

THESIS

GENETIC ANALYSIS OF A BLACK-TAILED PRAIRIE DOG (*CYNOMYS*
LUDOVICIANUS) METAPOPOPULATION WITHIN SHORTGRASS STEPPE

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR
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ABSTRACT OF THESIS

GENETIC ANALYSIS OF A BLACK-TAILED PRAIRIE DOG (*CYNOMYS LUDOVICIANUS*) METAPOPOPULATION WITHIN SHORTGRASS STEPPE

Black-tailed prairie dogs (*Cynomys ludovicianus*) in shortgrass steppe currently exist as a metapopulation. Habitat alteration, recreational shooting, agricultural control, and most recently, the introduction of sylvatic plague (*Yersinia pestis*) have contributed to local colony extinction and a steady decline of *C. ludovicianus* from its large and continuous historical range. Difficulties in quantifying dispersal have complicated efforts to document the degree of connectedness between isolated colonies. However, patterns of genetic similarity among populations, as measured by neutral molecular markers, provide an estimate of the degree of linkage within a metapopulation. We sampled 13 black-tailed prairie dog colonies in shortgrass steppe in Weld County, Colorado. The history of extinctions and recolonizations of the 13 colonies during the past 18 years is known. We examined 153 prairie dogs for variation at seven microsatellite loci and found moderate levels of genetic differentiation among prairie-dog populations ($F_{ST} = 0.118$). Akaike's Information Criterion was used to model prairie-dog dispersal as a function of genetic distance. Pairwise genetic distances between populations were related

to both the distances along drainages (potential dispersal corridors), and to the relative ages of the populations. Cluster analysis revealed that prairie-dog populations are not more closely related to nearest neighbors than to other populations, indicating that populations are not in genetic drift-migration equilibrium and that prairie dogs are likely to disperse among all populations.

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INTRODUCTION

A metapopulation is defined as a subdivided population linked by limited migration, extinctions of local populations, and establishment of new populations by dispersers (Levins, 1969, 1970). By their very nature, metapopulations are often highly fragmented, resulting in subdivided local populations (Hanski, 1997; Harrison, 1994; McCullough, 1996). Studies of metapopulation dynamics have focused on the theory of metapopulation models (e.g., Gyllenberg and Hanski, 1992; Hanski, 1991; Hastings, 1991; Howe et al., 1991) and modeling real populations (e.g., Beier, 1996; Gaona et al., 1998; Harrison et al., 1988; Lamberson et al., 1994; Lindenmayer et al., 1999; Price and Gilpin, 1996; Wootton and Bell, 1992). However, there is limited evidence that metapopulations exist in natural ecosystems (Harrison, 1991; Harrison and Taylor, 1997; Simberloff, 1995; but see McCullough, 1996), especially for long-lived animals (Gaona et al., 1998).

A metapopulation's persistence depends on the balance between the processes of extinction and recolonization (McCullough, 1996). An element to persistence is the dispersal of individuals within and among patches of suitable habitat (Lidicker and Koenig, 1996). Studies of metapopulation biology critically depend upon information on movement and dispersal (Lidicker and Koenig, 1996), and in particular on how dispersal

is affected by landscape structure, including dispersal corridors (Hanski and Thomas, 1994; Merriam, 1988; Wiens, 1996; Wiens et al., 1993). Experimental modeling may assist in conceptually linking landscape structure to metapopulation dynamics, but to better understand these dynamics, we need to examine natural populations in native environments (Hobbs, 1992; Wiens, 1996).

Black-tailed prairie dogs (*Cynomys ludovicianus*) are ideal for metapopulation studies because they exist in spatially isolated colonies that are connected by dispersing individuals. The dynamics of prairie-dog populations are influenced by local colony extinctions, which result from recreational shooting, agricultural control, habitat loss and alteration, and epidemics of sylvatic plague (*Yersinia pestis*). Dispersing prairie dogs are known to follow landscape features, such as roads and drainages (Garrett and Franklin, 1998; Knowles, 1985, 1986). Dispersal between black-tailed prairie dog colonies is characterized by: 1) occasional long-distance migrations, sometimes more than 5 kilometers, 2) movement of individuals into established or abandoned colonies rather than the establishment of new colonies, 3) dispersal by yearling males and adult females, 4) dispersal by individuals rather than groups, and 5) peak dispersal during the post-weaning period (June-August) (Garrett and Franklin, 1988; Garrett et al., 1982; Knowles, 1985). Despite the demographic studies on prairie-dog dispersal (Garrett and Franklin, 1988; Garrett et al., 1982; Knowles, 1985, 1986) and recolonization of experimentally-eradicated colonies (Cincotta et al., 1987), difficulties in observing and quantifying dispersal behavior have complicated efforts to document the degree of connectivity among colonies. Landscape connectivity refers to the extent to which the landscape

facilitates or impedes movement among patches (Taylor et al. 1993).

Patterns of genetic structure and genetic similarity among populations can provide insights into the processes of dispersal and recolonization. However, measures of genetic similarity are only indirect estimates of dispersal, and previous genetic studies of prairie dogs have yielded contrasting results. Foltz and Hoogland (1983) found little genetic differentiation among black-tailed prairie dog populations in the mixed-grass prairie of South Dakota, which suggests outbreeding and moderate to high rates of dispersal. McCullough and Chesser (1987) found little genetic differentiation and moderate rates of dispersal among three populations of Mexican prairie dogs (*C. mexicanus*). In contrast, Chesser (1983) reported significant inbreeding within and low dispersal rates among populations of black-tailed prairie dogs in the shortgrass steppe and semi-desert grassland of New Mexico. Daley (1992) also found moderate genetic differentiation among black-tailed prairie dog populations in mixed-grass prairie. Travis et al. (1997) found little evidence of significant gene flow between two populations of Gunnison's prairie dogs (*C. gunnisoni*). Dobson et al. (1997) concluded that although inbreeding did occur in black-tailed prairie dog populations, it occurred at a hierarchical level. Inbreeding was minimized at the level of breeding groups and random mating occurred within the subpopulation.

The social systems of *Cynomys* species differ, although they are all colonial, and this may, in part, explain the contrasting conclusions of these studies. Additionally, population structure of black-tailed prairie dogs may vary across grassland habitats. Most studies of black-tailed prairie dogs have focused on populations in mixed-grass prairie

(Cincotta et al., 1987; Daley, 1992; Dobson et al., 1997; Foltz and Hoogland, 1983; Garrett and Franklin, 1988; Halpin, 1987; Knowles, 1985, 1986). Foraging by prairie dogs reduces the amount of taller grasses in favor of perennial shortgrasses in mixed-grass prairie (Lauenroth et al., 1994), and this creates large patches of short vegetation within a matrix of taller vegetation (Stapp, 1998). In contrast, plant composition and vegetation height may not be different between uncolonized grasslands and prairie-dog colonies in shortgrass steppe (Koford, 1958; P. Stapp, in litt.). Black-tailed prairie dog colonies tend to be large, stable, and in close proximity to many neighboring colonies in the northern mixed-grass prairie (Halpin, 1987; Hoogland, 1995), but tend to be small, unstable, and isolated by distance and unsuitable habitat in shortgrass steppe and in areas of the eastern mixed-grass prairie (Halpin, 1987; M. Ball, pers. comm.). Therefore, dispersal may have different consequences for black-tailed prairie dogs across the range of grasslands.

Studies of metapopulations have become an important component of conservation biology, especially as habitats have become fragmented as a result of human intervention (Driscoll, 1998; Harrison, 1994; McCullough, 1996). Conservation of black-tailed prairie dogs is critical because they play a critical role in grassland ecosystems by altering plant succession and nutrient-cycling (Agnew et al., 1986; Ceballos et al., 1999; Koford, 1958; Miller et al., 1994; Reading et al., 1993; Whicker and Detling, 1988). They are also thought to increase regional species diversity of small mammals (Ceballos et al., 1999). Some authors have even considered the black-tailed prairie dog a keystone species (Ceballos et al., 1999; Miller et al., 1994; but see Stapp, 1998).

The grasslands of the Great Plains have suffered extensive alteration and fragmentation (Samson and Knopf, 1994). These changes have affected prairie-dog populations in this region. A recent ruling found that black-tailed prairie dogs warrant consideration for threatened status under the U. S. Endangered Species Act (Gober, 1999). Despite their broad distribution throughout the western Great Plains, black-tailed prairie dogs are thought to inhabit less than 10% of their historical range (Anderson et al., 1986). In general, fragmented and isolated populations have higher extinction rates (MacArthur and Wilson, 1967; Wilcox and Murphy, 1985). Thus, habitat fragmentation may increase the likelihood of local prairie-dog population extinction due to inbreeding and random demographic events (Wilcox and Murphy, 1985).

One of the most important and unpredictable constituents affecting prairie dogs is the widespread occurrence of sylvatic plague, a disease that is likely exotic to North America (Cully, 1993; Fitzgerald, 1993; Gober, 1999). Plague epizootics in mammalian populations were first recorded in North America in 1908 and spread to the western edge of the Great Plains, including Colorado, by 1940 (Barnes, 1982; Fitzgerald, 1993). Prairie dogs are extremely sensitive to sylvatic plague; affected black-tailed prairie dog colonies are eradicated in one season or faster (Center for Disease Control, Fort Collins, Colorado, in litt.; Fitzgerald, 1993; Rayor, 1985). The effects of sylvatic plague on black-tailed prairie dog colony size and connectivity need further study (Gober, 1999).

The objectives of this study were to: 1) determine whether landscape structures such as potential corridors affect dispersal in black-tailed prairie dogs in shortgrass steppe, 2) evaluate extinction and recolonization dynamics of prairie dogs with a

metapopulation structure, and 3) determine if the genetic structure of recently recolonized populations indicates that population bottlenecks have occurred. We studied: 1) the spatial arrangement of prairie-dog populations in relation to genetic similarity of the populations, 2) genetic differentiation within and among populations, and 3) prairie-dog dispersal inferred from genetic analyses.

METHODS

Study organism

Black-tailed prairie dogs (*Cynomys ludovicianus*) are nonhibernating, colonial burrowing rodents. Taxonomists currently recognize five species of prairie dogs: white-tailed, Utah, Gunnison's, Mexican, and black-tailed (Clark et al., 1971; Hall, 1981; Hollister, 1916; MacClintock, 1970; Pizzimenti, 1975), all of which occur in western North America. Black-tailed prairie dogs are the most widespread of the prairie dog species, ranging from Montana to northern Mexico from the Rocky Mountains east to the 100th meridian (Hoogland, 1995). Prairie-dog colonies are restricted by topographic features, including tall vegetation, water courses, and other barriers (King, 1955; Koford, 1958). Black-tailed prairie dogs are strictly colonial and are rarely observed away from established colonies (Koford, 1958; Smith, 1958). Within colonies, black-tailed prairie dogs live in coterries, or harem-polygynous territorial family groups composed of one adult male, 3-4 adult females, and their offspring (Hoogland, 1982, 1995). Male-biased natal dispersal within colonies, accompanied by female philopatry, may be a behavioral mechanism preventing inbreeding (Dobson et al., 1997; Halpin, 1987; Hoogland, 1982). Prairie dogs reach sexual maturity at two years of age when they weigh 700 to 1500

grams. The adult sex ratio is skewed in favor of females (Hoogland, 1981; King, 1955). Breeding occurs from late February through March, litter size ranges from 1-6, and the young emerge from their natal burrows in late May and June (Hoogland, 1982; King, 1955). The average life span of black-tailed prairie dogs is 3-4 years although some females have lived for up to 8 years (Hoogland, 1995).

Study area

The study site consisted of 13 black-tailed prairie dog colonies within a 264 km² area on the Central Plains Experimental Range and the Pawnee National Grassland in Weld County, Colorado, approximately 60 km northeast of Fort Collins (40° 35' N, 104° 45' W; Fig. 1). Mean elevation of the study area was 1700 m. The topography consisted primarily of shortgrass steppe interspersed with shallow swales and shrub-covered ridge tops. Typically, prairie-dog colonies exist in low-lying areas, such as swales and broad seasonal drainages, and are dominated by short, perennial bunchgrasses (*Bouteloua gracilis* and *Buchloe dactyloides*) and annual forbs. Upland areas separating prairie-dog colonies are also dominated by bunchgrasses, but have greater cover of small and large shrubs (*Eriogonum microthecum*, *Gutierrezia sarothrae*, and *Atriplex canescens*) than do prairie-dog colonies (Bonham and Lerwick, 1976). Hereafter, colonies are defined as the physical areas inhabited by prairie dogs and the populations refer to all prairie dogs inhabiting a colony.

Prairie-dog colonies have existed historically on the Pawnee National Grassland,

and have been monitored by the U.S. Forest Service since 1967. Annual assessments provide data on the location and active area of a colony, the time since establishment, periods of inactivity (extinction), and the time since recolonization after periods of inactivity (M. Ball, in litt.). Sylvatic plague epidemics, agricultural control efforts, and recreational shooting are major causes of local population extinction on the Pawnee National Grassland. Sylvatic plague first appeared in Colorado between 1945 and 1949 (Ecke and Johnson, 1952), but it is not known exactly when plague appeared on the Pawnee National Grassland. Data from U. S. Forest Service monitoring efforts indicate that sylvatic plague was present on the Pawnee National Grassland by 1967 and plague epidemics destroy a given prairie-dog population in 5-10 year cycles (M. Ball, pers. comm.). Colonies have historically occurred on Central Plains Experimental Range lands. However, information for these populations is limited to the presence or absence of prairie-dog activity (M. Ashby, pers. comm.).

Active area for each colony was estimated by calculating minimum polygon area (M. Ball, pers. comm.). The perimeter of each area was delineated by recording GPS coordinates at every active burrow along the colony edge. Active burrows were determined by sight or sound identification of prairie dogs, the presence of fresh feces, active diggings and/or tracks, and clipping of adjacent vegetation.

We did not use mark-recapture or visual counts to estimate population size on each of the 13 colonies. We did determine burrow densities by counting the number of active burrows in a 80 m x 150 m plot on 8 of 13 colonies. Estimated active burrow densities ranged from 55.8 burrows/ha to 90.8 burrows/ha (Appendix I). Initially, we

hoped to develop a relationship between population size and burrow density. Biggins et al. (1993) found a high correlation ($r = 0.95$) between estimates of white-tailed prairie dogs and counts of active burrows, but other studies have found that densities of burrow entrances may not be reliable indices of population size and densities for sciurid species (Cincotta et al., 1987; Hoogland, 1995; Powell et al., 1994; Van Horne et al., 1994). We did not estimate population size, but assumed that a greater number of prairie dogs inhabited larger colonies than smaller ones. Therefore, we used colony area as a relative indicator of population size.

Tissue collection, DNA extraction, and microsatellite genotype scoring

During June 1997 - January 1998, we live-trapped 153 prairie dogs in 13 populations. We recorded sex, age, reproductive status, and body mass of each animal. We collected a tail-clip from each individual for genetic analysis. After sampling, prairie dogs were marked with ear tags and released. Tissue samples were placed in an isotonic saline buffer (1X SSC: 0.15 M NaCl, 15 mM sodium citrate, 1 mM EDTA) and stored at -80°C for DNA extraction. DNA was isolated from the tail-clips by the CTAB (hexadecyltrimethylammonium bromide) procedure (Black and DuTeau, 1997). Primers for microsatellite analysis (IGS-1, IGS-6, CGS-14, CGS-17, CGS-22, CGS-25, CGS-26) were developed by May et al. (1997) and Stevens et al. (1997). We tried additional microsatellite primers (IGS-110b, IGS-BP1, CGS-12, CGS-20, and CGS-34), but they were not included in analysis because they were found to have either no product, a

monomorphic product, or too many stutter bands to score accurately.

PCR amplification of the loci was performed in a MJR PTC-100 thermocycler in 25- μ l volumes containing \approx 30 ng genomic DNA, 1.5 mM MgCl₂, 500 pm concentrations of forward and reverse primer, 100 μ M dNTPs, 1 X *Taq* buffer, and 0.5 U *Taq* polymerase. PCR cycling conditions for IGS-1 and IGS-6 were 94°C for 3 min followed by 34 cycles of 94°C for 1 min, 54°C for 30 s, and 72°C for 30 s followed by a final extension of 5 min at 54°C (May et al., 1997). Amplification conditions for CGS-14, CGS-17, CGS-22, CGS-25, and CGS-26 were 94°C for 1 min followed by two cycles of 94°C for 30 s, 58°C for 20 s, 72°C for 5 s followed by 33 cycles of 94°C for 15 s, 54°C for 20 s, 72°C for 5 s and then 72°C for 30 s (Stevens et al., 1997). Amplified samples were electrophoresed at 45 watts for 2-7 hours depending on the length of the fragment (Table 1) through 8% denaturing polyacrylamide gels as described in Sambrook et al. (1989). Each gel was fixed for 20 min in 2L of 10% glacial acetic acid, and DNA was visualized with silver stain as described in Black and DuTeau (1997). Individuals were assigned genotypes based on banding patterns from the silver-stained gels (Appendix II).

