The Spatial Genetic Variation of Black-tailed Prairie Dog (*Cynomys ludovicianus*) Populations on the Great Plains of North America: The effects of population control on gene flow and genetic differentiation.

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INTRODUCTION

Understanding the causes of spatial genetic heterogeneity in populations is a fundamental aspect of species conservation (Epperson 1993). The spatial distribution of populations implies both physical separation on the landscape while genetic heterogeneity is one potential result of that separation (Whitlock and McCauley 1990, Slatkin 1993, White and Svenden 1992, Whitlock 1992). Theoretical and empirical studies demonstrate that the spatial dynamics of populations are sensitive to the landscape features in which they are embedded and this sensitivity can be expressed by patterns of gene flow (the exchange of alleles), and genetic drift (the gradual random accumulations of genetic differences).

In colonial fossorial rodents, gene flow can be restricted by the distribution of colonies and by population groupings within the colony towns or group territories (Patton and Yang 1977). Fossorial rodents have been extensively examined for spatial variation of genetic parameters (Smith and Patton 1981, Chesser 1990, Stewart and Baker 1992, Stewart et al. 1993). Disjunct population distributions and territorial social systems make the colonial-fossorial rodents particularly suitable for studying spatial genetic variation. Black-tailed prairie dogs (*Cynomys ludovicianus*) disperse among coteries (territorial family groups) within a town (group of coteries) and among towns within a greater region (colony) (Garret and Franklin 1988). Male yearlings are the predominant dispersers for pdogs, they leave the natal harem-styled coteries and

disperse to other coteries within a town or among established towns (Hoogland 1985, Knowles 1985, Foltz and Hoogland 1983, Apa et al. 1990, Daley 1992).

Prairie dog (Pdog) colonies represent a unique model for examining spatial genetic and looking for relationships between human actions and genetic differentiation. Pdogs are unique because their colonies have distinct visual boundaries easily identified on remotely-sensed databases (McDonald et al. 1990, Schenbeck and Myre 1986, Bowser 1996a). In addition, pdog have been considered pests to western ranchers since the turn of the century, and pdog reduction programs initated since then are well documented in federal and state records (Clark et al. 1982, 1989, Forrest et al. 1988). However, pdog rapidly repopulate controlled areas with colonizers (possibly from neighboring colonies) or survivors. The potentially high dispersal rates among neighbors due to control programs could lead to high gene flow and low genetic differentiation (Chesser 1983, 1990, Daley 1992). Comparing the genetic diversity measures of towns with and without control efforts at differing geographic distances may reveal dispersal patterns and genetic relationships important to pdog population management.

In this paper, I evaluate the spatial genetic differentiation of pdog towns and colonies in Badlands National Park and Buffalo Gap National Grassland in South Dakota. Pdog colonies within Badlands have been uncontrolled since the establishment of the 60,000 acre Sage creek Wilderness area within the park (244,300 total acreage) in the late 1970's (McDonald et al. 1990). These colonies appeared to grow steadily from 1954 to 1991 based on aerial images of colony boundaries (Bowser 1996a). In contrast, pdogs on the neighboring Buffalo Gap National

Grasslands (591,260 acres) were controlled until the late 1980's when areas were set aside as potential black-footed ferret (*Mustela nigripes*) reintroduction sites (Uresk and Schenbeck 1987).

The extinction and recolonization of pdog colonies can structure genetic patterns by altering gene flow (Slatkin 1987). Within controlled areas (high extinction rates), I would expect towns to have similar genetic compositions (short genetic distances) to their immediate neighbors as gene flow would increase because of the large numbers of empty territories for dispersers to occupy. For the uncontrolled areas (low extinction rates), the physical separation should accurately predict genetic relationships, and genetic diversity should increase with greater distances. By using Wright's (1965) isolation by distance theorems and F-statistics, patterns of dispersal among towns and colonies, controlled or uncontrolled, can be elucidated.

The specific study objectives here are to: (1) describe genetic variation for pdog towns and colonies; (2) determine spatial groupings of PD populations; and (3) describe potential relationships of management actions (such as population control) with genetic patterns.

MATERIALS AND METHODS

Study site and species: This study was conducted on prairie dog colonies in Badlands National Park (BADL), South Dakota. Located on the mixed-grass prairie of the Great Plains, BADL was originally set aside in 1939 to preserve the unique badland walls first described by 18th century

French fur-trappers as "mauvaises terres a traverser" (bad lands to cross), and to conserve the Oligocene fossil deposites captured in the ancient seabeds now exposed by the badland walls. Pdogs are an integral part of the mixed-grass prairie ecosystem found in these badlands (King 1955, Cincotta and Uresk 1986). Pdogs actively alter the vegetation within their colonies, increasing the forb diversity and reducing graminoid species diversity and biomass (Cincotta et al. 1989, Bennett and Bock 1990). Pdogs originally existed in large colonies each covering several thousand hectares on mixed- and short-grass prairie from Saskatchewan, Canada to northern Mexico (Hoogland 1981, Cebellos et al. 1993); however, when pdogs were declared pests, these colonies were fragmented and isolated by aggressive population control efforts (Peterson 1987).

The presence of a variety of state and federal endangered animals on pdog colonies has important conservation implications (Sharps 1994). Pdogs are considered a keystone species as their colonies are preferentially used by a variety of species including bison (*bison bison*), Antelope (*Antilocarpa americana*), badgers (*Taxidea taxus*), burrowing owls (*Athene cunicularia*), ferruginous hawks (*Buteo regalis*), golden eagles (*Aquila chrysaetos*) (Campbell and Clark 1981, Sharps and Uresk 1990). The dynamics and stability of pdog colonies, especially through exchanging individuals and reducing extinction potential, are mechanisms important to the protection of all species (including threatened and endangered species) using pdog colonies.

