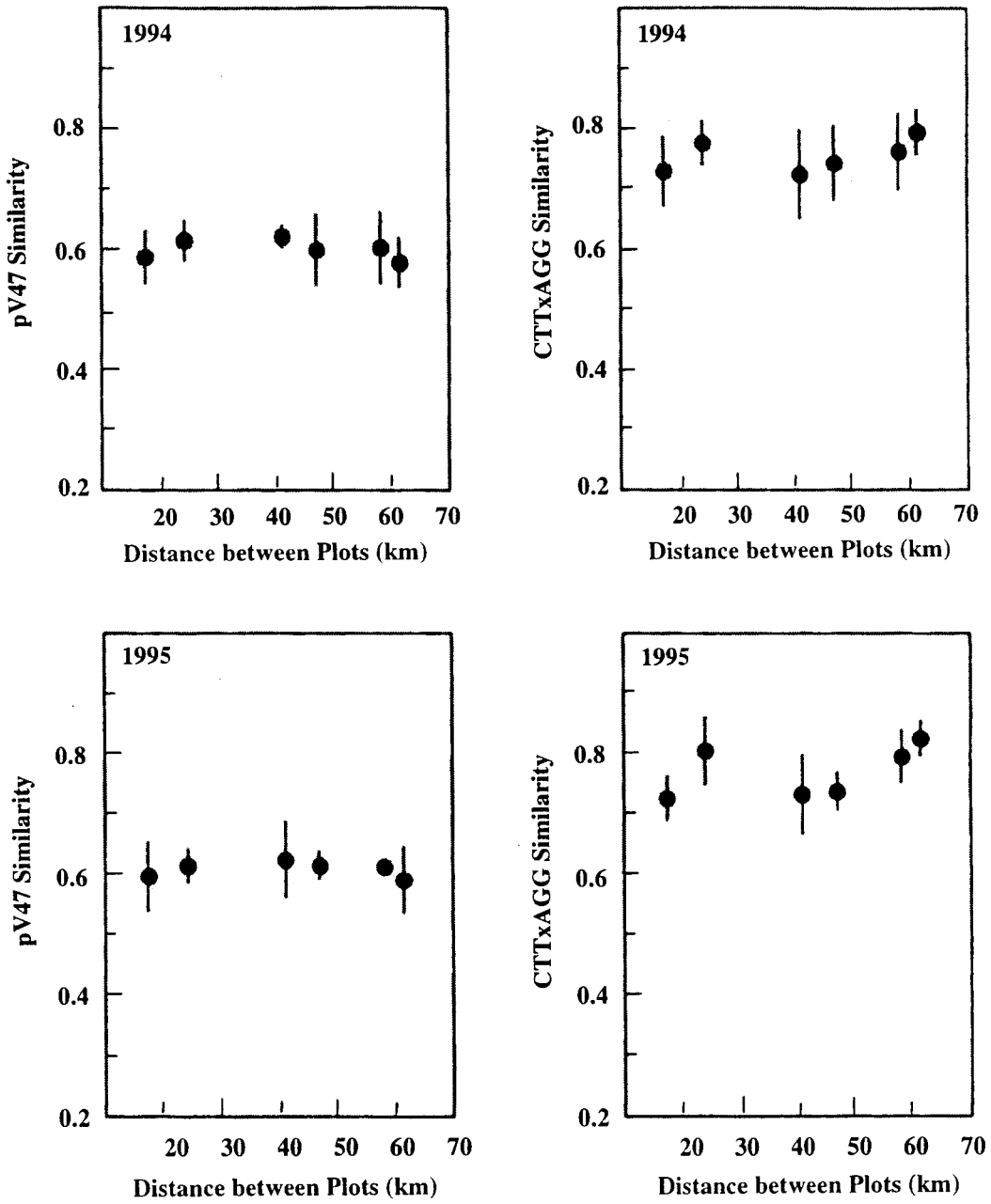


Fig. 1. Comparison of mean between-plot similarity indices ($\bar{S}$) calculated from pV47 and CTTxAGG DNA fingerprints and distances between plot centers for male striped skunks from the Southern High Plains, Texas, 1994–1995. Between-plot similarity indices have standard error bars.

during March–August, and the longest movement recorded was 7.2 km (Hansen 1997). Sargeant et al. (1982) recorded adult male striped skunks dispersing between 10 and 119 km in North Dakota. Less is known about adult female movements, although Sargeant et al. (1982) found that 43% of females trapped on a plot in the Northern Plains were present the next year, suggesting female philopatry. Dispersal rates appear to be inconsistent among populations of striped skunks, with relatively long-distance movements possible by individuals of

either sex. However, our observations of a tendency for females to be more genetically similar than males on a plot supports Seargent et al.'s (1982) conclusion of male-biased dispersal, at least on our study area.

Our results are consistent with the models of Avise (1995) and of Chesser and Baker (1996). The lack of spatial genetic structure in striped skunks indicates that at the scale of this study (≤60 km) gene flow of biparentally inherited genes of striped skunks is not distance-mediated. A high annual turnover of individuals in the population (Hansen 1997), lack of geographic barriers on the Southern High Plains, and the dispersal abilities of males appear to have resulted in a relatively outbred population of striped skunks within the 60-km range of our study. However, our finding of partitioning of genetic variation between sexes and the model of Chesser and Baker (1996) suggest that a study of maternally inherited genes, such as mitochondrial DNA, might document greater levels of spatial genetic differentiation in local striped skunk populations.

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