Data analysis

Population genetic structure

Observed genotype frequencies were tested for departures from Hardy-Weinberg equilibrium at each locus within each population using both Levene's (1949) correction

for small sample size and the exact probabilities options in BIOSYS-1 (Swofford and Selander, 1989). Within-population genetic diversity was assessed by examining the expected heterozygosity under Hardy-Weinberg equilibrium. We compared genetic diversity among recolonized and extant populations using the nonparametric Mann-Whitney U -statistic, with each population weighted equally. We analyzed genetic differentiation among and within populations in BIOSYS-1 using Weir and Cockerham's (1984) F -statistics. These parameters make explicit use of sample sizes, are well-suited to small data sets, and are related to Wright's (1965) F -statistics as $F = F_{IT}$ (the overall inbreeding coefficient), $\theta = F_{ST}$ (the subpopulation inbreeding coefficient), and $f = F_{IS}$ (the within population inbreeding coefficient). We calculated 95% confidence intervals about F -statistics by jackknifing across loci.

Tests of dispersal models

Pairwise genetic distances were calculated using three different distance metrics. We calculated the proportion of alleles shared between populations (Bowcock et al., 1994) (denoted D_A) using the program Microsat (<http://lotka.stanford.edu/microsat/microsat.html>). Cavalli-Sforza and Edwards' (1967) chord distance (denoted D_C) was also calculated between pairs of populations using BIOSYS-1 because it was found by Takezaki and Nei (1996) to have a higher probability of obtaining correct tree topologies for microsatellites under the stepwise mutation model than other distance measures. Finally, we calculated a distance measure using $F_{ST}/1-F_{ST}$

(Rousset, 1997) (denoted D_F) provided by the software package GENEPOP (Raymond and Rousset, 1995). In contrast to probabilities of identity, F_{ST} values are essentially independent of the rate and process of mutation and of total population size (Rousset, 1997). We then used the neighbor-joining (Saitou and Nei, 1987) procedure in the PHYLIP 3.51c package (Felsenstein, 1993) to construct dendrograms describing the relationship among populations using all three genetic distance measures. A majority-rule consensus tree was estimated from 1000 bootstrap replicates by resampling loci within each population. We also constructed a dendrogram using drainage geographic distance between prairie-dog populations to illustrate the physical relationship among populations.

Models of dispersal

We tested to see if populations fit an isolation-by-distance model (Slatkin, 1993). We incorporated measures of landscape structures into the analyses to determine if structures that promote dispersal better explain the genetic similarities between populations. We included linear distance between colonies because it has been widely used as a correlate with genetic distance (Baer, 1998; Haig et al., 1994; Hellberg, 1994; Pfenninger et al., 1996; Raybould et al., 1996). The importance of drainages and roads as potential dispersal corridors for black-tailed prairie dogs has been documented (Garrett and Franklin, 1988; Garrett et al., 1982; Knowles, 1985, 1986). We also chose to include the minimum drainage-road distance because prairie dogs may use both drainages and

roads during a dispersal event.

Using a planimeter and GPS coordinates, we calculated 78 pairwise distances for the 13 colonies. We used four individual distance measures: linear distance (denoted “linear”), drainage distance (denoted “drainage”), road distance (denoted “road”), and drainage and road distance combined (denoted “drainage-road”). Linear was determined by shortest straightline distance between each population, with no constraints. Drainage was measured by shortest distance, with the restriction that prairie dogs must follow swales and could not traverse open upland areas. Road was determined by shortest distance, with the restriction that prairie dogs must follow roads and could not travel across shrubland habitats. Drainage-road was measured by shortest distance, with the constraint that prairie dogs must follow the shortest route on roads and drainages. Pairwise geographic distances between colonies were used to construct four distance matrices.

We calculated least squares regressions for the three genetic distance metrics against \log_{10} of the four different geographical distances between colonies. Regressions were calculated for all pairs of colonies. The 95% confidence intervals for regression slopes were determined by using the number of populations rather than the number of pairwise comparisons for the degrees of freedom; simulations using Mantel’s randomization test (1967) showed that the two methods are in agreement (Hellberg, 1994). The relationships between D_A , D_C , or D_F and the four geographical distances between colonies were tested using Mantel’s general regression test. The statistical significance of the observed test statistic was found by comparing 1000 random

permutations of the geographical distance matrix, with a new test statistic each time. The significance level was designated as the proportion of permutations in which the test statistic was equal to or greater than the observed value.

The Mantel and least squares tests (at $\alpha = 0.05$ level of significance) were used to compare pairwise genetic and geographic distances, but we also wanted to incorporate colony age into our models of dispersal. We constructed a matrix for the pairwise differences in mean age between colonies. We predicted *a priori* that geographic distance measures would be better predictors of genetic distance, but that colony age would influence genetic similarity between populations and would explain additional variation in the genetic distance between populations. We tested mean age difference between colonies as an independent variable. We did not incorporate mean area difference between colonies into our models of dispersal.

We developed simple models expressing the relationship between genetic distance and intercolony distance and colony age. The independent variables for the nine models were: 1) colony age, 2) linear distance, 3) drainage distance, 4) road distance, 5) drainage-road distance, and 6)-9) the same geographic distances in models 2-5 with colony age as an additional variable. These models were compared for three genetic distance measures: D_A , D_C , and D_F . Model selection was based on least squares and Akaike's Information Criterion (AIC, see Akaike, 1973; Burnham and Anderson, 1998; Lebreton et al., 1992). AIC has a strong theoretical foundation in Kullback-Liebler (K-L) information theory (Burnham and Anderson, 1998). AIC measures the relative expected K-L distance between the approximating model and "reality". A set of candidate models is selected *a*

priori knowing that “reality” is not among them. AIC is computed for each of the approximating models in the set, and the model with the lowest AIC value is estimated to be closest to “reality”. This “best” model is the one that is chosen for inference. AIC is not a test in any sense, that is, no hypothesis (i.e., model) is the “null” and there is no arbitrary α level. Rather, AIC is based on the concept of inference, given the “best” approximating model, the data, and the set of *a priori* models (D. Anderson, pers. comm.). In contrast, traditional hypothesis testing lacks the theory to make sound inferences for vigorous model selection (Akaike, 1981; Burnham and Anderson, 1998; Royall, 1997). We compared the set of *a priori* models by comparing models based on their AIC values, rather than relying on the hypothesis-testing approach. A first-order linear approximation seemed most appropriate because this study was based on a relatively small sample set (Royall 1997; D. Anderson, pers. comm.).

Adjusted R^2 statistics were used to determine whether or not a particular model provided an adequate description of the data set. The adjusted R^2 statistic is an alternative to the correlation coefficient R^2 , and is adjusted for the number of model parameters (SAS Institute, 1989) and is calculated as

$$\text{adj } R^2 = 1 - [((n-i)(1-R^2))/(n-K)],$$

where n = number of observations used in fitting the model, K is the number of parameters in the model, and i is an indicator variable that is 1 if the model includes an intercept, and 0 otherwise. We used AIC to select a “best” model for the data. The “best” model weighs parsimony against more highly parameterized models.

Parsimonious models are simple and contain fewer parameters. Calculations of AIC,

AIC_c, and AIC_c weights were after Burnham and Anderson (1998). AIC values can be calculated from least squares estimates with normally distributed errors from the equation

$$AIC = n \log(\hat{\sigma}^2) + 2K,$$

where $\hat{\sigma}^2 = \sum \epsilon_i^2 / n$ and ϵ_i are the estimated residuals for a particular candidate model

and K is the number of parameters. To adjust for small sample size, we calculated AIC_c (Hurvich and Tsai 1989) using the equation

$$AIC_c = AIC + 2K(K + 1)/(n-K-1),$$

where n is the number of pairwise distance measures. Lower AIC_c values indicate “better” models. Because AIC and AIC_c are on a relative scale, Burnham and Anderson (1998) recommend computing the AIC differences,

$$\Delta_i = AIC_i - \min AIC,$$

over all candidate models in the set. As a general guideline, Δ_i values differing by ≤ 2 have substantial support and should receive consideration in making inferences, whereas models with Δ_i values between 4 to 7 have less support. Models with Δ_i values > 10 have almost no support and fail to explain substantial variation in the data. The procedure for assigning relative importance of various predictors is based on estimates of expected Kullback-Leibler information (Burnham and Anderson, 1998). The information-theoretic approach allow estimates of the formal likelihood of each model, given the data (x_i) , $(\mathcal{L}(M_i | x_i))$. Normalizing these likelihoods to sum to 1, one can obtain the set of Akaike weights. The AIC_c weight of a given model is calculated as:

$$w_i = e^{-0.5\Delta_i} / \sum e^{-0.5\Delta_i}.$$

AIC_c weights are summed for all models with a particular predictor variable to provide a “strength of evidence” for the various predictors. The sum of weights ranges from 0 to 1. Predictors with sums of weights closer to 1 have more support. To assess model selection uncertainty, we calculated 95% confidence sets for the three genetic distance measures. Akaike weights (w_i) for each genetic distance measure were summed from largest to smallest until that sum was ≥ 0.95 . The resulting set of models can be viewed as a confidence set on the K-L “best” model (Burnham and Anderson, 1998). All estimates, test statistics, and AIC values were computed using SAS (SAS Institute, 1989).

RESULTS

Black-tailed prairie dog metapopulation dynamics

We studied 13 colonies on the Central Plains Experimental Range and the Pawnee National Grassland during 1997-98. Maximum pairwise colony distance was 24 km and nearest-neighbor distances varied from 1.4 to 5.7 km (Table 2). Active area of colonies varied from 2.4 ha to 52 ha. Colonies that had been recently reestablished tended to be smaller (Table 2). Seven of the study colonies were recolonized within the past 1-2 years and six colonies had been active within the last 4-10 years (Table 2). U. S. Forest Service records documented prairie-dog activity on our study colonies on the Pawnee National Grassland prior to 1981, but these colonies were extinct when Mark Ball began annual monitoring in 1981. Colonies remained vacant until colony 66 in the Owl Creek area (Fig. 1) was recolonized in 1988 (Table 3). Subsequent recolonization of other prairie-dog populations within our study area on the Pawnee National Grassland occurred during the following years (Table 3). Prairie-dog colonies were active from 1990 to 1993 on the Central Plains Experimental Range. Before the onset of prairie-dog reproduction in 1994, all populations on the Central Plains Experimental Range were eradicated either by a sylvatic plague epizootic or control efforts (M. Ashby, pers. comm.). We also

documented the near extinction of two large prairie-dog populations on the Pawnee National Grassland after sample collection had been completed. A sylvatic plague epizootic extirpated almost all prairie dogs in colony 80 sometime between August and late October 1998 and colony 69 almost completely vanished due to a plague epidemic in February 1999.

Sample collection

We collected tissue samples from 3-16 individuals per colony. We were not able to sample more prairie dogs because the live-trapping effort was so intensive; on average, 35 trap-days (no. traps x no. days) were required to obtain each sample. Trap success (individuals/trap-day x 100) was greater for colonies on the Central Plains Experimental Range (5.1%) than for colonies on the Pawnee National Grassland (1.7%), which we attribute to differences in recreational shooting pressure between these areas and timing of trapping. Only three individuals were captured from colony 81 because no more than six prairie dogs inhabited the colony.

Population genetic structure

The number of alleles per locus ranged from four to 13 for the seven microsatellite loci analyzed. Allele frequencies are given in Appendix III. We found no evidence for deviations from Hardy-Weinberg equilibrium within populations, suggesting

random mating and a lack of Wahlund's (1928) effect within each population sampled. Considering that we found no heterozygote deficiencies in any of the populations, we concluded that no null alleles were segregating at high frequency in these populations (Pemberton et al., 1995).

Mean heterozygosity within populations ranged from 0.386 to 0.705 (Table 4), but did not differ between old or young colonies (mean heterozygosity for recolonized populations = 0.577, for extant populations = 0.587; Mann-Whitney $Z = 0.214$, $P = 0.830$). We observed no excess of homozygotes or heterozygotes within populations (mean $f = 0.014$, Table 5). θ values revealed moderate levels of genetic differentiation among colonies (mean $\theta = 0.118$) (Table 5).

Tests of models of dispersal

We constructed neighbor-joining trees of pairwise genetic distances between populations (Fig. 2) using three genetic distance matrices D_A , D_C , and D_F (Tables 6 and 7). The topologies of the trees from the genetic distance measures differed slightly and few branches had greater than 50% bootstrap support. In addition, the topologies of the neighbor-joining trees did not resemble the topology of the dendrogram for drainage geographic distance (Fig. 2). Although the mean θ value indicated that genetic differentiation occurs among populations, there was little support for an isolation-by-distance relationship because nearby colonies did not cluster with each other.

We calculated Mantel correlations from the pairwise genetic distance matrices

(Tables 6 and 7) and the pairwise geographic distance matrices (Tables 8 and 9). Results for the Mantel test show that drainage distance explained more of the variance in genetic distance ($r = 0.398$) than did the other three geographic distances (linear $r = 0.198$, road $r = 0.197$, drainage-road $r = 0.238$; Table 10). Regressions of genetic distance against drainage revealed significant relationships (D_A : $F_{1,12} = 7.59$, $P = 0.017$; D_C : $F_{1,12} = 5.163$, $P = 0.042$; D_F : $F_{1,12} = 7.576$, $P = 0.018$; Table 11), whereas the regressions of genetic distance and other geographic distances were not statistically significant (Table 11). The 95% confidence intervals on the regression slopes of genetic distance against linear, road, and drainage-road distance overlapped zero (Figs. 3, 4, and 5).

Information-theory framework was used to model prairie-dog dispersal as a function of genetic distance. The AIC_c model that included drainage and age was selected as the “best” model when D_A and D_C were the response variables (Tables 12 and 13). The most parsimonious model for D_F was drainage (Table 14). We defined 95% confidence sets of 9 models based on Akaike weights (w_i). Confidence sets included 5 models for D_A , 5 models for D_C , and 8 models for D_F (Tables 12, 13, and 14). The 95% confidence sets for both D_A and D_C contained all models which included age as a predictor variable. The models for all genetic distance measures highlight the importance of drainage as a predictor variable and provide weak support for linear, road, and drainage-road as predictors of genetic distance.

We assessed the importance of five predictor variables using the AIC_c weights. Age and drainage were the best predictors of genetic distance among populations for all three genetic distance measures (D_A : age $w_i = 0.966$, drainage $w_i = 0.722$; D_C : age $w_i =$

0.987, drainage $w_i = 0.542$; D_F : drainage $w_i = 0.677$, age $w_i = 0.486$; Fig. 6). Because age was an important predictor of genetic distance, we calculated least squares regressions for D_C (as a representative of all three genetic distance measures) against mean age of a colony pair to illustrate the relationship between age and genetic distance. Regressions were calculated for all pairs of colonies. We found a significant negative relationship between genetic distance and mean age of a colony pair ($F_{1,12} = 11.6$, $P = 0.001$; Fig. 7).

DISCUSSION

Population genetic structure

In this study, we found moderate genetic differentiation among black-tailed prairie dog populations ($\theta = 0.118$). This conclusion is consistent with the results of studies conducted on a similar spatial scale as our study. Chesser (1983) found moderate genetic differentiation ($F_{ST} = 0.103$) among 21 populations of black-tailed prairie dogs in New Mexico. Moderate genetic differentiation ($F_{ST} = 0.115$) was also found among eight black-tailed prairie dog populations in South Dakota (Daley, 1992). Chesser (1983) and Daley (1992) found a lack of association between genetic and linear distances and differences in allele frequencies among populations and concluded that dispersal among black-tailed prairie dog populations was infrequent. Chesser (1983) and Daley (1992) also concluded that the presence of unique alleles in neighboring populations of black-tailed prairie dogs was a result of founder effect and genetic drift. Genetic studies of Mexican (McCullough and Chesser, 1987) and Gunnison's (Travis et al., 1997) prairie dogs described similarly moderate differentiation ($F_{ST} = 0.07$ and $F_{ST} = 0.11$, respectively) and inferred low rates of dispersal. In contrast, relatively low genetic differentiation was found between two black-tailed prairie dog populations in the mixed-grass prairie of

South Dakota ($F_{ST} = 0.028$), suggesting that dispersal rates among populations were high (Foltz and Hoogland, 1983).