Comparative sites: Three national parks on the Great Plains were chosen as comparison sites for the badlands data (Figure 1). Wind Cave National Park (WICA), South Dakota, presently preserves two small (less than 100 hectares) colonies as research sites (see Hoogland 1982, Foltz

and Hoogland 1983, Garret and Franklin 1988, Daley 1992). These colonies were last reduced during the late 1970s and the genetic structures have been well documented since then (R. Klukas, Resource Management Specialist, WICA). Theodore Roosevelt National Park (THRO), North Dakota, and Devil's Tower National Monument (DETO), Wyoming, both actively control their pdog populations with annual or biannual reductions. DETO has a single isolated colony thought to be highly inbred (recolonization is slow and probably by survivors of the biannual poison-efforts--J. Gyra, DETO Natural Resource Specialist, pers. commun.). THRO has several large colonies annually reduced by shooting; these colonies rapidly recolonize apparently from populations on neighboring National Forest Service lands.

Field Sampling: Twelve towns from three colonies were sampled from BADL (Figure 2). Twenty individuals per town were sampled such that each individual was from a separate coterie to prevent familial relationships from distorting genetic parameters (Daley 1992). Small towns (fewer than 20 coteries) were sampled up to the number of identifiable coteries. In some cases several neighboring populations were combined to make a single sample of 20; in other cases, the sample size fell below 20 for scattered and isolated populations. Coteries were identified by observing territorial displays (smaller colonies) or visual inspection of mound distribution (larger colonies); each presumed coterie was marked with flagging and one individual was collected from the immediate vicinity of the flagging.

Pdogs were either captured using Sherman Live traps baited with Sweetchop (molasses and oat mixture) or shot. Blood samples were collected by toe-nail clipping or directly from the body

cavity, placed in 250 microliter heparinized tubes, and immediately stored on dry ice to prevent protein degradation. Small patches of fur were shaved from each trapped animal to prevent re-sampling.

All blood samples were shipped on dry ice to the laboratory of Dr. V. Sork, University of Missouri-St. Louis where they were stored in an ultracold (minus 70 Fahrenheit) freezer until genetic analyses.

Electrophorectic studies: Allozyme analysis generally followed methods described by Richardson et al. (1986), Aquaah (1992), and A.Templeton and V. Sork (pers. commun.). Gel and electrode buffer systems and staining recipes are described in Richardson et al. (1986) and Pasteur et al. (1988). Each sample was ground with a chilled mortar and pestle, mixing the blood with distilled water and a mild stabilizing buffer for animal materials as described by Richardson et al. (1986). The resulting mix was absorbed onto filter paper-wicks (0.6 X 0.4 cm) and stored in ultracold freezer until electrophorectic analysis.

Electrophoresis was conducted on 11 or 12 % potato starch (Sigma S-4501) gels with 10% sucrose and NADP added as stabilizers (Richardson et al. 1986). Three gel and tray buffering systems were used: Tris continuous (pH 8.0, Templeton et al. pers. commun.), Tris discontinuous with pH 6.3/6.7 tray/gel buffer (Richardson et al. 1986, Pasteur et al. 1988); and Poulik pH 8.0 (Sork et al. pers. commun., Richardson et al. 1986). All gels were covered with ice packs and run in a cold chamber for 4 to 18 hours depending on band separation and migration distances.

Twenty presumptive loci were surveyed using the different buffering systems. Proteins examined were: acid phosphase (ACPH), alcohol dehydrogenase (ADH), alanopine dehydrogenase (ALD), fluorescent esterase (Fest), glucose-6-phosphate isomerase (PGI), glucose dehydrogenase (GDH), gluctamic oxalacetic transminase (GOT), isocitrate dehydrogenase (IDH), lactate dehydrogenase (LDH-1, LDH-2), leucine aminopeptidase (LAP), malate enzyme (ME), malate dehydrogenase (MDH-1, MDH-2), mannose phosphate isomerase (MPI), nucleoside phosphorlase (NP), peroxidase (Per), phosphoglucomutase (PGM-1, PGM-2), phosphogluconate dehydrogenase (6PGD), sorbital dehydrogenase (SDH), triose phosphate isomerase (TPI), and xanthine dehydrogenase (XDH).

Data Analysis: Genetic analyses were conducted on towns within and among colonies in BADL and among regions (BADL versus DETO, WICA, and THRO). Over two hundred samples from twelve towns (maximum of 20 individuals per town) within BADL were examined (see Table 1 for actual sample sizes used for analyses). Samples from DETO (19), WICA (20) and THRO (20) were all from a single colony within the respective region. The BADL data were also divided into two sections; controlled (poison or hunt) and uncontrolled.

Genetic diversity measures were obtained using BIOSYS-1 (Swofford and Selander 1981) as background information on genetic sub-division among sub-populations. Genetic measures obtained included mean heterozygosity per locus based on Hardy-Weinberg expectations, the observed heterozygosity, mean number of alleles per locus, and the proportion of polymorphic

locus (assuming a locus is polymorphic if the frequency of the common allele is <99%). Variances for F-statistic measures were obtained by using a FORTRAN 77 program for Jackknifing each locus independently (Weir 1990) compiled in a Sun Sparkstation 5 UNIX computer.

Allele frequencies were calculated to estimate population exchange (within towns, among towns within colonies, among colonies within a region, and among regions), heterozygosity, F-statistics, and genetic distances. Genetic distances were also used as a metric measure to calculate principal component vectors and to generate clusters using weighted averaging (WPGMA) clustering techniques (Whitlock and McCauley 1990). WPGMA was used specifically to reduce the distortion of the data from chaining--a problem when the group reassignment is recalculated from the centroid of a pre-existing group (Pimental 1979, Romesberg 1984, Jackson 1986, SAS Manual--SAS Corporation 1989). BIOSYS-1 was used to calculate genetic parameters (Wright's F-statistics and genetic distances) among both towns and colonies. SYSTAT was used to perform multivariate statistics on genetic parameters because of it's detailed clustering procedures.

The inbreeding coefficients F_{is} (correlation of genes within individuals), F_{it} (correlation of genes within individuals within a population), and F_{st} (correlation of genes of different individuals) were calculated from allele frequencies of polymorphic loci using both BIOSYS-1 and a FORTRAN 77 compiled jackknifing procedure (Weir 1990). The FORTRAN program estimates the variance of the estimators by using each locus as independent replicates (Weir and Cockerham 1984). F_{st} was used as an indirect measure of the variance in allele frequencies due to differences among

populations (Slatkin 1987, Wayne et al. 1991). Dispersal distance is a direct measure of population exchange and is often assumed to be analogous with geographic or euclidean distances; thus, if population extinction increases gene flow, population isolation can be tested by comparing genetic (indirect) and geographic (direct) distances among populations (Bowser 1996b).

F_{st} was also used as a measure of genetic differentiation among populations, with each locus tested for statistical significance using the chi square statistic and Fisher's exact probablity (Swofford and Selander 1981). To reduce impacts of founder events and population bottlenecks on measures of genetic diversity, town age was estimated by examining 50 years of aerial photography of the towns using GRASS GIS on a SunSpark 5 (Leberg 1990, Bowser 1996a). Small towns less than 50 years old were combined with their nearest neighbor--if the neighbor was a potential source of dispersers.

Matrices of genetic and geographic distances were checked for correlation using SYSTAT and SPLUS3 (on UNIX systems). Principal Component Analysis (PCA) of the genetic distances was performed by SPLUS to determine the first three principal components. These were used to create clusters in a similarity dendrogram that elucidates groups (Stewart and Baker 1992, Stewart et al. 1993).

RESULTS

Genetic diversity measures indicate different levels of genetic variation for the twelve populations in BADL (Table 1). Fourteen loci were monomorphic, had inconsistent banding difficult to interpret (peroxidases and esterases), were unreadable (some of the dehydrogenases like SDH and XDH), or had poor migration (GDH and MPI). The mean percentage of polymorphic loci was 39.38% and the average number of alleles per locus ranged between 1.4 and 1.9 for the polymorphic loci. The mean heterozygosity over loci ranged from 0.061 in Ba to 0.169 in Bi, and the expected heterozygosity ranged from 0.060 in Ba to 0.202 at Bi. Note that Ba also had the smallest sample size (7) as the colony was isolated with no immediate neighbors, and had only seven widely-scattered coteries. Sample sizes for all populations examined ranged from 7 to 20 with a mean sample size of 17.1.

Analyses of genetic structure for populations within BADL show an estimated mean inbreeding coefficient F_{is} across loci with BADL to be 0.081 with considerable variation among loci. Jack-knifed mean inbreeding of 0.95 with standard deviation of 0.192 (Table 2). Of the polymorphic loci used to calculate the inbreeding coefficients, IDH and LAP showed opposite results: IDH had significant excess of heterozygotes (Fisher's exact probability <0.05); while LAP had significant excess of homozygotes (Fisher's Exact Probability <0.001). LAP had a rare allele that appeared at Co and Ha. The number of effective migrants per generation ranged from 0.24 for PGM-2 to 2.95 for IDH.

Analyses of macrogeographic genetic structure (F_{st}) show significant variation among loci with a mean F_{st} of 0.330. Jack-knifing across populations produced slightly higher mean F_{st} of 0.348 with a standard deviation of 0.114 (Table 2). Two loci, PGI-1 and PGM-2 had high F_{st} values suggesting low migration rates (N_m 0.49 and 0.24 migrants per generation respectively). Mean value of F_{st} (.330) across all loci suggests a gene flow rate of 0.51 migrants per generation.

Analyses of the hierarchical structure of genetic diversity using five polymorphic loci (removing rare (private) allele LAP-- Slatkin 1987) indicated significant structuring of genetic variation among coteries within towns (F_{tc}=0.312). The lowest explanatory structure for genetic diversity was colonies among regions (F_{cT}) where the mean F_{cT} was -0.12 (Table 3).

Analyses of uncontrolled populations indicated some difference from all populations with genetic differentiation among populations of 0.287, lower than F_{st} (0.330) for all populations (Table 4). Controlled towns also had the lowest observed heterozygosity (0.061 at Ba). The addition of regional populations combined with BADL did little to change F_{st} values from all of BADL towns (F_{st}=0.328); however, regional populations alone (WICA, DETO, THRO, and BADL) had a F_{st} value of 0.281 (jack-knifed F_{st}.0.348, standard deviation of 0.113) uncorrected for differences in sample size. There were a couple of rare and regional alleles both within BADL (LAP-1 at Co and Ha) and between BADL and THRO (MDH-1).

Modified Rogers genetic distances for towns within BADL showed Ha to have large genetic distances to Km (0.508) and Ko (0.455) (Table 5). Towns with the lowest genetic distances were

Ba to Tw (0.063), La to Ts (0.122), Ts to Tw (0.106), and Tw to Ty (0.100). The shortest geographic distance among towns were Bw to Bu (<1000 meters), Ts to Ty (1900 meters), and Ha to Ty (4700 meters). The longest geographic distances among towns were Ko to Bi (24000 meters) and Ko to Ba (22800 meters).