We found a significant association between genetic and geographic distances, similar allele frequencies among populations, and few unique alleles within populations. There was no evidence of founder effect or genetic drift within newly recolonized populations despite their young age and small colony size; mean heterozygosity did not differ between old and young populations, and recently reestablished populations were not devoid of alleles found in extant populations. These results suggest that although moderate genetic differentiation among black-tailed prairie dog populations does occur, the rate of dispersal among populations is high.

Models of dispersal

Our study is the first attempt to incorporate landscape features, such as dispersal corridors, into a population genetic study of black-tailed prairie dogs. The importance of population genetic structure has not been examined in studies using direct measures of dispersal in black-tailed prairie dogs (e.g., Cincotta, 1987; Garrett and Franklin, 1988; Garrett et al., 1982; Halpin et al., 1987; Knowles, 1985, 1986). Conversely, previous genetic studies of black-tailed prairie dogs have estimated dispersal (gene flow) from measures of genetic differentiation, but they have not investigated the effects of landscape features on dispersal (e.g., Chesser, 1983; Daley 1992; Dobson et al., 1997; Foltz and Hoogland, 1983). Although genetic distance is an indirect measure of dispersal, genetic

distances between populations can provide insights into dispersal (Koenig et al., 1996). We linked three genetic distance measures to four geographic features and the age of prairie-dog colonies using *a priori* models.

Our results suggest that drainage is an important predictor of dispersal. Drainages may function as dispersal corridors because vegetated swales provide concealment for dispersing prairie dogs (Garrett and Franklin, 1988; Knowles, 1985). Black-tailed prairie dog colonies are typically located in swales and broad seasonal drainages, so dispersing prairie dogs may have a greater likelihood of encountering a colony along drainages (Garrett and Franklin, 1988). The importance of drainages as dispersal corridors could also be a result of habitat selection, differential survival, or other factors that affect dispersal.

Linear distance is a poor predictor of dispersal. Linear distance measures assume that the habitat matrix between populations is homogeneous and that the distance between colonies is the only “cost” associated with dispersal (Wiens, 1996). In reality, the habitat between colonies is heterogeneous and gene flow is related to both the isolation and the connectivity of populations in the landscape. Detectability of colonies, the proximity of a colony to favorable habitat, and possible habitat barriers might influence dispersal in black-tailed prairie dogs.

We found little support for roads as a predictor of genetic distance. This result contradicts the findings of other studies which have indicated that roads are important dispersal corridors for black-tailed prairie dogs (Knowles, 1985, 1986; Koford, 1958). Reading and Matchett (1997) predicted that prairie-dog density and colony area would be

related to distance to nearest road because of the importance of roads as dispersal corridors reported in previous studies (e.g., Knowles, 1985, 1986; Koford, 1958). The results of their study, however, revealed that a colony's proximity to roads was not related to either population density or colony area. Prairie dogs traveling along roadways may have great mortality risks because recreational shooters access colonies by and remain near existing roads (Reading and Matchett, 1997; U.S. Bureau of Land Management, in Reading and Matchett, 1997). Furthermore, if researchers frequent roads, then prairie dogs may be observed more on roads than open prairie and roads would be presumed to be important dispersal corridors.

Drainage-road is not an important predictor of dispersal, although we hypothesized *a priori* that it would be the best predictor because it minimizes the distance a prairie dog travels along two potential dispersal corridors. We found that the correlation between pairwise drainage-road distance measures and pairwise road distance measures ($r = 0.933$) was greater than the correlation between pairwise drainage-road distance measures and pairwise drainage distance measures ($r = 0.590$). Although drainage is an important predictor of genetic distance among populations, road has relatively little importance and may account for the lack of importance of drainage-road.

Colony age is an important predictor of genetic distance among black-tailed prairie dog populations. Recently recolonized populations may be more genetically distant from each other because they are not in migration-drift equilibrium (McCauley, 1991). Genetic drift proceeds faster in small populations and, unless opposed by gene flow, reduces genetic variation within a population (Hartl and Clark, 1997). Likewise,

dispersal homogenizes populations if not opposed by genetic drift (Hartl and Clark, 1997). Allele frequencies within a population will eventually reach an equilibrium between gene flow and genetic drift. However, populations that have only recently been reestablished may have not yet had time to differentiate by drift and will not be in migration-drift equilibrium (Hartl, 1988).

Metapopulation dynamics

There is little evidence that metapopulations occur in natural ecosystems (Harrison, 1991; Harrison and Taylor, 1997; Simberloff, 1995; Wiens, 1996; but see McCullough, 1996) and information on the dynamics of naturally-existing metapopulations is limited (Harrison, 1991; Wiens, 1996). Few empirical studies have examined dispersal within metapopulations (e.g., Debinski, 1994; Meyer et al., 1998; Neve et al., 1996; Peacock and Smith, 1997; Sinsch, 1997; Sutcliffe et al., 1996). Important factors that may influence dispersal, such as landscape connectivity, are rarely incorporated into empirical studies (Hanski and Thomas, 1994; Merriam, 1988; Wiens, 1996; Wiens et al. 1993).

We conclude that black-tailed prairie dogs in our study occur as a metapopulation. The data from this study, coupled with the documented history of extinctions and recolonization, indicate that prairie dogs in shortgrass steppe exist as subpopulations that are subject to local population dynamics (e.g., extinction and recolonization) and are connected via dispersal. Geographic distance and colony age are related to the time since

recolonization. The genetic differentiation among populations fits an isolation-by-distance relationship, suggesting that populations are close to migration-drift equilibrium. However, data also provide evidence that recently recolonized populations are not in migration-drift equilibrium.

Local populations are prone to extinction from recreational shooting, agricultural control, habitat loss, and particularly sylvatic plague. Large, extant prairie-dog populations might be predicted to serve as extinction-resistant “mainland” populations when, in fact, larger colonies may be more prone to extinction from sylvatic plague epidemics. High population densities among prairie dogs provide greater opportunities for the exchange of plague-infected fleas and increase the rate with which plague moves through a population (Barnes, 1993). Thus, the black-tailed prairie dog metapopulation persists through dispersal and the recolonization of extinct populations.

Genetic consequences of metapopulation dynamics

Dispersal plays a critical role in determining a metapopulation’s persistence (Hamilton and May, 1977; Hastings, 1993; McCullough, 1996; Roff, 1974, 1975) and the genetic differentiation among local populations (Olivieri et al., 1995). Very little dispersal (gene flow) appears to be necessary to prevent considerable genetic differentiation among local populations (Hanski, 1996). The processes of extinction and recolonization can also limit the rate and extent to which genetic differentiation occurs in populations (McCauley, 1991; Whitlock and McCauley, 1990).

The genetic consequences of extinction and recolonization have been described by theoretical models including Slatkin's (1977) 'island'-type models of population structure: the 'propagule pool' model and the 'migrant pool' model. The 'propagule pool' model assumes that founding individuals of a recolonized population are from the same source population. In contrast, the 'migrant pool' model suggests that a given founding group is comprised of individuals drawn at random from all possible source populations. These patterns of recolonization can have very different genetic consequences for population structure. Extinction and recolonization increase local genetic differentiation in a 'propagule'-founded population (Wade and McCauley, 1988). However, in a 'migrant'-founded population, extinction and recolonization can either increase or decrease the genetic differentiation depending on the size of the founding population and the amount of dispersal among established populations (Wade and McCauley, 1988).

The dispersal patterns of black-tailed prairie dogs are better described by the 'migrant pool' model of recolonization, indicating that recently reestablished populations are comprised of individuals from many source populations. We would expect to observe a strong isolation-by-distance relationship and similar tree topologies between genetic distance measures and drainage geographic distance measures if the dispersal patterns of prairie dogs were described by the 'propagule pool' pattern of recolonization. We do not find a strong isolation-by-distance relationship within the metapopulation, although there is a significant association between drainage distance and genetic distance. Additionally, neighbor-joining trees revealed that recently reestablished populations are not more

closely related to any one source population than to all other source populations. We would also expect an inflated measure of genetic differentiation, θ , if neighboring populations were more closely related to each other than to other local populations (Wade and McCauley, 1988). Although we detected a moderate level of genetic differentiation among populations, this value was not highly inflated. These data suggest that prairie dogs most likely disperse to neighboring populations along drainage corridors but continuous dispersal among all local populations occurs throughout the metapopulation.

Management recommendations

A metapopulation can persist as long as the rate of recolonization exceeds the rate of extinction, even though no local population may survive continuously over time (McCullough, 1996). This black-tailed prairie dog metapopulation persists because of the continuous dispersal between populations. A disruption of dispersal opportunities and an increase in colony isolation will have genetic repercussions. For instance, a loss of genetic diversity can, in some cases, lead to inbreeding depression and a decreased ability for a population to respond to changing environmental conditions (McCauley, 1991). If the group of prairie dogs that establishes a new population is small and homogeneous, founder effect or a population bottleneck may occur (Hartl and Clark, 1997).

The ability of prairie dogs to disperse among colonies is critical because recolonization of local extinctions is essential for the regional persistence of metapopulations (Fahrig and Merriam, 1994). Short-term dispersal is necessary to ensure

recolonization of unoccupied colonies, and long-term dispersal among populations may ensure continual survival of the metapopulation. Our data suggest that potential dispersal corridors, such as drainages, need to be maintained to ensure recolonization of unoccupied colonies and continuous dispersal among populations.

For many species, it is assumed that the smallest populations within a metapopulation are likely to disappear first when habitat is decreased and isolation is increased; the species will survive longer in larger populations (Hanski, 1996; Hanski et al., 1996). This assumption, however, does not consider the effects that disease dynamics have on metapopulation structure. The fact that sylvatic plague epidemics are more likely to eradicate large prairie-dog colonies contradicts the above assumption. The dynamics of sylvatic plague in black-tailed prairie dog populations need to be better understood before sound management plans can be recommended. Sylvatic plague does not spread readily from one black-tailed prairie dog colony to another (Koford, 1958; Rayor, 1985), but it is difficult to predict which populations will persist because we do not understand how plague is spread within and between colonies (Cully, 1993).

The management of black-tailed prairie dogs should be based on regional species' persistence and not on a colony-by-colony basis. The management of individual colonies will not only affect the colony of concern, but neighboring colonies as well. Because we cannot predict the persistence of any given prairie-dog population, we need to ensure that populations are connected by dispersal so that extinctions may be recolonized. As habitats become more fragmented, prairie-dog colonies will become more isolated; isolation may lead to more differentiated populations and a greater potential for

inbreeding. We are in a better position to advocate landscape designs that include size, quantity, and spatial distribution of black-tailed prairie dog populations if we know in advance what black-tailed prairie dogs need to persist as a metapopulation.

LITERATURE CITED

- Agnew, W., D. W. Uresk, and R. M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. *Journal of Range Management*, 39:135-139.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pp. 267-281, *in* International Symposium on Information Theory, Second Edition (B. N. Petran and F. Csaki, eds.). Akademiai Kiado, Publishers, Budapest, Hungary.
- Akaike, H. 1981. Likelihood of a model and information criteria. *Journal of Econometrics*, 16:3-14.
- Anderson, E., S. Forrest, T. W. Clark, and L. Richardson. 1986. Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (*Audubon and Bachman*), 1851. *Great Basin Naturalist memoirs*, 8:11-62.
- Baer, C. F. 1998. Population structure in a south-eastern US freshwater fish, *Heterandria formosa*. II. Gene flow and biogeography within the St. Johns River drainage. *Heredity*, 81:404-411.
- Barnes, A. M. 1982. Surveillance and control of bubonic plague in the United States. *Symposia of the Zoological Society of London*, 50:237-270.

- Barnes, A. M. 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. Pp. 28-37 *in* Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret (J. L. Oldemeyer, D. E. Biggins, and B. J. Miller, eds.). U.S. Department of the Interior Biological Report 13, 96 pp.
- Beier, P. 1996. Metapopulation models, tenacious tracking and cougar conservation. Pp. 293-324 *in* Metapopulations and Wildlife Conservation (D. R. McCullough, ed.). Island Press, Washington, District of Columbia, 429 pp.
- Biggins, D. E., B. J. Miller, L. R. Hanebury, B. Oakleaf, A. H. Farmer, R. Crete, and A. Dood. 1993. A technique for evaluating black-footed ferret habitat. Pp. 73-78 *in* Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret (J. L. Oldemeyer, D. E. Biggins, and B. J. Miller, eds.). U.S. Department of the Interior Biological Report 13, 96 pp.
- Black, W. C. IV and N. M. DuTeau. 1997. RAPD-PCR and SSCP Analysis for insect population genetic studies. Pp. 361-373 *in* The Molecular Biology of Insect Disease Vectors: A Methods Manual (J. Crampton, C. B. Beard, and C. Louis., eds.). Chapman and Hall Publishers, New York, 578 pp.
- Bonham, C. D. and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. *Journal of Range Management*, 29:221-225.
- Bowcock, A. M., A. Ruiz-Linares, J. Romföhrde, E. Minch, J. R. Kidd, and L. L. Cavalli-Sforza. 1994. High resolution of human evolutionary trees with polymorphic microsatellites. *Nature*, 368:455-457.

- Burnham, K. P. and D. R. Anderson. 1998. Model Selection and Inference. A Practical Information-Theoretic Approach. Springer-Verlag, New York, 349 pp.
- Cavalli-Sforza, L. L., A. W. F. Edwards. 1967. Phylogenetic analysis: models and estimation procedures. *American Journal of Human Genetics*, 19:233-257.
- Ceballos, G., J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *Journal of Arid Environments*, 41:161-172.
- Chesser, R. K. 1983. Genetic variability within and among populations of the black-tailed prairie dog. *Evolution*, 37:320-331.
- Cincotta, R. P., D. W. Uresk, and R. M. Hansen. 1987. Demography of black-tailed prairie dog populations reoccupying sites treated with rodenticide. *Great Basin Naturalist*, 47: 339-343.
- Clark, T. W., R. S. Hoffman, and C. F. Nadler. 1971. *Cynomys leucurus*. *Mammalian Species*, 7:1-4.
- Cully, J. F. 1993. Plague, prairie dogs, and black-footed ferrets. Pp. 38-49 in *Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret* (J. L. Oldemeyer, D. E. Biggins, and B. J. Miller, eds.). U.S. Department of the Interior Biological Report 13, 96 pp.
- Daley, J. G. 1992. Population reductions and genetic variability in black-tailed prairie dogs. *Journal of Wildlife Management*, 56:212-220.
- Debinski, D. M. 1994. Genetic diversity assessment in a metapopulation of the butterfly *Euphydryas gillettii*. *Biological Conservation*, 70:25-31.

- Dobson, F. S., R. K. Chesser, J. L. Hoogland, D. W. Sugg and D. W. Foltz. 1997. Do black-tailed prairie dogs minimize inbreeding? *Evolution*, 51:970-978.
- Driscoll, D. A. 1998. Genetic structure, metapopulation processes and evolution influence the conservation strategies for two endangered frog species. *Biological Conservation*, 83:43-54.
- Ecke, D. H. and C. W. Johnson. 1952. Plague in Colorado. Pp. 1-37 in *Plague in Colorado and Texas*. U. S. Public Health Service, Public Health Monograph 6.
- Fahrig, L. and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology*, 8:50-59.
- Felsenstein, J. 1993. PHYLIP: a phylogenetic inference package, version 3.51c. University of Washington, Seattle, 150 pp. (on disk).
- Fitzgerald, J. P. 1993. The ecology of plague in Gunnison's prairie dogs and suggestions for the recovery of black-footed ferrets. Pp. 50-59 in *Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret* (J. L. Oldemeyer, D. E. Biggins, and B. J. Miller, eds.). U.S. Department of the Interior Biological Report 13, 96 pp.
- Foltz, D. W. and J. L. Hoogland. 1983. Genetic evidence of outbreeding in the black-tailed prairie dog (*Cynomys ludovicianus*). *Evolution*, 37:273-281.
- Gaona, P., P. Ferreras, and M. Delibes. 1998. Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). *Ecological Monographs*, 68:349-370.
- Garrett, M. G. and W. L. Franklin. 1988. Behavioral ecology of dispersal in the black-

- tailed prairie dog. *Journal of Mammalogy*, 69:236-250.
- Garrett, M. G., J. L. Hoogland, and W. L. Franklin. 1982. Demographic differences between an old and a new colony of black-tailed prairie dogs (*Cynomys ludovicianus*). *The American Midland Naturalist*, 108:51-59.
- Gober, P. 1999. Endangered and threatened wildlife and plants; 90-day finding for a petition to list the black-tailed prairie dog as threatened. *Federal Registrar* 64:14424-14428. (25 March 1999).
- Gyllenberg, M. and I. Hanski. 1992. Single-species metapopulation dynamics: a structured model. *Theoretical Population Biology*, 42:35-61.
- Haig, S. M., J. M. Rhymer, D. G. Heckel. 1994. Population differentiation in randomly amplified polymorphic DNA of red-cockaded woodpeckers *Picoides borealis*. *Molecular Ecology*, 3:581-595.
- Hall, E. R. 1981. *The Mammals of North America*. Second ed. John Wiley and Sons, New York.
- Halpin, Z. T. 1987. Natal dispersal and the formation of new social groups in a newly established town of the black-tailed prairie dogs (*Cynomys ludovicianus*). Pp. 104-118 in *Mammalian Dispersal Patterns: the effects of social structure on population genetics* (B. D. Chepko-Sade and Z. T. Halpin, eds.). University of Chicago Press, Chicago, Illinois, 342 pp.
- Hamilton, W. D. and R. M. May. 1977. Dispersal in stable habitats. *Nature*, 269:578-581.
- Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and

- observations. *Biological Journal of the Linnean Society*, 42:17-38.
- , 1996. Metapopulation ecology. Pp. 13-43 *in* Population dynamics in ecological space and time (O. E. Rhodes, Jr., R. K. Chesser, and M. H. Smith, eds.). University of Chicago, Chicago, Illinois, 388 pp.
- Hanski, I. and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pp. 5-26 *in* Metapopulation Biology: Ecology, Genetics, and Evolution (I. A. Hanski and M. E. Gilpin, eds.). Academic Press, San Diego, California, 512 pp.
- Hanski, I. and C. D. Thomas. 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biological Conservation*, 68:167-180.
- Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conservation Biology*, 10:578-590.
- Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society*, 42:73-88.
- , 1994. Metapopulations and conservation. Pp. 111-128 *in* Large-Scale Ecology and Conservation Biology (P. J. Edwards, R. M. May, and N. R. Webb, eds.). Blackwell, Oxford, United Kingdom, 375 pp.
- Harrison, S. and Hastings, A. M. 1996. Genetic and evolutionary consequences of metapopulation structure. *Trends in Ecology and Evolution*, 11:180-183.
- Harrison, S. and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics.

- Pp. 27-42 in *Metapopulation biology: ecology, genetics and evolution* (I. A. Hanski and M. E. Gilpin, eds.). Academic Press, San Diego, California, 512 pp.
- Harrison, S., D. D. Murphy, and P. R. Ehrlich. 1988. Distribution of the Bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *American Naturalist*, 132:360-382.
- Hartl, D. L. 1988. *A Primer of Population Genetics*, Second Edition. Sinauer Associates, Inc. Sunderland, Massachusetts, 305 pp.
- Hartl, D. L. and A. G. Clark. 1997. *Principles of Population Genetics*, Third Edition. Sinauer Associates, Inc. Sunderland, Massachusetts.
- Hastings, A. 1991. Structured models of metapopulation dynamics. *Biological Journal of the Linnean Society*, 42:57-71.
- Hastings, A. 1993. Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology*, 74:1362-1372.
- Hastings, A. and S. Harrison. 1994. Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics*, 25:167-188.
- Hellberg, M. E. 1994. Relationships between inferred levels of gene flow and geographic distance in a philopatric coral *Balanophyllia elegans*. *Evolution*, 48:1829-1854.
- Hollister, N. 1916. A systematic account of the prairie dogs. *North American Fauna*, 40:1-37.
- Hoogland, J. L. 1981. Nepotism and cooperative breeding in the black-tailed prairie dogs (Sciuridae: *Cynomys* spp.) Pp. 283-310 in *Natural Selection and Social*

- Behavior (R. D. Alexander and D. W. Tinkle, eds.). Chiron Press, New York, 532 pp.
- , 1982. Prairie dogs avoid extreme inbreeding. *Science*, 215:1639-1641.
- , 1995. The black-tailed prairie dog: social life of a burrowing mammal. The University of Chicago Press, Chicago, Illinois, 557 pp.
- Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of "sink" populations. *Biological Conservation*, 57:239-255.
- Hurvich, C. M. and C. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika*, 76:297-307.
- King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairiedog town in the Black Hills of South Dakota. *Contributions, Laboratory of Vertebrate Biology, University of Michigan*, 67:1-126.
- Knowles, C. J. 1985. Observations on prairie dog dispersal in Montana. *Prairie Naturalist*, 17:33-40.
- Knowles, C. J. 1986. Some relationships of black-tailed prairie dogs to livestock grazing. *Great Basin Naturalist*, 46:198-203.
- Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution*, 11:514-517.
- Koford, C. B. 1958. Prairie dogs, white faces, and blue grama. *Wildlife Monographs* 3, 78 pp.
- Lamberson, R. H., B. R. Noon, C. Voss, and K. S. McKelvey. 1994. Reserve design for

- territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. *Conservation Biology*, 8:185-195.
- Lauenroth, W. K., D. G. Milchunas, J. L. Dodd, R. H. Hart, R. K. Heitschmidt, and L. R. Rittenhouse. 1994. Effects of grazing on ecosystems of the Great Plains. Pp. 69-100 *in* Ecological implications of livestock herbivory in the West (M. Vavra, W. A. Laycock, and R. D. Pierper, eds.). Society for Range Management, Denver, Colorado, 297 pp.
- Lebreton, J-D, K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monograph*, 62:67-118.
- Levene, H. 1949. On a matching problem arising in genetics. *Annals of Mathematics and Statistics*, 20:91-94.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomology Society of America*, 15:237-240.
- , 1970. Extinction. *Lecture in Mathematics in the Life Sciences*, 2:75-107.
- Lidicker, W. Z. Jr. and W. D. Koenig. 1996. Responses of terrestrial vertebrates to habitat edges and corridors. Pp. 85-109 *in* Metapopulations and wildlife conservation (D. R. McCullough, ed.). Island Press, Washington, District of Columbia, 429 pp.
- Lindenmayer, D. B., M. A. McCarthy, and M. L. Pope. 1999. Arboreal marsupial incidence in eucalypt patches in south-eastern Australia: a test of Hanski's

- incidence function metapopulation model for patch occupancy. *Oikos*, 84:99-109.
- MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, New Jersey, 203 pp.
- MacClintock, D. 1970. *Squirrels of North America*. Van Nostrand Reinhold, New York, 184 pp.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research*, 27:209-220.
- May, B., T. A. Gavin, P. W. Sherman, and T. M. Korves. 1997. Characterization of microsatellite loci in the Northern Idaho ground squirrel *Spermophilus brunneus brunneus*. *Molecular Ecology*, 1997: 399-400.
- McCauley, D. E. 1991. Genetic consequences of local population extinction and recolonization. *Trends in Ecology and Evolution*, 6:5-8.
- McCullough, D. A. and R. K. Chesser. 1987. Genetic variation among populations of the Mexican prairie dog. *Journal of Mammalogy*, 68:555-560.
- McCullough, D. R. 1996. *Metapopulations and wildlife conservation*. Island Press, Washington, District of Columbia, 529 pp.
- Merriam, G. 1988. Landscape dynamics in farmland. *Trends in Ecology and Evolution*, 3:16-20.
- Meyer, J. S., L. L. Irwin, and M. S. Boyce. 1998. Influence of habitat abundance and fragmentation on northern spotted owls in western Oregon. *Wildlife Monographs*, 0:5-51.
- Miller, B., G. Ceballos, R. Reading. 1994. The prairie dog and biotic diversity.

- Conservation Biology, 8:677-681.
- Neve, G., B. Barascud, R. Hughes, J. Aubert, H. Descimon, P. Lebrun, and M. Baguette. 1996. Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclissiana eunomia* (Lepidoptera: Nymphalidae). Journal of Applied Ecology, 33:14-22.
- Olivieri, I., Y. Michalakis, and P.-H. Gouyon. 1995. Metapopulation genetics and the evolution of dispersal. American Naturalist, 146:202-228.
- Peacock, M. M. and A. T. Smith. 1997. The effect of habitat fragmentation on dispersal patterns, mating behavior, and genetic variation in a pika (*Ochotona princeps*) metapopulation. Oecologia, 112:524-533.
- Pemberton, J. M., J. Slate, D. R. Bancroft, J. A. Barrett. 1995. Nonamplifying alleles at microsatellite loci: a caution for parentage and population studies. Molecular Ecology, 4: 249-252.
- Pfenninger, M., A. Bahl, B. Streit. 1996. Isolation by distance in a population of a small land snail *Trochoidea geyeri*: evidence from direct and indirect methods. Proceedings of the Royal Society of London, Biological Series, 263:1211-1217.
- Pizzimenti, J. J. 1975. Evolution of the prairie dog genus *Cynomys*. Occasional Papers of the Museum of Natural History, The University of Kansas, no. 39, Lawrence, Kansas.
- Powell, K. L., R. J. Robel, K. E. Kemp, and M. D. Nellis. 1994. Aboveground counts of black-tailed prairie dogs: temporal nature and relationship to burrow entrance density. Journal of Wildlife Management, 58:361-366.

- Price, M. V. and M. Gilpin. 1996. Modelers, mammalogists, and metapopulations: designing Stephen's kangaroo rat reserves. Pp. 217-240 in *Metapopulations and Wildlife Conservations* (D. R. McCullough, ed.). Island Press, Washington, District of Columbia, 529 pp.
- Raybold, A. F, R. J. Mogg, R. T. Clarke. 1996. The genetic structure of *Beta vulgaris* ssp. *maritima* (sea beet) populations: RFLPs and isozymes show different patterns of gene flow. *Heredity*, 77:245-250.
- Raymond, M and F. Rousset. 1994. GENEPOP. Vers. 1.2: a population genetics software for exact tests and ecumenicism (on disk).
- Rayor, L. S. 1985. Dynamics of a plague outbreak in Gunnison's prairie dog. *Journal of Mammalogy*, 66:194-196.
- Reading, R. P. and R. Matchett. 1997. Attributes of black-tailed prairie dog colonies in northcentral Montana. *Journal of Wildlife Management*, 61:664-673.
- Reading, R. P., J. J. Grensten, S. R. Beissinger, T. W. Clark. 1993. Pp. 9-10 in *Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret* (J. L. Oldemeyer, D. E. Biggins, B. J. Miller, and R. Crete, eds.). U.S. Department of the Interior Biological Report 13, 96 pp.
- Roff, D. A. 1974. The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. *Oecologia*, 15:259-275.
- , 1975. Population stability and the evolution of dispersal in a heterogeneous environment. *Oecologia*, 19:217-237.

- Rousset, F. 1997. Genetic differentiation and estimation of gene flow from *F*-statistics under isolation by distance. *Genetics*, 145:1219-1228.
- , 1997. Statistical evidence: a likelihood paradigm. Chapman and Hall, London, United Kingdom.
- SAS Institute. 1989. SAS/STAT user's guide, Version 6. Fourth edition. Volume 2. SAS Institute, Cary, North Carolina.
- Saitou, N. and M. Nei. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution*, 4: 406-425.
- Sambrook, J., Fritsch, E. F., Maniatis, T. 1989. *Molecular Cloning: a Laboratory Manual*, Second ed. Cold Spring Harbor Laboratory Press, New York.
- Samson, F. B. and F. L. Knopf. 1994. *Prairie conservation in North America*. Bioscience, 44:418-421.
- Simberloff, D. 1995. Habitat fragmentation and population extinction of birds. *Ibis*, 137:105-111.
- Sinsch, U. 1997. Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. *Oecologia*, 112:42-47.
- Slatkin, M. 1977. Gene flow and genetic drift in a species subject to frequent local extinctions. *Theoretical Population Biology*, 12:253-262.
- , 1993. Isolation by distance in equilibrium and non-equilibrium populations. *Evolution*, 47:264-279.
- Smith, R. E. 1958. Natural history of the prairie dog in Kansas. *Miscellaneous Publications, Museum of Natural History, University of Kansas*, 49:1-39.

- Stapp, P. 1998. A reevaluation of the role of prairie dogs in Great Plains grasslands. *Conservation Biology*, 12:1253-1259.
- Stevens, S., J. Coffin, and C. Strobeck. 1997. Microsatellite loci in Columbian ground squirrels *Spermophilus columbianus*. *Molecular Ecology*, 6: 493-395.
- Sutcliffe, O. L., C. D. Thomas, and D. Moss. 1996. Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology*, 65:85-95.
- Swofford, D. L. and R. B. Selander. 1989. BIOSYS-1. Release 1.7. University of Illinois Press, Urbana, Illinois. (on disk).
- Takezaki, N. and M. Nei. 1996. Genetic distances and reconstruction of phylogenetic trees from microsatellite DNA. *Genetics*, 144:389-399.
- Taylor, P. D., L. Hahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos*, 68:571-573.
- Travis, S. E., C. N. Slobodchikoff, and P. Keim. 1997. DNA fingerprinting reveals low genetic diversity in Gunnison's prairie dog (*Cynomys gunnisoni*). *Journal of Mammalogy*, 78:725-732.
- Van Horne, B., R. L. Schooley, S. T. Knick, G. S. Olson, K. P. Burnham. 1997. Use of burrow entrances to indicate densities of Townsend's ground squirrels. *Journal of Mammalogy*, 61:92-101.
- Wade, M. J. and D. E. McCauley. 1988. Extinction and recolonization: their effects on the genetic differentiation of local populations. *Evolution*, 42:995-1005.
- Wahlund, S. 1928. Zusammensetzung von populationen und korrelationsercheinungen vom standpunkt der vererbungslehre aus betrachtet. *Hereditas*, 11:65-106.

- Weir, B. S. and C. C. Cockerham. 1984. Estimating F -statistics for the analysis of population structure. *Evolution*, 38:1358-1370.
- Whicker, A. D. and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. *BioScience*, 38:778-785.
- Whitlock, M. C. and D. E. McCauley. 1990. Some population genetic consequences of colony formation and extinction: genetic correlations within founding groups. *Evolution*, 44:1717-1724.
- Wiens, J. A. 1996. Wildlife in patchy environments: metapopulations, mosaics, and management. Pp. 53-84 *in* *Metapopulations and Wildlife Conservation* (D. R. McCullough, ed.). Island Press, Washington, District of Columbia, 529 pp.
- Wiens, J. A., N. C. Stenseth, B. Van Horne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. *Oikos*, 66:369-380.
- Wilcox, B. A. and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist*, 125:879-887.
- Wootton, J. T. and D. A. Bell. 1992. A metapopulation model of the peregrine falcon in California: viability and management strategies. *Ecological Applications*, 2:307-321.
- Wright, S. 1965. The interpretation of population structure by F -statistics with special regard to systems of mating. *Evolution*, 19: 395-420.

TABLES AND FIGURES

Table 1. Repeat motif, fragment size, number of alleles, electrophoresis time (at 45 Watts), and primer sequences for seven microsatellite loci in *Cynomys ludovicianus*, the black-tailed prairie dog. IGS primers were developed by May et al. (1997) and CGS primers were developed by Stevens et al. (1997) .

Locus	Motif	Size range (bp)	Number of alleles	Gel run time (hr)	Primer sequence (5'-3')
IGS-1	(CA) ₂₀	103-112	6	3.5	ATAACAGCACCTGCTCCAC AATCCATCCTCTACCTGTAATGC
IGS-6	(CA) ₂₈	123-137	12	4	GGGCATTAATTCCAGGACTT GGGCTGGAATTAAAGGTATCA
CGS-14	(TG) ₃₀	237-281	7	7	CAGGTGGGTCCATAGTGTTAC TTGTGCCTCAGCATCTCTTC
CGS-17	(TG) ₁₆	143-169	9	4	CAATTCGTGGTGGTTATATC CTGTCAACCTATATGAACACA
CGS-22	(TG) ₁₈	174-192	6	4.5	TCCCAGAGAACAACATCAACAG TCCGCACAGGTCTTGGACTT
CGS-25	(TG) ₁₇	116-152	7	4	CCAGCATGGGGGAGAGAGAG CTTGTCATTTATCCATTCATAG
CGS-26	(TG) ₁₇	112-117	4	4	CCCAGGGACCACATAGGAGGTA AGGACTGGGGTTGTAGGTGAGT

Table 2. Area, age (years since recolonization) and nearest-neighbor distance for 13 *Cynomys ludovicianus* populations on the Central Plains Experimental Range (colonies 5-35) and Pawnee National Grassland (colonies 66-81) in Weld County, Colorado, 1997-98.