Principal Component Analysis (PCA) of BADL populations using allele frequencies for seven loci (including one rare (LAP-1) and one regional allele MDH-1 at THRO) showed 76% of the variance can be explained by the two eigenvectors (Table 6). The separation of populations along the first two principal component axes can be explained by differences in the first axes of PGI-1 frequencies ($r = -0.904$; $p = 0.001$) and in PGM-2 ($r = -0.825$; $p = 0.001$) for the second axis.

DISCUSSION

Black-tailed prairie dog populations exhibit considerable genetic variability and population sub-division. The organization of pdogs into coteries as social territorial groups may have important effects on the genetic differentiation of populations; genetic variation was higher among coteries within a town ($F_{ct} = 0.312$) than either among towns ($F_{tT} = 0.303$) or regions ($F_{cT} = -0.12$). As the coteries can be small and have a skewed sex ratio (usually one dominant male and several females), genetic drift and inbreeding would be predictably higher within populations than among regions (Chesser 1983). Similarily Daley (1992) found high F_{st} values ($F_{st} = 0.115$) along with a lack of correlation between genetic and geographic distances suggesting that even high migration

rates were insufficient to override population subdivision. As the samples from BADLs were evenly distributed among males, females, juveniles and adults, the high genetic diversity found is not likely to be biased by oversampling males or females, young or old.

Regional F_{st} values were also compatible to patterns found in pocket gophers *Thomonys* species (F_{st} values ranged from 0.232 to 0.752) with similar social structures as pdogs (Patton and Feder 1981, Carraway and Kennedy 1993). F-statistics for fossorial colonial animals are expected to be elevated beyond other species; Patton and Yang (1977) describe the genetic diversity of fossorial rodents as "...a broad mosaic with sharp discontinuities often between adjacent populations but with different patterns of discontinuities exhibited at nearly every locus."

The genetic diversity of Pdog towns within BADL did not appear to match expected distributions based on geographic distances. Genetic and geographic distances had no significiant relationship ($r^2 = 0.038$, $df = 85$, $p > 0.07$ for all possible pairs of towns. Figure 2). Clustering populations based on genetic distances using weighted average pair group assignment (WPGMA) also did not produce patterns predicted by the physical arrangement of populations on the landscape as smaller genetic distances are assumed to indicate higher levels of gene flow (Slatkin 1985a). Figure 3 demonstrates the lack of congruence between clusters expected by geographic distances and those by genetic distances. There are four groups (and two isolated towns) produced by clustering; while all the towns in the Tyree Basin colony (Ty, Tw, and Ts) clustered together as expected, other expected clusters like the Burns Basin colony (Bw, Bu) and the eastern colony (Bi and Ba) did not. The cluster of Bi and Bu is interesting as Bi is a controlled town and Bu is the nearest

uncontrolled town. Potentially the movement of dispersers from Bu to Bi is one example of management control pdog towns changing the genetic diversity among towns by increasing gene flow and decreasing genetic drift.

Regional towns clustered with BADL towns (Figure 4) and there was little evidence of clusters distinct within BADL or among regions. This result is consistent with that noted by Daley (1992) and Chesser (1983)--the genetic diversity within pdog towns was greater than the diversity among regions or among towns. Clustering towns on the first three prinicipal components (Figure 5) also did not produce strong groups suggestive of the patterns indicated in Figure 3. There were no clear groups produced by the three-dimensional clustering with PCA eigenvectors, nor were any patterns suggestive of alternative explanations.

The impact of population control was predicted as one mechanism (akin to random population fisson and fusion events) to reduce genetic differentiation (Slatkin 1985a, Whitlock and McCauley 1990, Whitlock 1992). Extinction events for social territorial animals can increase gene flow among subdivided populations in that immigrants would meet less resistence in re-establishing controlled populations (Daley 1992). In addition, if population bottlenecks decreased genetic diversity through founder effects, the inbreeding coefficient among populations would rise (Leberg 1990). In the case of pdogs, the frequent human-caused extinctions could increase gene flow among towns within a colony; but the coteries themselves could still tend towards inbreeding (Daley 1992). However, a small amount of mixing--such as a few survivors from a control effort mixed with dispersers--in the formation of a colonizing group can cause F_{st} to be "...non-linear

and monotonically increasing." (Whitlock and McCauley 1990). In such cases, linear relationships between genetic diversity and geographic distances would not be expected because of the influence of social systems on immigration and emigration (Patton and Yang 1977, White and Svenden 1992).

Pdog population control appeared to have little affect on the population subdivision enforced by the coterie system. The extreme population subdivision appeared to persist and the frequent extinction and recolonizations had little overall effect on genetic diversity (of uncontrolled populations). Figure 4 illustrates this point--clustering genetic distances for all populations does not separate inter-regional populations from intra-regional ones suggesting genetic diversity within a region can exceed that among regions. Extinction events, such as population control, were not sufficient to reverse the effects of genetic drift intra-regionally potentially because a very limited number of survivors in a colonized town could counter-act the effects of gene flow among that town and its neighboring populations encouraged by the extinction event (Slatkin 1985, Slatkin 1987, Whitlock and McCauley 1990, Whitlock 1992). The differing ratios of homozygote and heterozygote alleles (indicative of population isolation--Britten and Brussard 1993) complement this theory of control-survivors counteracting gene flow effects. Private alleles found within BADL at Co and Ha also promote the idea of survivors mixing with immigrants for pdog populations.

Landscape features were not examined in this study and their effects on pdog dispersal were not estimated. One probable explanation of the high genetic diversity within colonies of BADL may

be landscape barriers (like the badland walls) or limits to colony establishment such as soil types or slope (Bowser 1996b). Landscape features can change the actual distance an animal travels between two populations, thus the genetic distance may be reflective of the actual dispersal paths the animals follow around landscape features and different barriers. To examine this hypothesis that landscape complexity dictates genetic diversity, actual dispersal distances would need to be created based on ecological parameters of pdogs (Bowser 1996b, 1996c). These paths would be expected to better reflect the levels of gene flow among populations then estimates based on the euclidean distances among populations.