Colony	Area (ha)	Age (yr)	Distance to nearest colony (km)
5	6.12	2	5.7
22	3.75	1	1.5
27	2.75	2	1.5
29	3.09	1	1.8
30	2.20	2	1.8
35	2.37	2	2.2
66	51.96	10	1.4
69	31.90	8	1.4
76	7.56	4	4.2
78	7.93	4	4.2
79	3.97	4	4.3
80	17.95	4	2.0
81	1.02	1	2.9

Table 4. Genetic variability estimates^a for thirteen populations of *Cynomys ludovicianus* on the Central Plains Experimental Range and the Pawnee National Grassland, 1997-98.

Colony	n _t	n _s	n _a	Mean heterozygosity	
				Observed	Expected under H-W
5	15	14.9 (0.1)	3.7 (0.4)	0.587 (0.062)	0.562 (0.052)
22	11	10.6 (0.4)	4.1 (0.6)	0.562 (0.068)	0.663 (0.052)
27	14	13.9 (0.1)	3.0 (0.2)	0.496 (0.096)	0.507 (0.065)
29	16	15.3 (0.4)	5.1 (0.6)	0.666 (0.049)	0.698 (0.048)
30	10	10.0 (0.0)	4.3 (0.5)	0.686 (0.106)	0.614 (0.071)
35	15	14.9 (0.1)	3.6 (0.7)	0.519 (0.069)	0.495 (0.062)
66	15	14.7 (0.2)	4.1 (0.3)	0.705 (0.061)	0.654 (0.036)
69	11	10.7 (0.3)	4.1 (0.6)	0.646 (0.095)	0.659 (0.060)
76	12	11.9 (0.1)	3.0 (0.8)	0.386 (0.096)	0.400 (0.091)
78	10	9.7 (0.3)	4.4 (0.6)	0.507 (0.090)	0.627 (0.061)
79	15	14.9 (0.1)	3.9 (0.7)	0.627 (0.094)	0.608 (0.076)
80	8	7.9 (0.1)	4.1 (0.7)	0.651 (0.084)	0.678 (0.084)
81	3	3.0 (0.0)	3.1 (0.3)	0.524 (0.143)	0.657 (0.075)

^an_t = sample size per population n_s = mean sample size per locus, n_a = mean number of alleles per locus; standard errors are indicated in parentheses.

Table 5. Weir and Cockerham's (1984) F -statistics for each microsatellite locus from 13 *Cynomys ludovicianus* populations combined; significance tested by the jackknifed 95% confidence interval.

Locus	F^a	f^b	θ^c
IGS-1	0.072	-0.025	0.095
IGS-6	0.170	0.049	0.127
CGS-14	0.245	0.114	0.148
CGS-17	0.153	-0.034	0.124
CGS-22	0.111	-0.015	0.124
CGS-25	-0.048	-0.119	0.064
CGS-26	0.138	0.015	0.124
Mean	0.130	0.014	0.118
95% Confidence Interval	0.116 - 0.144	0.002 - 0.025	0.114 - 0.121

^a F denotes F_{IT} , ^b f denotes F_{IS} , ^c θ denotes F_{ST} .

Table 6. Pairwise estimates of genetic distance between 13 black-tailed prairie dog populations based on $F_{ST}/1-F_{ST}$ (above diagonal) and Cavalli-Sforza and Edwards' chord distance (below diagonal).

Population	5	22	27	29	30	35	66	69	76	78	79	80	81
5	_____	0.071	0.189	0.143	0.154	0.160	0.142	0.067	0.136	0.125	0.057	0.097	0.069
22	0.351	_____	0.097	0.045	0.049	0.102	0.060	-0.013	0.169	0.031	0.050	0.037	0.025
27	0.453	0.438	_____	0.130	0.170	0.255	0.207	0.085	0.288	0.185	0.141	0.139	0.215
29	0.450	0.378	0.473	_____	0.107	0.157	0.088	0.050	0.240	0.087	0.063	0.036	0.096
30	0.404	0.390	0.508	0.404	_____	0.203	0.135	0.074	0.308	0.114	0.142	0.153	0.160
35	0.389	0.376	0.481	0.426	0.446	_____	0.157	0.114	0.176	0.045	0.128	0.149	0.099
66	0.431	0.365	0.518	0.364	0.369	0.414	_____	0.053	0.160	0.087	0.086	0.067	0.087
69	0.348	0.311	0.408	0.387	0.379	0.362	0.346	_____	0.118	0.051	0.009	-0.001	0.035
76	0.396	0.482	0.526	0.531	0.588	0.441	0.435	0.399	_____	0.145	0.123	0.140	0.109
78	0.413	0.391	0.466	0.384	0.444	0.323	0.388	0.382	0.425	_____	0.088	0.089	-0.050
79	0.332	0.359	0.443	0.349	0.399	0.387	0.383	0.279	0.408	0.390	_____	0.019	0.077
80	0.407	0.363	0.437	0.351	0.465	0.406	0.370	0.272	0.418	0.404	0.336	_____	0.057
81	0.417	0.455	0.514	0.483	0.540	0.481	0.466	0.418	0.388	0.360	0.441	0.436	_____

Table 7. Pairwise estimates of genetic estimates between 13 *Cynomys ludovicianus* populations based on the proportion of shared alleles.

Population	5	22	27	29	30	35	66	69	76	78	79	80	81
5	—												
22	0.361	—											
27	0.584	0.466	—										
29	0.582	0.394	0.566	—									
30	0.522	0.404	0.605	0.541	—								
35	0.766	0.756	0.584	0.780	0.776	—							
66	0.490	0.399	0.682	0.455	0.489	0.712	—						
69	0.342	0.237	0.427	0.399	0.417	0.649	0.361	—					
76	0.426	0.640	0.755	0.809	0.873	0.873	0.542	0.482	—				
78	0.494	0.403	0.587	0.548	0.550	0.649	0.496	0.403	0.553	—			
79	0.336	0.344	0.515	0.390	0.489	0.640	0.414	0.251	0.444	0.448	—		
80	0.452	0.387	0.580	0.418	0.617	0.741	0.459	0.264	0.491	0.525	0.279	—	
81	0.461	0.498	0.691	0.652	0.727	0.815	0.597	0.476	0.447	0.331	0.512	0.514	—

Table 8. Pairwise estimates of shortest distance along drainages between black-tailed prairie dog colonies (\log_{10} km, above diagonal) and shortest linear distance between populations (\log_{10} km, below diagonal).

Population	5	22	27	29	30	35	66	69	76	78	79	80	81
5	-----	33.50	32.00	22.50	23.00	31.00	19.00	19.50	44.00	24.50	18.00	16.75	23.75
22	13.36	-----	1.50	9.50	8.00	3.75	16.00	15.50	52.00	33.25	20.25	17.50	33.25
27	14.13	3.44	-----	11.00	9.50	2.50	14.50	14.00	50.50	31.75	18.75	16.00	31.75
29	12.33	7.96	8.05	-----	27.50	13.25	12.00	12.50	43.25	24.00	10.00	5.50	23.25
30	10.94	6.57	6.66	4.71	-----	11.00	13.00	13.50	43.00	25.00	11.00	6.50	24.00
35	14.59	4.25	4.34	8.39	7.01	-----	13.50	12.50	49.00	30.25	17.25	14.50	30.25
66	21.77	17.40	17.49	11.50	12.59	13.41	-----	2.00	39.00	20.00	7.50	4.00	19.00
69	20.66	16.29	16.38	10.38	11.48	12.30	1.89	-----	40.25	21.25	8.75	5.00	20.25
76	24.22	21.97	22.06	14.82	17.62	18.44	13.22	12.21	-----	32.00	37.50	38.25	32.50
78	19.21	16.97	17.06	9.82	13.72	17.40	15.17	14.06	6.83	-----	18.75	18.50	7.25
79	23.25	20.80	20.89	13.65	16.19	17.01	5.46	6.36	10.17	12.02	-----	4.75	18.00
80	19.00	14.63	14.72	8.72	9.82	10.64	3.89	2.78	11.27	12.49	7.49	-----	17.75
81	21.43	19.19	19.27	12.04	14.87	15.69	11.29	10.18	6.26	4.46	17.01	8.52	-----

Table 9. Pairwise estimates of geographic distance along roads between 13 *Cynomys ludovicianus* populations (log₁₀ km, above diagonal) and shortest drainage-road distance between colonies (log₁₀ km, below diagonal).

Population	5	22	27	29	30	35	66	69	76	78	79	80	81
5	-----	13.50	14.25	12.50	11.00	14.50	21.75	20.75	24.25	19.25	23.25	19.00	21.50
22	12.00	-----	3.50	8.00	6.50	4.25	17.50	16.25	22.00	17.00	20.75	14.50	19.25
27	12.00	1.50	-----	8.00	6.75	4.50	17.50	16.50	22.00	17.00	21.00	14.75	19.25
29	8.00	7.00	7.50	-----	4.75	8.50	11.50	10.50	14.75	9.75	13.75	8.75	12.00
30	10.00	4.50	6.00	2.75	-----	7.00	12.50	11.50	17.50	13.75	16.25	9.75	14.75
35	13.50	3.00	2.00	8.00	4.00	-----	13.50	13.00	18.50	17.50	17.00	10.75	15.75
66	15.50	13.50	12.00	8.25	9.75	13.00	-----	2.00	13.25	15.25	5.50	4.00	11.25
69	16.00	12.00	10.50	8.50	9.50	12.00	1.50	-----	12.25	14.00	6.50	2.75	10.25
76	20.00	20.00	21.00	16.50	18.50	24.50	11.00	10.75	-----	6.75	10.25	11.25	6.25
78	16.00	15.00	15.25	9.75	15.00	16.00	12.50	12.25	7.00	-----	12.00	12.50	4.50
79	18.00	17.50	16.00	9.75	13.00	17.00	4.50	4.75	10.00	10.00	-----	7.50	17.00
80	12.50	12.50	12.50	5.25	8.00	10.00	3.00	3.25	12.00	12.50	4.50	-----	8.50
81	14.50	14.00	13.25	8.00	10.50	15.00	12.50	12.75	8.00	8.00	10.50	10.50	-----

Table 10. Mantel correlations for pairwise estimates of three genetic distance measures with four measures of geographic distance.

Genetic distance measure ^a	Mantel correlation (<i>P</i>)			
	Drainage distance	Road distance	Drainage-road distance	Linear distance
D _A	0.362 (0.002)	0.114 (0.289)	0.245 (0.001)	0.173 (0.115)
D _C	0.405 (0.002)	0.225 (0.002)	0.231 (0.001)	0.197 (0.030)
D _F	0.426 (0.002)	0.222 (0.031)	0.239 (0.002)	0.224 (0.031)
Mean	0.398	0.187	0.238	0.198

^aD_A denotes the proportion of alleles shared between populations, D_C denotes Cavalli-Sforza and Edwards' chord distance between colonies, and D_F denotes $F_{ST}/1-F_{ST}$ distance measure between populations.

Table 11. F-test values and correlations (r) for least-squares regressions of genetic distance against geographic distance.

Geographic distance	F-test _{1,12} (P) correlation r		
	Cavalli-Sforza and Edwards chord distance (D _C)	F _{ST} /1-F _{ST} (D _F)	Proportion of shared alleles (D _A)
Linear	1.034 (0.329)	3.083 (0.105)	2.646 (0.130)
	0.116	0.197	0.183
Drainage	5.163 (0.042)	7.576 (0.018)	7.594 (0.017)
	0.406	0.301	0.301
Road	4.374 (0.058)	3.796 (0.075)	2.986 (0.110)
	0.233	0.218	0.194
Drainage-road	3.094 (0.104)	3.472 (0.087)	3.018 (0.108)
	0.198	0.209	0.195

Table 12. Results of Akaike's Information Criterion (AIC) model selection for black-tailed prairie dog dispersal on the Central Plains Experimental Range and the Pawnee National Grassland in Weld County, Colorado, 1997-98 as a function of the proportion of shared alleles.

Model	K	adjusted R ²	AIC _c	Δ_i	w_i^a
Drainage distance and age	2	0.164	-307.985	0	0.681
Linear distance and age	2	0.117	-303.856	4.289	0.080
Age	1	0.101	-303.352	4.634	0.067
Drainage-road distance and age	2	0.110	-303.130	4.855	0.060
Road distance and age	2	0.110	-303.084	4.901	0.059
Drainage distance	1	0.079	-301.496	6.489	0.027
Road distance	1	0.021	-296.737	11.248	0.003
Linear distance	1	0.021	-296.737	11.248	0.003
Drainage-road distance	1	0.018	-296.588	11.450	0.002

^a95% model confidence set in bold.

Table 13. Results of Akaike's Information Criterion (AIC) model selection for *Cynomys ludovicianus* dispersal on the Cental Plains Experimental Range and the Pawnee National Grassland in Weld County, Colorado, 1997-98 as a function of Cavalli-Sforza and Edwards' chord distance.

Model	K	adjusted R ²	AIC _c	Δ _i	w _i ^a
Drainage distance and age	2	0.159	-455.140	0	0.529
Age	1	0.121	-452.868	2.327	0.165
Road distance and age	2	0.126	-452.167	2.973	0.120
Linear distance and age	2	0.119	-451.548	3.592	0.088
Drainage-road distance and age	2	0.116	-451.290	3.850	0.077
Drainage distance	1	0.051	-446.855	8.285	0.008
Road distance	1	0.016	-444.018	11.122	0.002
Linear distance	1	0.004	-442.779	12.361	0.002
Drainage-road distance	1	0.000	-442.755	12.385	0.002

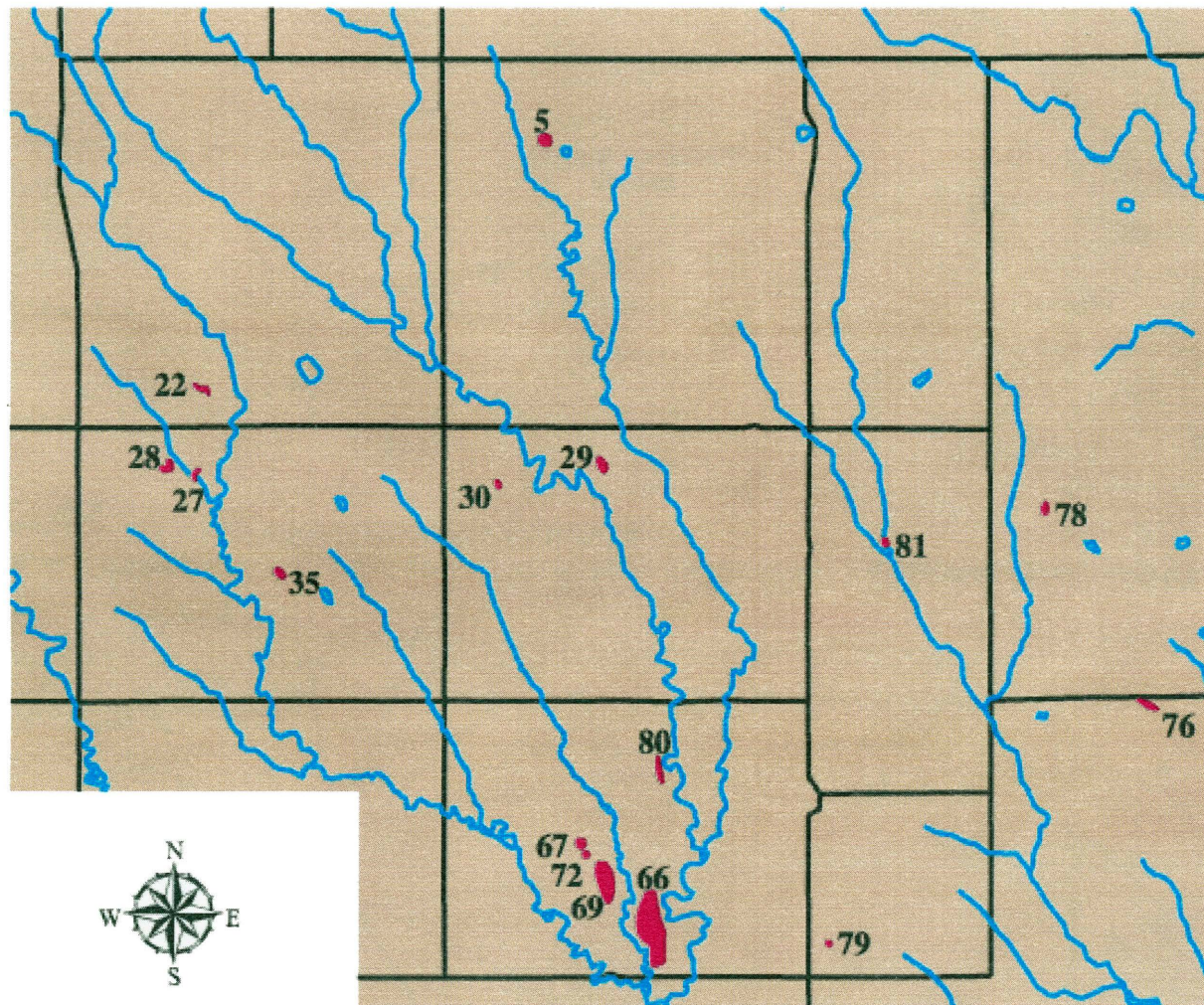
^a95% model confidence set in bold.