The genetic diversity of pdog populations on the Great Plains is high and there is no relationship between the genetic and geographic distances for towns within colonies or among colonies and regions. Population control efforts do not appear to have counter-acted the tendency for prairie dogs, as fossorial animals, to be more isolated in space due to their fossorial habit. The next step to explain spatial genetic distributions of pdog populations would be an examination of the actual dispersal paths animals follow among towns--assuming that the true distance among populations is not a straight line, but a circuitous route that avoids barriers or certain habitats. A spatial genetic test likely to elucidate spatial patterns for pdogs could be used in the planning for effective population controls while maintaining long-term population genetic diversity.

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Table 1. Summary of genetic diversity measures for isozyme loci observed in *Cynomys ludovicianus* populations in Badlands National Park, South Dakota.

Population	**Ha**	**Bi**[*1]	**Ba**[1]	**Bu**	**Bw**[2]	**Co**[2]	**Ts**	**Tw**	**Ty**	**Ko**	**La**	**Km**
Sample Size	20	20	7	20	13	18	18	13	20	16	20	20
% polymorphic alleles	42.9	42.9	28.6	42.9	28.6	42.9	42.9	42.9	71.4	28.6	42.9	42.9
Mean number of alleles	1.9	1.4	1.4	1.7	1.7	1.4	1.4	1.6	1.9	1.4	1.4	1.6
standard error	0.4	0.2	0.3	0.4	0.4	0.2	0.2	0.3	0.3	0.3	0.2	0.3
Mean heterozygosity												
Observed	.155	.169	.061	.133	.124	.099	.074	.107	.103	.131	.150	.110
standard error	.087	.109	.042	.063	.072	.076	.037	.062	.046	.106	.075	.079
Expected	.142	.202	.060	.148	.174	.147	.113	.117	.120	.121	.166	.106
standard error	.072	.097	.041	.074	.106	.076	.060	.058	.039	.096	.080	.065

* = controlled towns (bi-annual reductions by park staff).
1 = towns on private lands (controlled annually by landowner).
2 = towns on National Forest Service lands controlled by annual permit hunts.
Population abbreviations: Ha=Haybutte; Bi=Bigfoot, Ba=Baysinger; Bu=Burns Basin; Bw=Burns West; Co=Conata Basin; Ts=Tyree South; Tw=Tyree Southwest; Ty=Tyree Basin; Ko=Kocher Flats; La=Larsons; Km=Kocher Main.

Table 2. Summary of single and multi-locus F-statistics calculated for colonies within Badlands National Park, South Dakota using BIOSYS-1 (Swofford and Selander 1981). Calculations were based on polymorphic loci following Carraway and Kennedy (1993). Jack-knifed variances are calculated from Weir, (1990) FORTRAN program. Number of migrants (N_m) is calculated following formula used by Wayne et al. (1991). $F_{st} = 1/(4N_m + 1)$

Locus	F_{is}	F_{it}	F_{st}	N_m
6PGD	.188	.337	.183	1.51
IDH	.356	.407	.078	2.95
PGI-1	.024	.354	.338	0.49
PGM-1	.079	.201	.133	1.63
PGM-2	.034	.524	.507	0.24
LAP	-.200	-.014	.155	1.36
Mean	.081	.384	.330	0.51
Jack-knifed over all populations*	.095	.402	.348	
(SE)	(.192)	(.125)	.114	
Confidence limits	-.170 - .396	.197 - .582	.194 - .526	

* Weir's formula corrects for sample sizes and calculates the mean F-statistics slightly higher than Swofford and Selander (1981) BIOSYS-1 program. Weir and Cockerham (1984) and Whitlock (1992) discuss some of the differences in calculating F-statistics.

Table 3. Hierarchical breakdown of genetic diversity measures calculated by BIOSYS-1 (Swofford and Selander 1981) using five polymorphic loci for black tailed prairie dog *(Cynomys ludoviciamus)* populations within Badlands National Park, South Dakota.

Locus	F_{tc}[1]	F_{tT}[2]	F_{cT}[3]
6PGD	.039	.153	.119
IDH-1	.035	.046	.012
PGI-1	.373	.300	-.117
PGM-1	.055	.109	.057
PGM-2	.489	.487	-.004
Mean	.312	.304	-.012

1. Hierarchical F-statistics for towns (t) within colonies (c); 2. Hierarchical F-statistics for towns (t) within regions (T); 3. Hierarchical F-statistics for colonies (c) among regions (T).

Table 4. Summary of single and multilocus F-statistics for uncontrolled prairie dog colonies in Badlands National Park, South Dakota. F-statistics were calculated using BIOSYS-1 (Swofford and Selander 1981) based on six polymorphic loci.

LOCUS	F_{is}	F_{it}	F_{st}
6PGD	.175	.222	.053
IDH	.356	.402	.071
PGI-1	-.118	.267	.344
PGM-1	.157	-.056	.087
PGM-2	.183	.607	.519
LAP	-.200	-.021	.149
MEAN	.025	.304	.287
Jack-knifed over all populations	.163	.406	.293
(SE)	(.051)	(.043)	(.067)
Confidence Limits	.052 - .266	.315 - .493	.145 - .397

Table 5. Modified Rogers genetic distance from allele frequencies of six polymorphic loci from 12 prairie dog (*Cynomys ludovicianus*) towns in Badlands National Park, South Dakota (rare and regional alleles were not included in this analysis--see discussion in Britten and Brussard 1992).