Table 14. Results of Akaike's Information Criterion (AIC) model selection for black-tailed prairie dog dispersal on the Central Plains Experimental Range and the Pawnee National Grassland, 1997-98 as a function of $F_{ST}/1-F_{ST}$.

Model	K	adjusted R^2	AIC _c	Δ_i	w_i^a
Drainage distance	1	0.079	-381.078	0	0.361
Drainage distance and age	2	0.088	-380.806	0.273	0.316
Road distance	1	0.035	-377.468	3.610	0.059
Road distance and age	2	0.045	-377.169	3.909	0.051
Drainage-road distance	1	0.031	-377.151	3.927	0.051
Distance-road distance and age	2	0.043	-377.006	4.072	0.047
Linear distance and age	2	0.041	-376.841	4.237	0.043
Linear distance	1	0.026	-376.768	4.310	0.042
Age	1	0.017	-376.040	5.038	0.029

^a95% model confidence set in bold.

Fig. 1. Distribution of black-tailed prairie dog populations on the Central Plains Experimental Range and Pawnee National Grassland in Weld County, Colorado, May 1997-January 1998. Populations 28, 67, and 72 were not included in study.



- Prairie Dog Towns
- Study Area
- Drainages
- Roads

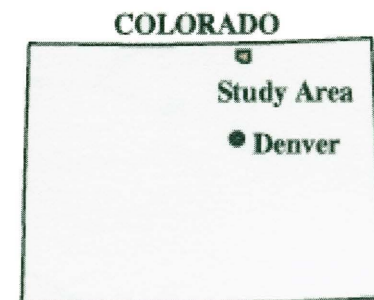


Fig. 2. Dendrogram of drainage geographic distance and neighbor-joining trees of microsatellite data using three different distance measures. Bootstrap values above 50% are indicated.

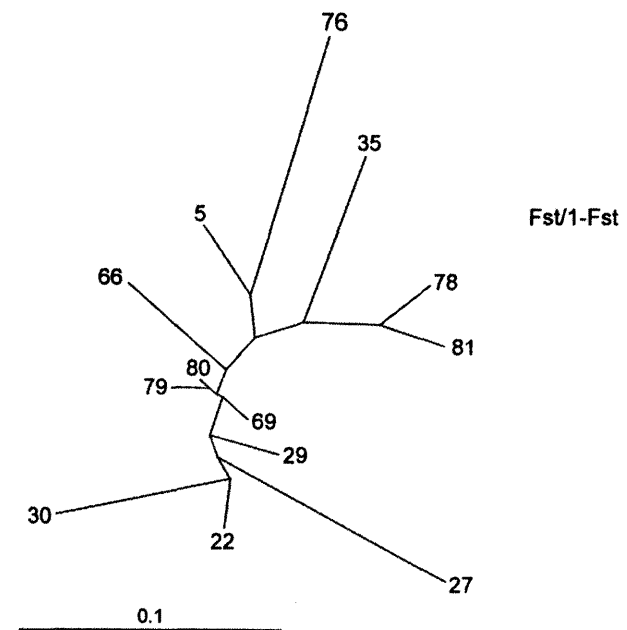
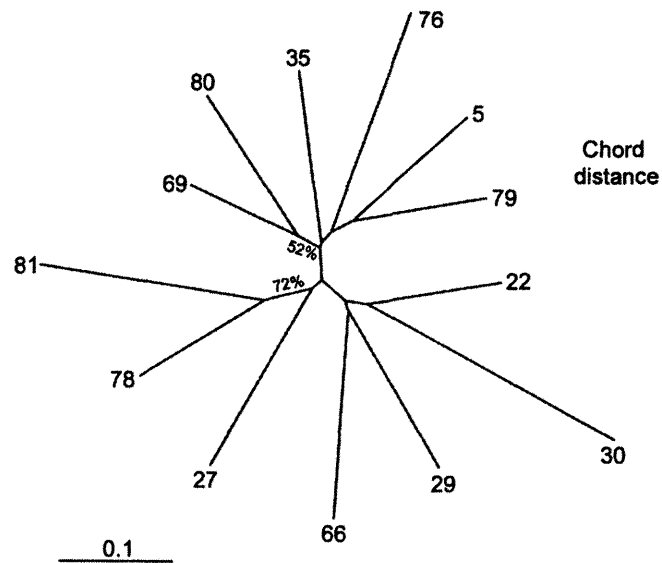
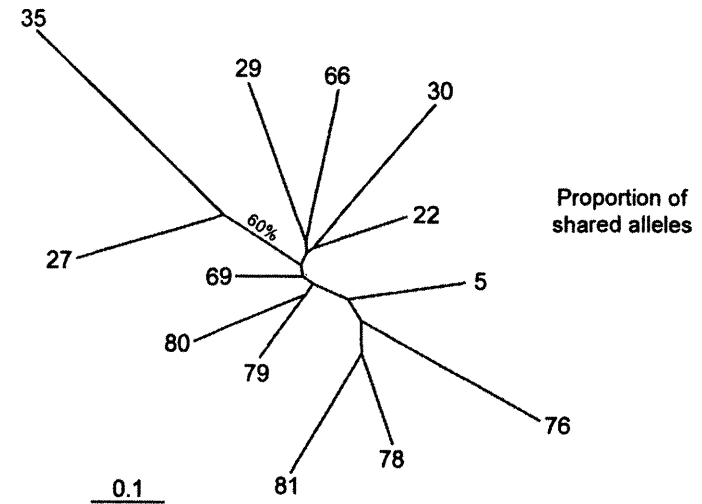
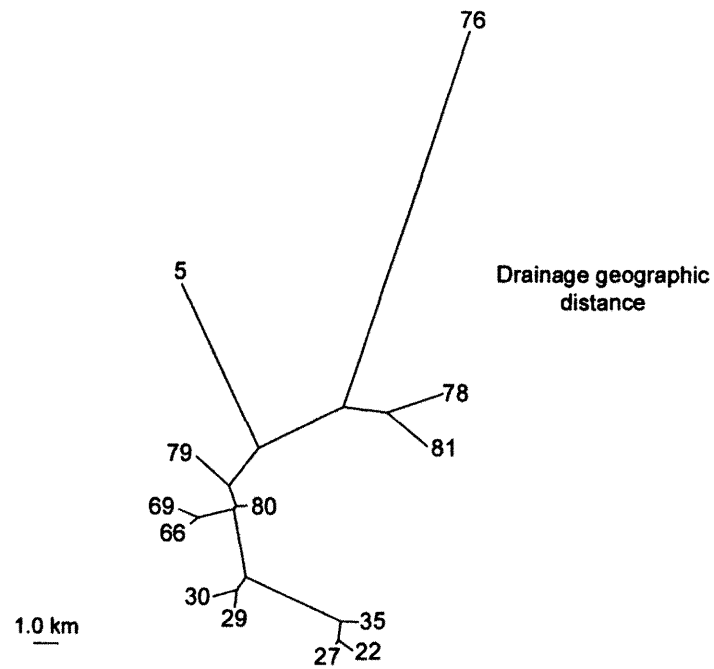


Fig. 3. Regressions of the genetic distance measure proportion of shared alleles (D_A) on $\log_{10}(\text{distance})$. Slopes with significance level greater than $\alpha = 0.05$ are indicated by a solid line. (a) linear: $y = 0.11x + 0.49$, 95% slope CL = (-0.03, 0.24); (b) drainage: $y = 0.14x + 0.36$, 95% slope CL = (0.04, 0.23); (c) road: $y = 0.12x + 0.39$, 95% slope CL = (-0.02, 0.27); (d) drainage-road: $y = 0.11x + 0.41$, 95% slope CL = (-0.02, 0.24).

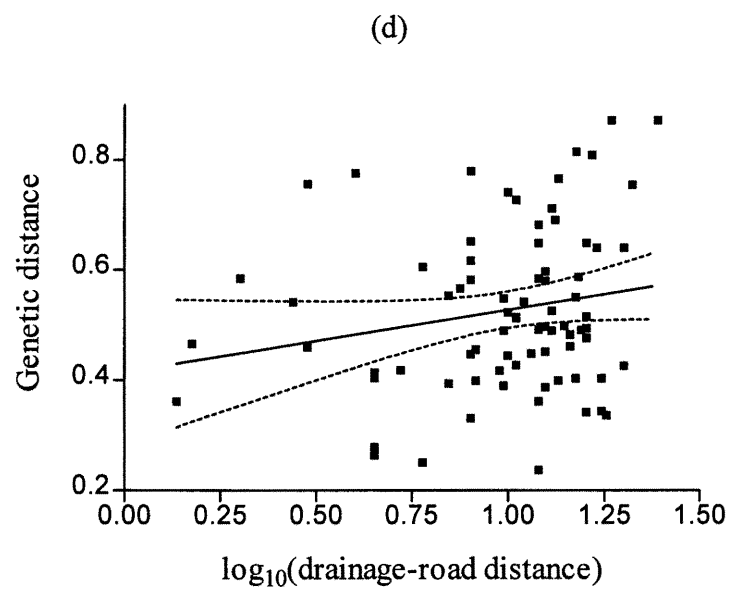
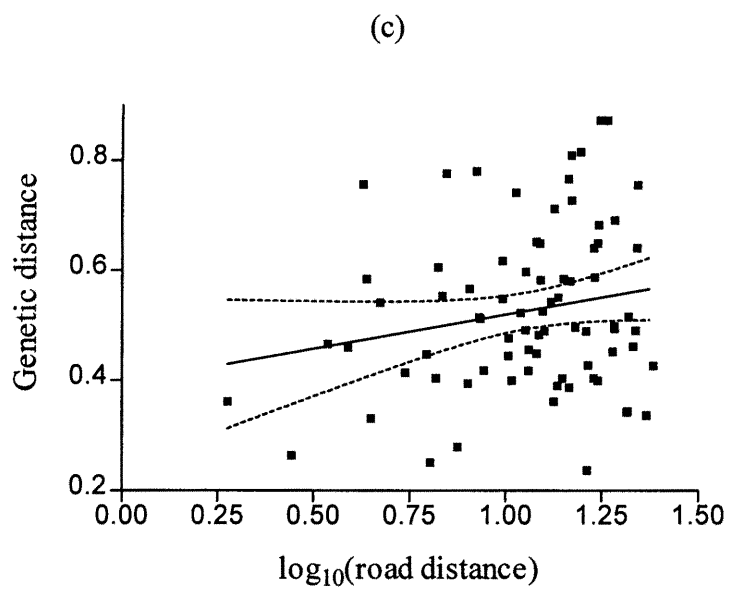
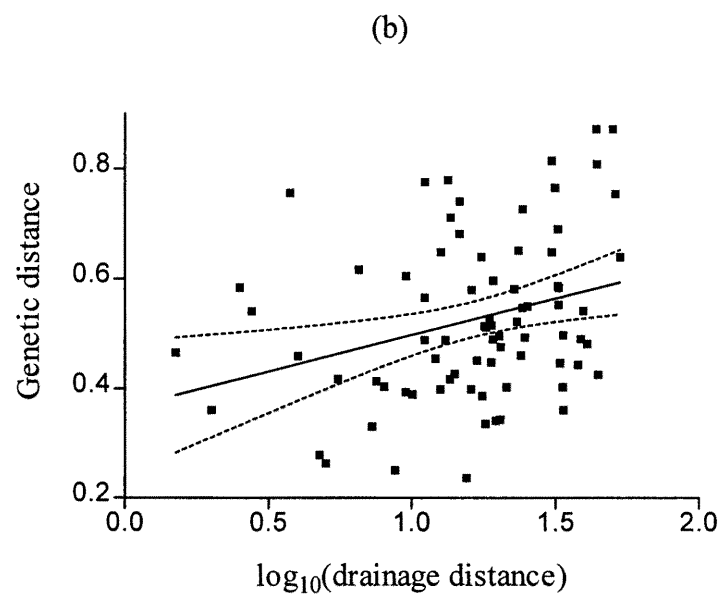
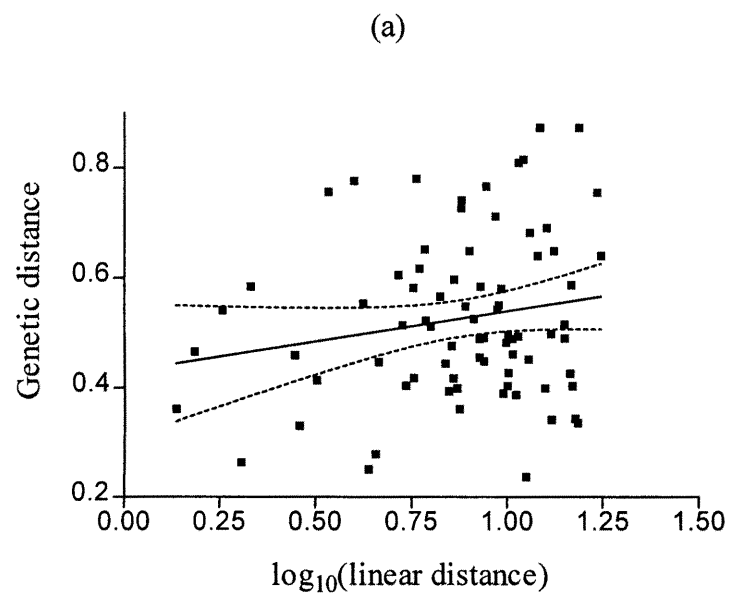


Fig. 4. Regressions of the genetic distance measure chord distance (D_C) on $\log_{10}(\text{distance})$. Slopes with significance level greater than $\alpha = 0.05$ are indicated by a solid line. (a) linear: $y = 0.03x + 0.04$, 95% slope CL = (-0.03, 0.08); (b) drainage: $y = 0.06x + 0.34$, 95% slope CL = (0.02, 0.09); (c) road: $y = 0.06x + 0.35$, 95% slope CL = (0.00, 0.11); (d) drainage-road: $y = 0.05x + 0.37$, 95% slope CL = (-0.01, 0.10).