Location	Bi	Bu	Bw	Ba	Co	Ha	Ts	Tw	Ty	Ko	La	Km
Bi	****											
Bu	0.137	****										
Bw	0.217	0.185	****									
Ba	0.385	0.346	0.410	****								
Co	0.316	0.279	0.383	0.470	****							
Ha	0.298	0.369	0.308	0.563	0.455	****						
Ts	0.237	0.174	0.272	0.416	0.202	0.346	****					
Tw	0.235	0.169	0.228	0.413	0.280	0.317	0.106	****				
Ty	0.260	0.162	0.240	0.364	0.313	0.375	0.138	0.100	****			
Ko	0.300	0.267	0.161	0.475	0.379	0.270	0.252	0.203	0.245	****		
La	0.214	0.212	0.264	0.445	0.272	0.247	0.122	0.146	0.186	0.242	****	
Km	0.324	0.285	0.357	0.063	0.419	0.508	0.358	0.356	0.311	0.424	0.387	****

Table 6. Principal Component Analysis (PCA) Axes from variance-covariance matrix of allele frequencies from seven polymorphic loci (including all rare and regional alleles) for 15 prairie dog (*Cynomys ludovicianus*) from four regional populations on the Great Plains of North America. Stars indicate which locus significantly explains for most of the variation in towns for each axis. Numbers in parentheses indicate the percent variance explained by that vector.

Locus	Vector 1* (43.360)	Vector 2** (32.606)	Vector 3*** (10.926)
6PGD	0.1804	-0.3418	0.8706
MDH-1[a]	-0.0178	-0.1065	0.0648
IDH-1	0.0916	0.0212	0.0776
PGI-1	-0.8464	0.4054	0.3241
PGM-1	0.1054	-0.0261	0.1608
PGM-2	-0.4792	-0.8400	-0.2166
LAP	0.0408	0.0270	-0.2324

*= PGI-1 (r=-0.904, p=0.000).

**=PGM-2 (r=-0.825, p=0.000)

***=6PGD (r=0.772, p=0.000)

a= MDH-1 was a regional allele, polymorphic only in THRO and is included in all regional comparisions.

Figure 1. Black tailed prairie dog (Cynomys ludovicianus) colony distributions in Badlands National Park, South Dakota

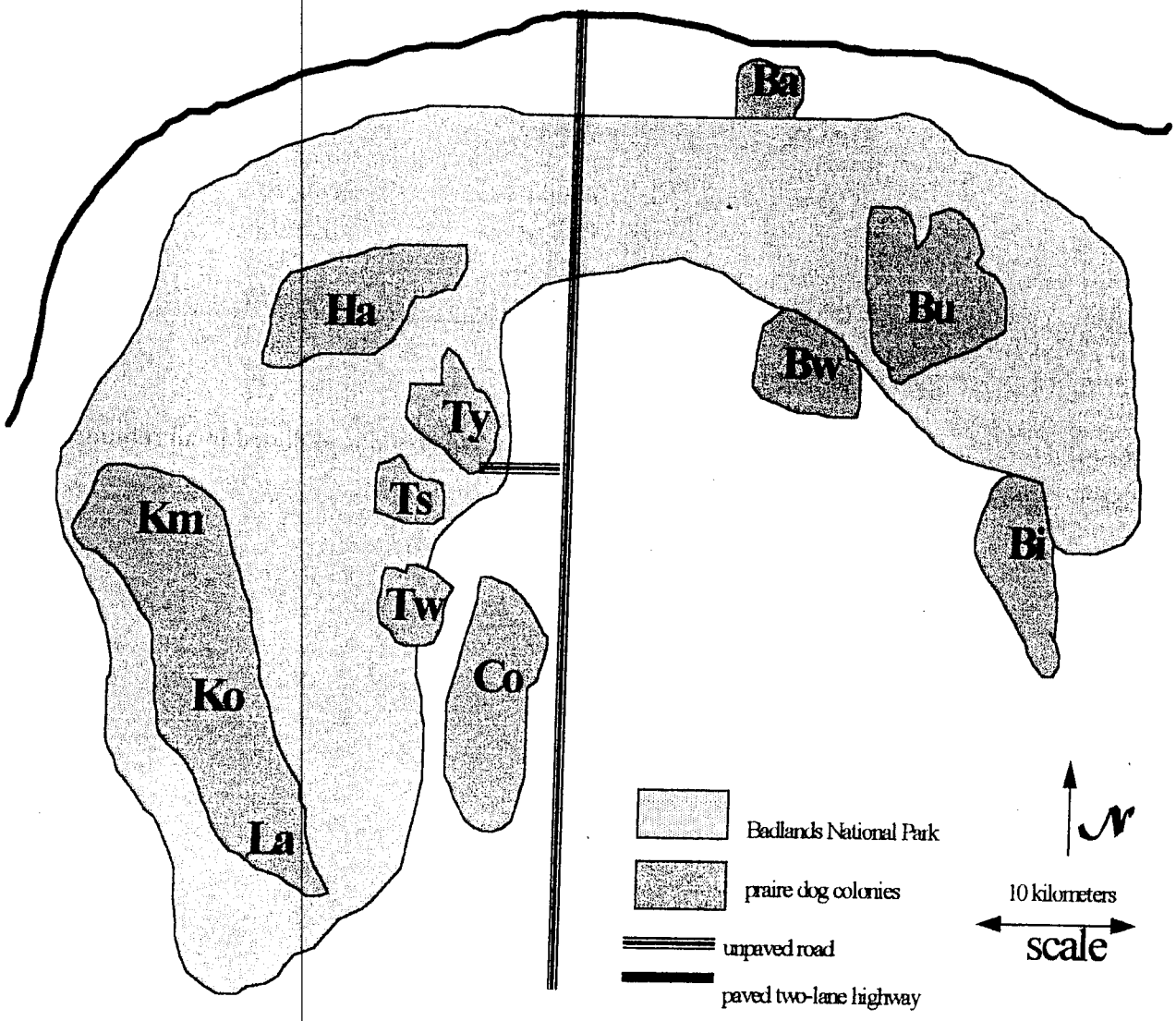
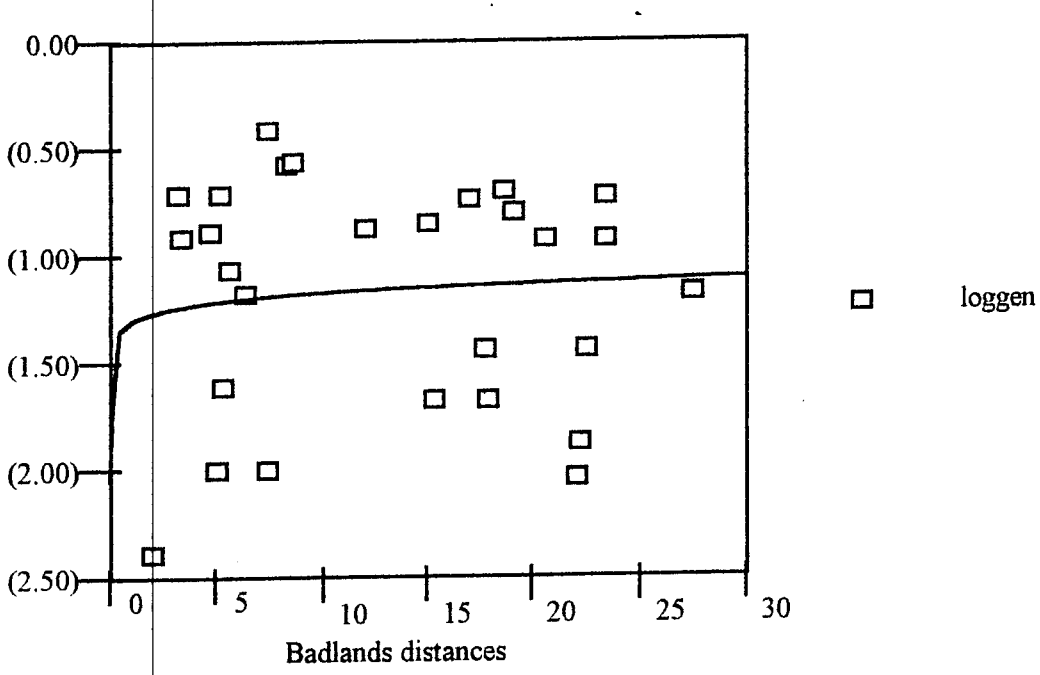