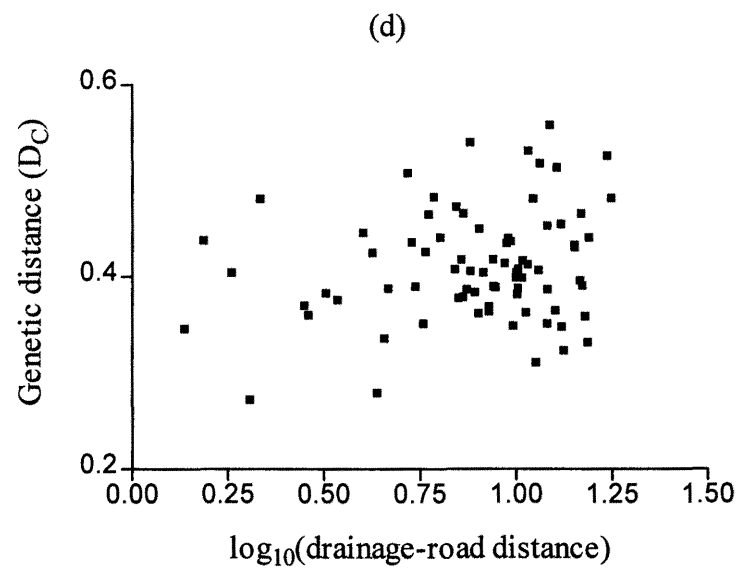
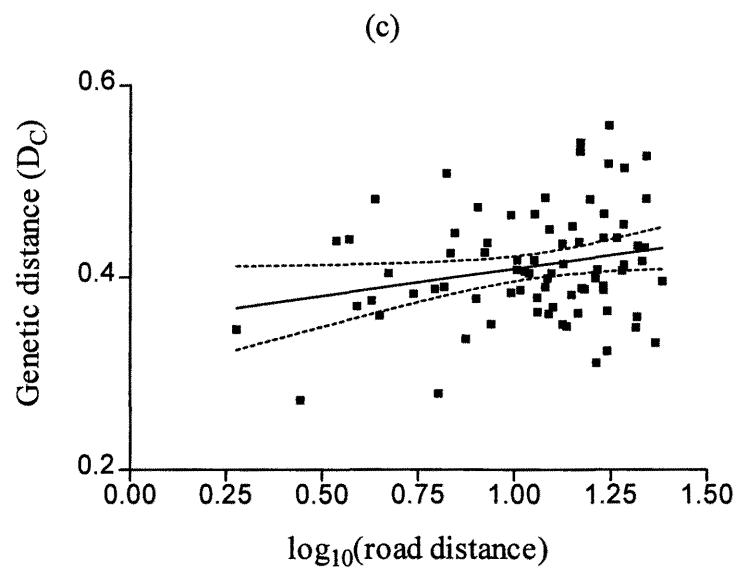
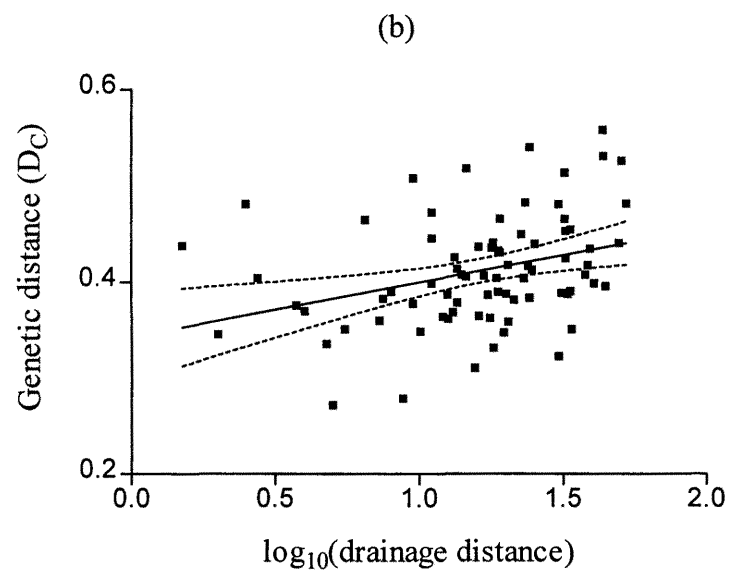
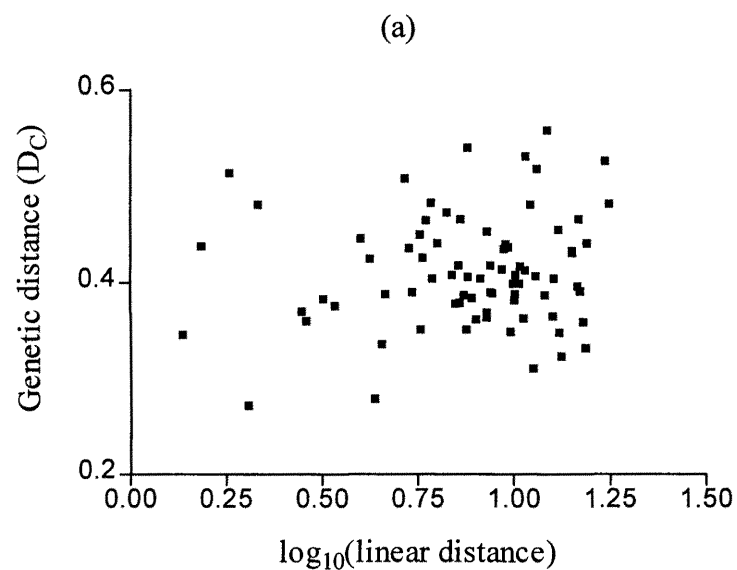
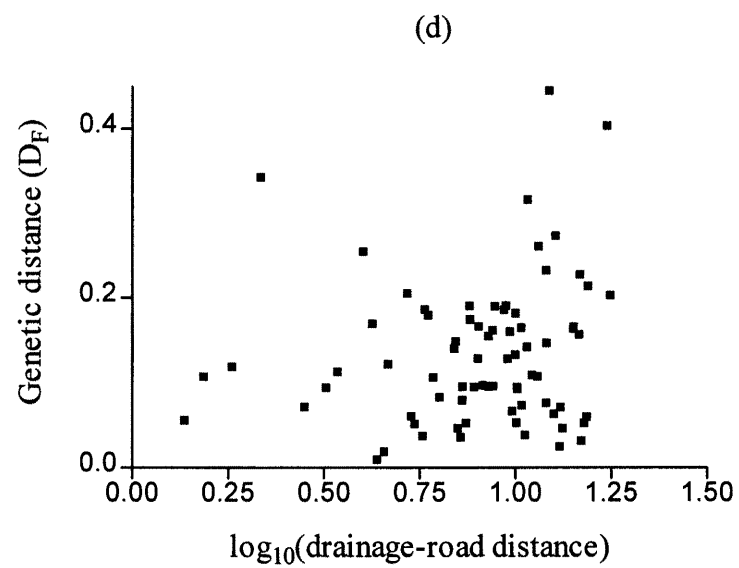
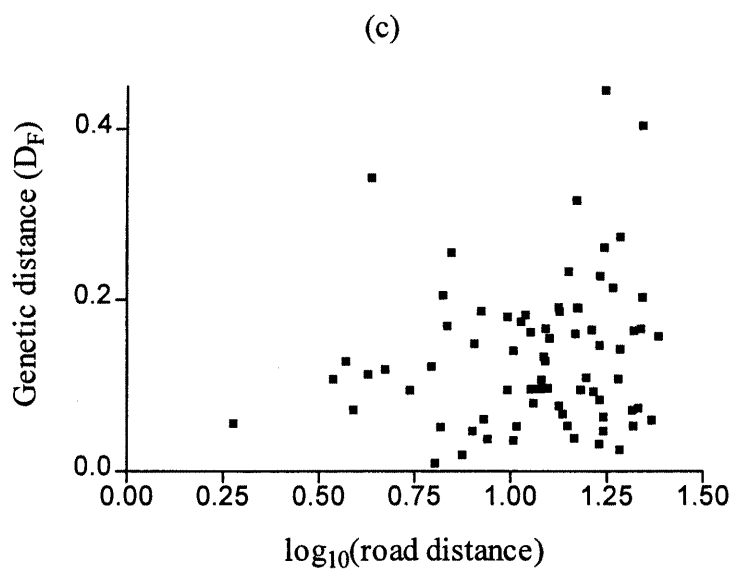
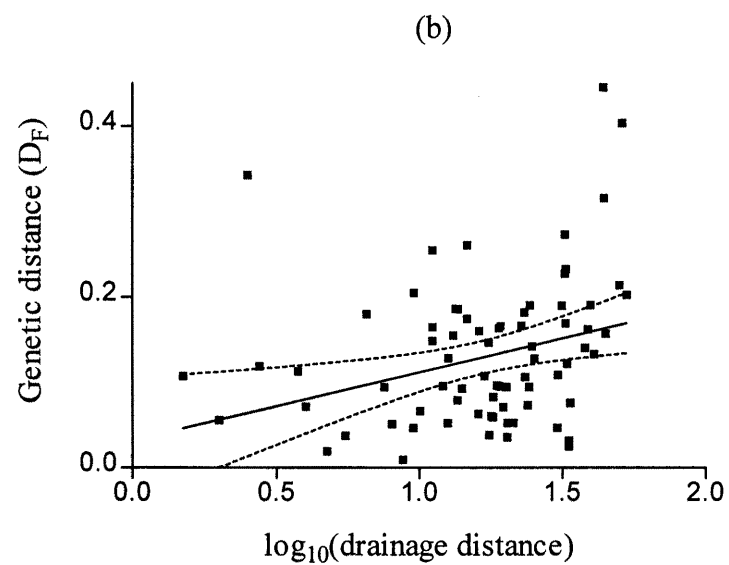
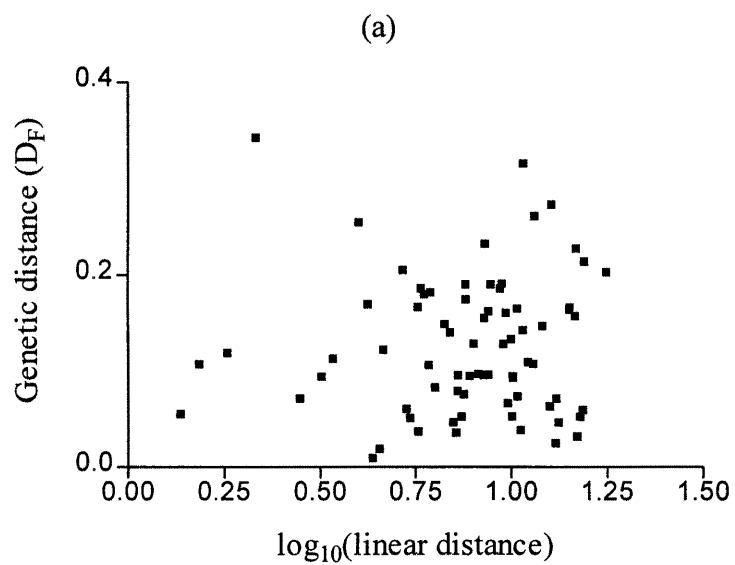


Fig. 5. Regressions of the genetic distance measure $F_{ST}/1-F_{ST}$ (D_F) on $\log_{10}(\text{distance})$. Slopes with significance level greater than $\alpha = 0.05$ are indicated by a solid line. (a) linear: $y = 0.07x + 0.07$, 95% slope CL = (-0.01, 0.15); (b) drainage: $y = 0.08x + 0.03$, 95% slope CL = (0.02, 0.14); (c) road: $y = 0.08x + 0.04$, 95% slope CL = (0.00, 0.16); (d) drainage-road: $y = 0.07x + 0.06$, 95% slope CL = (-0.01, 0.15).



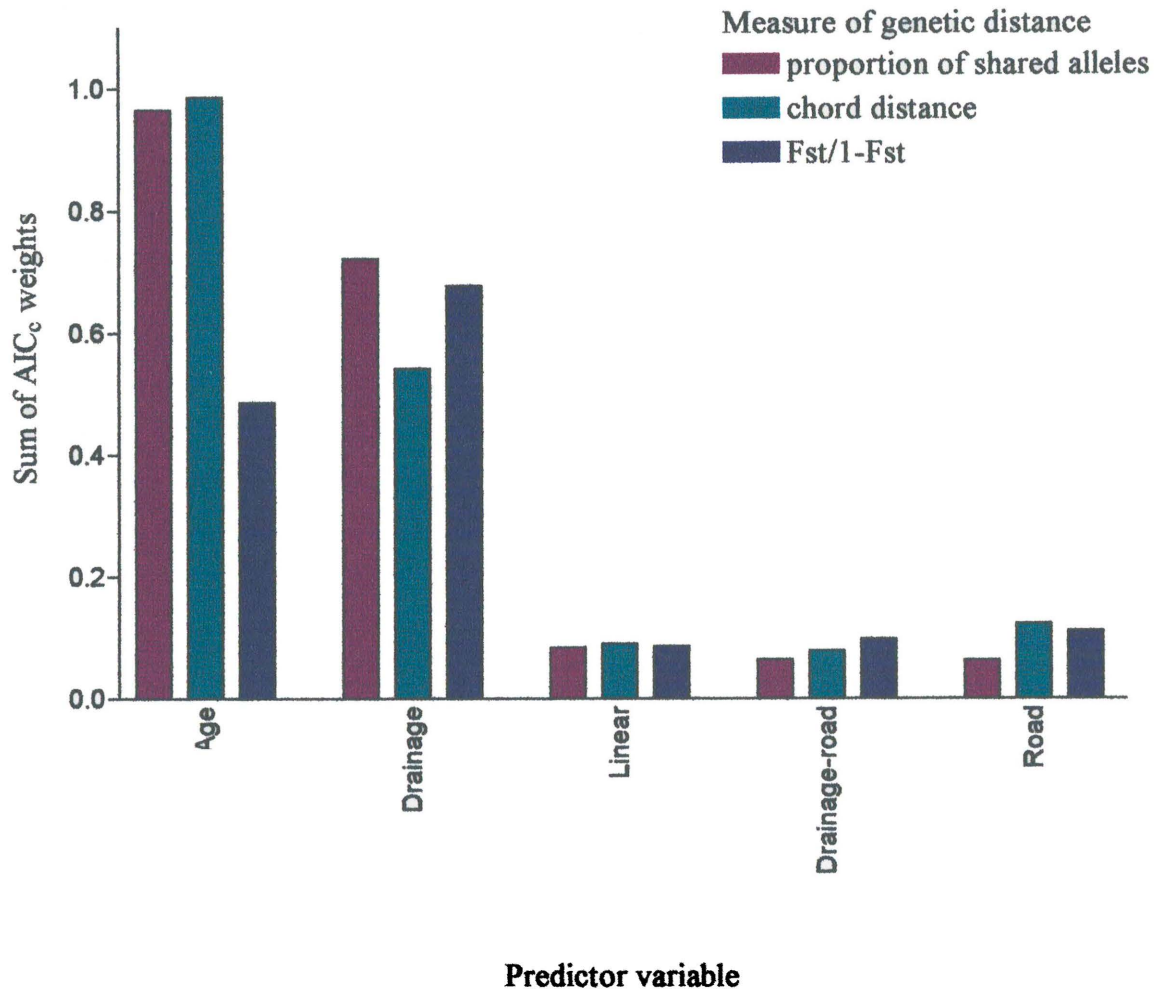


Fig. 6. Relative importance of five predictors of genetic distance measures for black-tailed prairie dogs on the Central Plains Experimental Range and the Pawnee National Grassland in Weld County, Colorado, 1997-98. Importance is measured by summing the AIC_c weights.