Figure 2. Log-transformed genetic (loggen) versus linear distances for black-tailed prairie dog (*Cynomys ludovicianus*) populations within Badlands National Park, South Dakota. Loglinear regression line drawn to show non-significant relationship between genetic and geographic distances.



$y = 0.132LOG(x) - 1.314 \quad r^2 = 0.006$

Figure 3. Weighted Pair Group Method Averaging (WPGMA) using Modified Rogers Genetic distance data on six polymorphic loci for prairie dog populations in Badlands National Park, South Dakota. See text for population abbreviations.

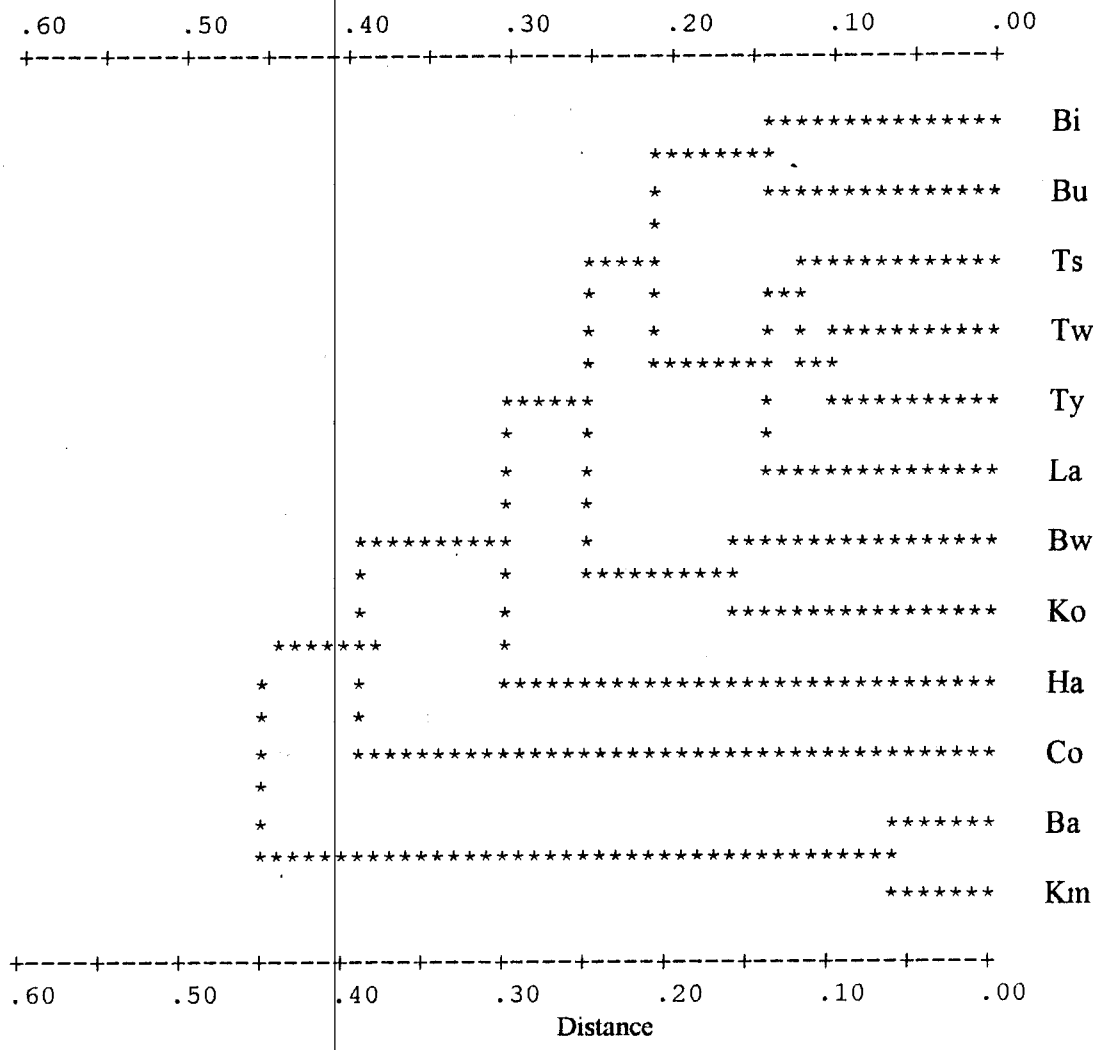


Figure 4. Weighted Pair Group Method Averaging (WPGMA) clusters of genetic distances for seven alleles (including rare and regional alleles) among towns and regions of prairie dog populations on the Great Plains of North America. See text for population abbreviations.

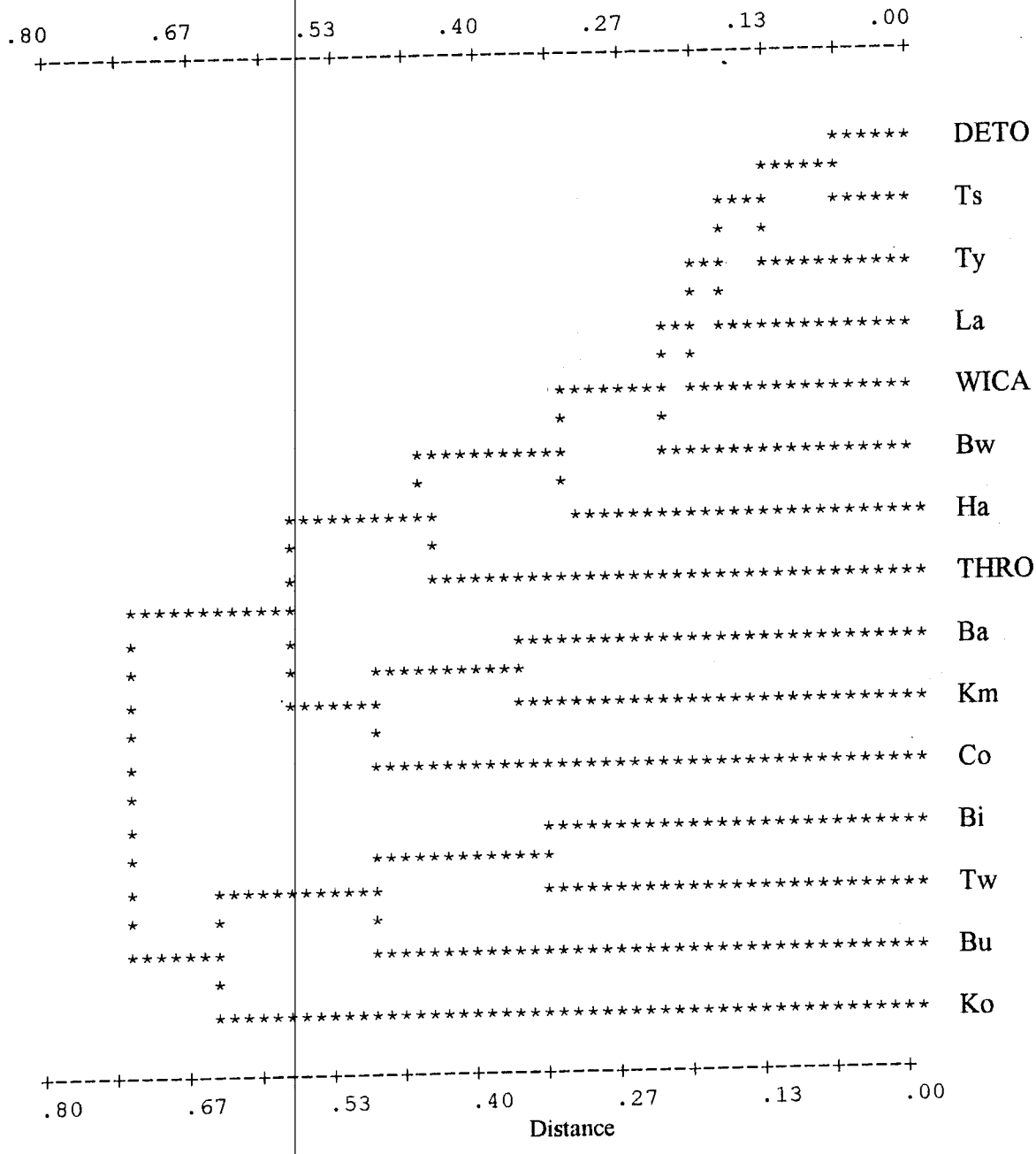


Figure 5. Cluster three-dimension diagram based on the first three principal components from PCA of allele frequences for seven polymorphic loci in 15 prairie dog towns in four regions on the Great Plains of North America.