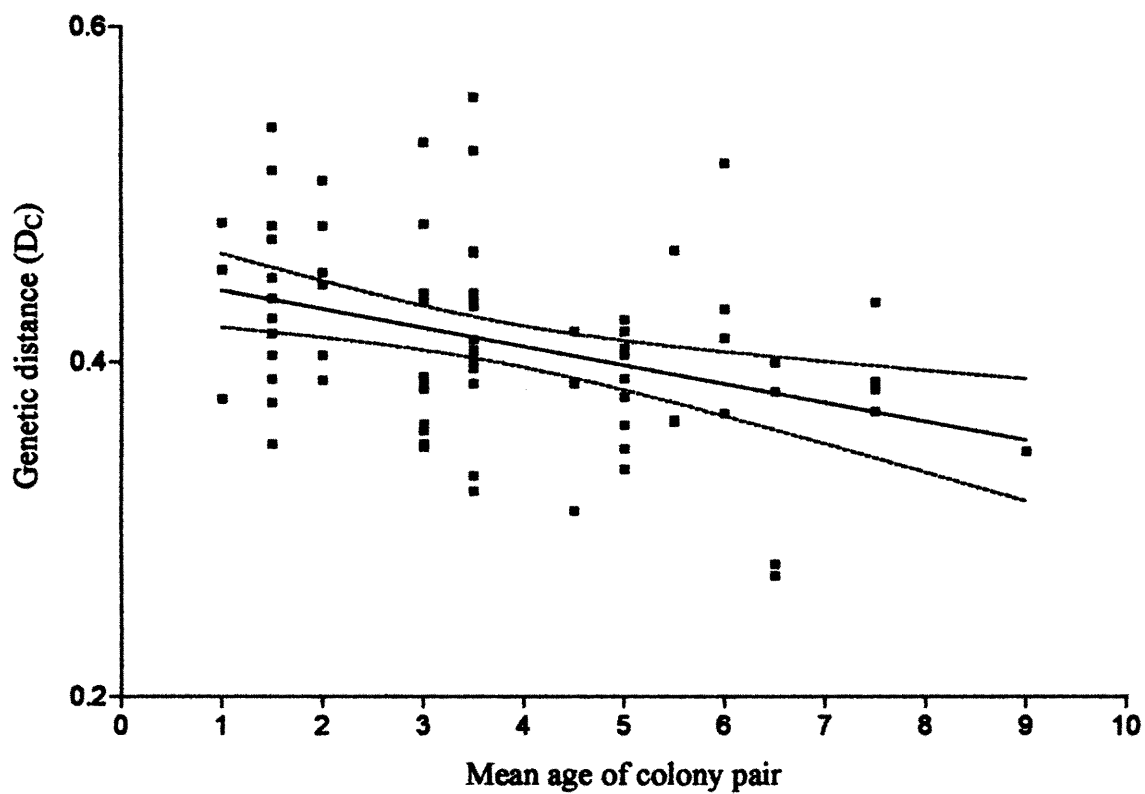


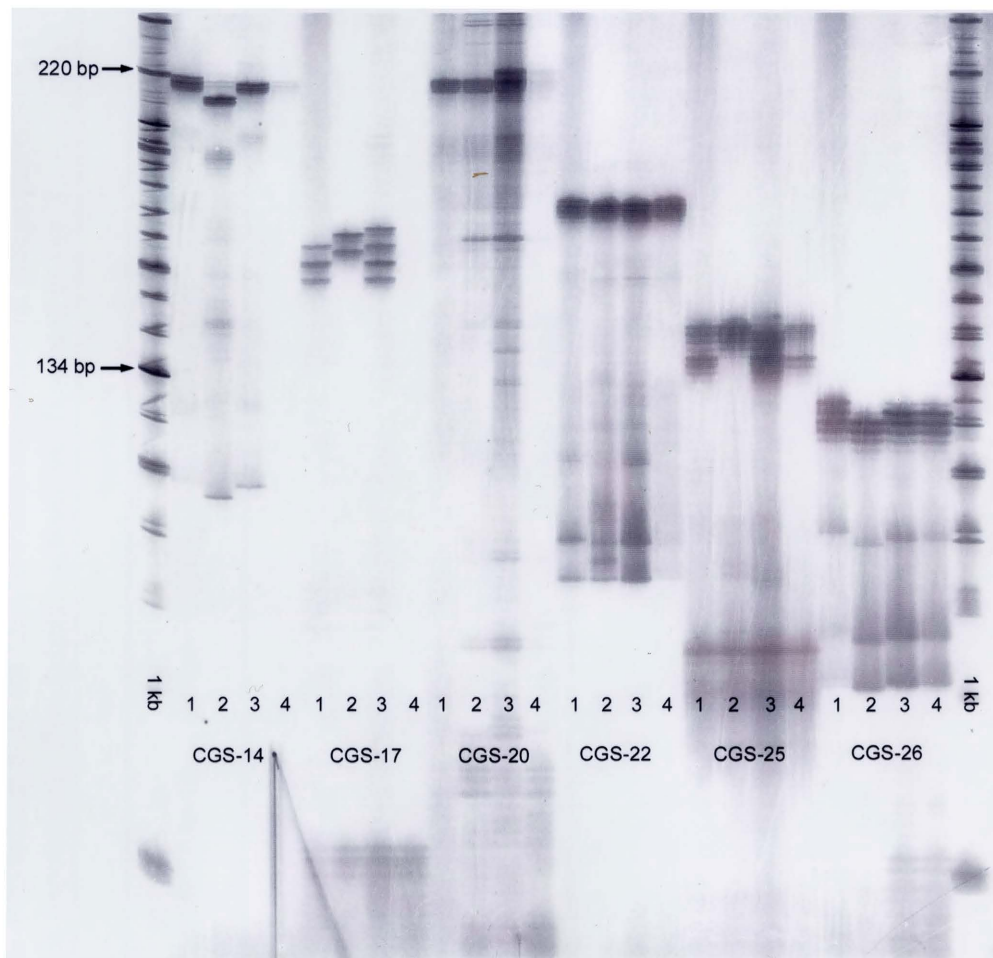
Fig. 7. Regression of the genetic distance measure chord distance (D_C) on the mean age of a colony pair. $y = -0.01x + 0.45$. 95% slope CL = $(-0.02, -0.00)$.

APPENDICES

Appendix I.

Table of township, range, and section location and active burrow density (burrows/ha) for 13 *Cynomys ludovicianus* colonies on the Central Plains Experimental Range (colonies 5-35) and the Pawnee National Grassland (colonies 66-81) in Weld County, Colorado, 1997-98.

Colony	Location	Burrow density
5	T10NR65WS5	82.5
22	T10NR66WS22	NA
27	T10NR66WS27	69.2
29	T10NR65WS29	NA
30	T10NR65WS29	NA
35	T10NR66WS35	NA
66	T9NR65WS21	55.8
69	T9NR65WS20	69.2
76	T9NR64WS8	81.6
78	T10NR64WS30	90.8
79	T9NR652S23	77.5
80	T9NR65WS9	77.5
81	T10NR65WS35	NA



Appendix II. PCR products for six microsatellite loci from four black-tailed prairie dogs resolved on a denaturing polyacrylamide gel. Primers were designed by Stevens et al. (1997).

Appendix III. Table of allele frequencies. Alleles are listed in order of increasing mobility (A = slowest). Each letter represents a decrease in size by 2 basepairs. Populations 5-35 are Central Plains Experimental Range prairie-dog populations, populations 66-81 are Pawnee National Grasslands populations. Population locations are illustrated in Fig. 1.

Locus IGS-1 Allele	Population												
	5 (n=15)	22 (n=11)	27 (n=14)	29 (n=16)	30 (n=10)	35 (n=15)	66 (n=15)	69 (n=11)	76 (n=12)	78 (n=10)	79 (n=15)	80 (n=8)	81 (n=3)
A										0.050			
B				0.281	0.200	0.033	0.133	0.091		0.050	0.100	0.125	
C	0.100	0.273	0.107	0.281	0.200	0.067	0.367	0.227		0.200	0.233	0.188	0.167
D	0.100	0.045	0.357	0.063				0.091		0.050		0.188	0.167
E	0.800	0.636	0.536	0.313	0.550	0.900	0.400	0.545	1.000	0.650	0.633	0.500	0.667
F		0.045		0.063	0.050		0.100	0.045			0.033		

Locus IGS-6 Allele	Population												
	5 (n=15)	22 (n=11)	27 (n=14)	29 (n=16)	30 (n=10)	35 (n=15)	66 (n=15)	69 (n=11)	76 (n=12)	78 (n=10)	79 (n=15)	80 (n=8)	81 (n=3)
A						0.033		0.056				0.188	
B	0.143	0.250	0.577			0.100	0.036	0.278	0.333	0.188	0.143	0.125	0.167
C	0.036	0.188	0.115	0.231	0.100		0.071	0.111	0.042	0.063	0.179	0.188	0.167
D	0.571			0.115	0.050			0.056	0.333	0.063	0.179		0.500
E	0.214	0.250	0.308	0.077	0.600	0.500	0.179	0.167	0.042	0.375	0.143	0.063	
F	0.036	0.063		0.115	0.100	0.133	0.179	0.167	0.083		0.107	0.250	0.167
G		0.125						0.167	0.083			0.125	
H					0.050						0.179		
I		0.063		0.192	0.050	0.067	0.536			0.125			
J				0.077						0.125			
K		0.063		0.038	0.050	0.067							
L				0.154		0.100			0.083	0.063	0.071	0.063	

[illegible]

[illegible]

Locus CGS-22 Allele	Population												
	5 (n=15)	22 (n=11)	27 (n=14)	29 (n=16)	30 (n=10)	35 (n=15)	66 (n=15)	69 (n=11)	76 (n=12)	78 (n=10)	79 (n=15)	80 (n=8)	81 (n=3)
A		0.045		0.063	0.050		0.233			0.200			0.167
B			0.036		0.050					0.100			0.167
C	0.600	0.273	0.321	0.438		0.700	0.433	0.500	0.750	0.250	0.733	0.750	0.333
D	0.400	0.591	0.643	0.469	0.900	0.300	0.300	0.500	0.250	0.450	0.267	0.250	0.333
E		0.091		0.031									
F							0.033						

[illegible]

Appendix IV. Information on black-tailed prairie dog live-trapping

We captured and sampled 129 black-tailed prairie dogs on the Central Plains Experimental Range (CPER) and the Pawnee National Grassland (PNG) from May 1997 to January 1998. The number of prairie dogs captured on CPER colonies ($n = 80$) was significantly greater than the number captured on PNG colonies ($n = 49$) (Wilcoxon 2-sample test: $Z = 2.95$, $P = 0.0033$; Table 1). We also found that the number of trap-days (no. traps x no. days) until first capture was significantly greater on PNG colonies than on CPER colonies (Wilcoxon 2-sample test: $Z = 2.94$, $P = 0.0033$; Table 2). The cumulative trap effort (number of trap-days necessary to obtain 10-15 prairie dogs) was always greater for populations on the PNG than for populations on the CPER (Fig. 1).

We hypothesized that the difference in trap success (individuals/trap-day x 100) (CPER: 5.1%, PNG: 1.7%) was a result of differences in human shooting pressures between the CPER and the PNG. The PNG is U. S. Forest Service public land, and as long as one has a small-game license, there are no regulations on recreational shooting of black-tailed prairie dogs. CPER land is managed by the Agricultural Research Service and is a Long-Term Ecological Research site. This land is continually frequented by scientists and ARS land managers; therefore, prairie-dog populations are usually not subject to recreational shooting. Prairie dogs inhabiting colonies subject to recreational shooting may be more wary of humans and therefore more difficult to trap.

Vosburgh and Irby (1998) investigated the effects of recreational shooting on prairie-dog colonies in central Montana and found that prairie dogs could be approached more closely in nonhunted colonies than hunted colonies.

Although our data suggest that difference in trap success was a result of differences in human shooting pressures, we cannot rule out the effect that other factors, such as timing of trapping, may have on trap success. We did not design this study to investigate differences in trap success between CPER and PNG prairie-dog colonies. Thus, trapping efforts for the CPER and PNG were not the same in some months (Table 3). We combined the data for the summer months (May-August) and for the winter months (September-January) in an attempt to account for the effect of timing of trapping on trap success. The number of captured prairie dogs did not differ between the CPER and PNG (Wilcoxon 2-sample test: $Z = 0.87$, $P = 0.38$).

Future studies on black-tailed prairie dogs on the CPER and PNG should consider potential effects of human shooting pressures and timing of trapping in their study designs. Trap effort may be very intensive (35 trap-days/individual on average in our study) and trap success fairly low (4.35% on average in our study) and may make demographic studies difficult to conduct.

LITERATURE CITED

Vosburgh, T. C. and L. R. Irby. 1998. Effects of recreational shooting on prairie dog colonies. *Journal of Wildlife Management*, 62:363-372.

Appendix IV. Table 1. Live-trapping data from black-tailed prairie dog populations on the Central Plains Experimental Range and the Pawnee National Grassland in Weld County, Colorado, May 1997-January 1998.

Population	Trap period	Days	Trapdays ^a	Adult males	Juvenile males	Adult females	Juvenile females	Total individuals	Total captures ^b
Central Plains Experimental Range populations									
5	07/30-08/14	10	261	3	4	1	7	15	26
22	11/16-12/14 01/17-01/22	13	338	1	3	1	6	11	15
27	06/15- 06/17 07/30-08/28	18	365	2	3	6	2	13	38
29	11/06-12/12	9	204	5	5	4	2	16	23
30	08/18-09/04 10/22-11/06	14	332	5	1	1	3	10	41
35	08/20-09/02	7	175	3	3	0	9	15	40
Total		71	1675	19	19	13	29	80	182

Population	Trap period	Days	Trapdays ^a	Adult males	Juvenile males	Adult females	Juvenile females	Total individuals	Total captures ^b
Pawnee National Grassland populations									
51	05/21-05/29	4	110	0	0	0	0	0	0
66	09/30-10/21 06/22-06/28 07/07-07/17	25	589	4	5	2	4	15	44
76	07/18-07/23 09/30-11/20	25	605	4	0	7	0	11	30
78	07/07-07/23 09/04-09/17	19	447	0	0	0	0	0	0
79	06/19-06/28 07/07-07/17	15	509	4	4	5	2	15	32
80	06/09-06/18 07/18-07/23 10/11-10/23	19	559	1	0	1	3	5	6
81	09/09-09/17 09/30-10/08	9	183	2	0	1	0	3	16
Total		116	3002	15	9	16	9	49	128

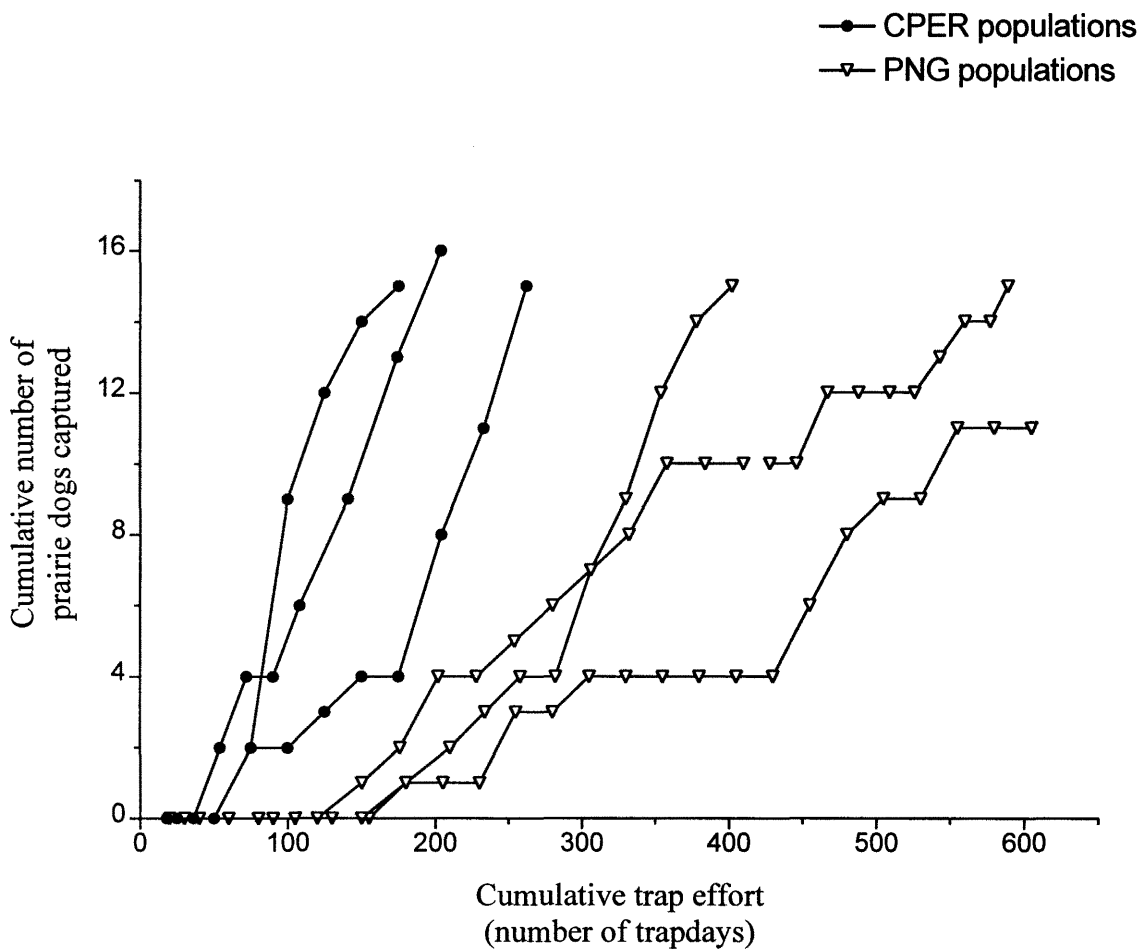
^aTrapdays equals the number of days trapped x the number of traps used. ^bTotal captures equals the total number of capture, including recaptures.

Appendix IV. Table 2. Trap success for black-tailed prairie dogs on the Central Plains Experimental Range and the Pawnee National Grassland in Weld County, Colorado, May 1997-January 1998.

Population	Number of trapdays until first capture	% individual trap success (number of prairie dogs captured per trapday after first capture)	% total trap success (number of total captures per trapday after first capture)
Central Plains Experimental Range populations			
5	49	15/212 = 7.08%	26/212 = 12.26%
22	30	11/308 = 3.57%	15/308 = 4.87%
27	12	12/260 = 4.60%	34/260 = 13.08%
29	36	16/168 = 9.52%	23/168 = 13.69%
30	1	9/144 = 6.25%	21/144 = 14.50%
35	50	15/125 = 12%	40/125 = 32%
Mean	29.67 ± 19.81	7.17% ± 3.14%	15.07% ± 9.0%
Pawnee National Grassland populations			
66	120	15/469 = 3.20%	44/469 = 9.38%
76	75	11/450 = 2.4%	30/450 = 6.67%
78	447	0	0
79	150	15/252 = 5.95%	31/252 = 12.3%
80	200	5/359 = 1.39%	6/359 = 1.67%
81	50	3/75 = 4%	16/75 = 21%
Mean	173.67 ± 144.13	2.82% ± 2.07%	8.50% ± 7.66%

Appendix IV. Table 3. The number of black-tailed prairie dogs captured per month on the Central Plains Experimental Range (CPER) and the Pawnee National Grassland (PNG) in Weld County, Colorado, May 1997-January 1998.

Month	Number of individuals captured	
	CPER	PNG
June	1	6
July	1	21
August	52	0
September	1	3
October	0	12
November	8	8
December	16	0
January	4	0



Appendix IV. Fig. 1. Cumulative number of prairie dogs captured as a function of cumulative trap effort (number of trap-days). Data from three Central Plains Experimental Range and three Pawnee National Grassland populations were chosen to illustrate the relationship.