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GENETIC STRUCTURE OF A METAPOPULATION OF BLACK-TAILED PRAIRIE DOGS

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Habitat alteration, agricultural control, recreational shooting, and most recently, sylvatic plague (caused by *Yersinia pestis*) contributed to local extinctions and a steady decline of black-tailed prairie dog (*Cynomys ludovicianus*) throughout its range. As a consequence, prairie dogs currently live in metapopulations, where their overall persistence will depend on a balance between extinction of colonies and recolonization from extant colonies. Patterns of genetic similarity among colonies, as measured by neutral molecular markers, provide an estimate of the dispersal and gene flow among colonies within prairie dog metapopulations. We sampled 13 colonies of black-tailed prairie dogs in short-grass prairie of northern Colorado, 100-km east of Fort Collins, Colorado. We used historical records and genetic analysis to show that colonies undergo regular extinctions, which subsequently are recolonized by individuals from multiple source colonies. We examined 155 individuals for variation at 7 microsatellite loci and found moderate levels of genetic differentiation among colonies (Θ [$=F_{ST}$] = 0.118). We also used assignment and exclusion tests based on multilocus genotypes of individuals to determine the probability that individuals originated from the same colony in which they were captured. About 39% of individuals could not be assigned to colonies where they were captured, indicating they were either immigrants (adults) or the offspring of immigrants (adults and juveniles). We tested for genetic isolation by distance among colonies by comparing genetic distances to geographic distances between colonies. Akaike's Information Criterion for model selection revealed that dispersal most likely occurred along low-lying dry creek drainages connecting isolated colonies. Genetic distances between colonies were also related to ages of colonies; older colonies were more similar genetically than younger colonies. This underscores the importance of dispersal among prairie dog colonies and has important implications for persistence of prairie dog metapopulations, in which all colonies, regardless of size, are vulnerable to extinction from plague.

Key words: conservation genetics, *Cynomys ludovicianus,* dispersal corridors, landscape ecology, metapopulations, population genetics

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Metapopulations exist in a series of discontinuous habitats, linked by limited migration, where the number of occupied habitat patches is determined by extinction and recolonization of local populations (Hanski 1999; Hanski and Simberloff 1997; Harrison and Taylor 1997; Levins 1969). Long-term persistence of a metapopulation depends on balance between extinction and recolonization of habitat fragments (Hanski 1999; McCullough 1996), and dynamics of metapopulations depend on individual dispersal within and between suitable habitats (Lidicker and Koenig 1996). In turn, move-

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ment is affected by physical aspects of the surrounding landscape (Hanski 1999; Merriam 1988; Wiens 1996). Although simulation models may aid in conceptually linking landscape structure to metapopulation dynamics, a more complete understanding of dynamics of natural populations requires knowledge of actual rates and mechanisms of dispersal in the field (Hobbs 1992; Wiens 1996). An increasingly popular approach for estimating dispersal rates involves use of genetic markers (Koenig et al. 1996; Peacock and Smith 1997). In this approach, gene flow is inferred from patterns of genetic similarity among hypothesized subpopulations, under the assumption that these patterns reflect movement of individuals rather than forces like selection or mutation.

We describe the population genetic structure of black-tailed prairie dogs (*Cynomys ludovicianus*) on short-grass prairie of north-central Colorado, relative to landscape features and recent history of extinction and recolonization of colonies. Black-tailed prairie dogs were distributed widely on short-grass and mixed-grass prairies of central North America, but they currently exist in spatially isolated colonies connected to different degrees by dispersal (Hoogland 1995). The decline of prairie dogs has resulted from a combination of habitat loss, poisoning, and recreational shooting. Moreover, dynamics of prairie dog colonies have been altered greatly by introduction of plague, which is caused by the bacterial pathogen, *Yersinia pestis.* Plague first appeared in Colorado in the late 1940s (Barnes 1993) and subsequently has dispersed throughout the state. Prairie dogs are extremely sensitive to plague, and prairie dog colonies are extirpated by plague every 5–10 years (M. Ball, pers. comm.; Cully 1993). As a consequence, prairie dogs currently exist as metapopulations, where colonies become extinct after plague epizootics and are recolonized later. Population genetic studies have demonstrated moderate levels of subdivision between colonies ($F_{ST} > 0.10$). However, these studies have not incorporated either landscape effects or history of extinctions and colonization in their analyses.

The black-tailed prairie dog is the most widespread of 5 recognized species of prairie dog, ranging from southern Canada (Saskatchewan) to northern Mexico (Chihuahua), and from the Rocky Mountains east to the 100th meridian (Hoogland 1995). Black-tailed prairie dogs are strictly colonial and are rarely observed away from established colonies (Koford 1958). Within colonies, individuals form coteries, territorial harem—polygynous family groups comprising 1 adult male, 3–4 adult females, and their offspring (Hoogland 1995). Because females are philopatric, coteries contain highly related females (M. F. Antolin and D. W. Tripp, in litt.; Hoogland 1995) and genetic differentiation between coteries can be as high as the differentiation between colonies (Chesser 1983; Dobson et al. 1997). Dispersal is male biased, with yearling males moving within colonies and thus reducing levels of inbreeding in the colony as a whole (Dobson et al. 1997; Halpin 1987; Hoogland 1995). Dispersal also occurs between colonies and is characterized by: solitary rather than group movements; peak dispersal during a postweaning period (June–August); dispersal mostly by yearling males, although both adult males and females also move between colonies; occasional long-distance movements (>5 km); and dispersal to established or abandoned colonies rather than to new locations (Garrett and Franklin 1988; Garrett et al. 1982; Knowles 1985, 1986). In a study of recolonization of colonies after experimental eradication, prairie dogs formed new coteries in the center of what had been a large colony (Cincotta et al. 1987).

Physical and ecological variability in the landscapes inhabited by prairie dogs likely influences dispersal and gene flow among colonies. Most studies of black-tailed prairie dogs have been conducted in mixed-grass prairie (Daley 1992; Foltz and Hoog-

land 1983; Garrett and Franklin 1988; Knowles 1985, 1986), where colonies are generally large, stable, and in close proximity to one another (Halpin 1987; Hoogland 1995). In contrast, colonies in short-grass prairie are generally smaller, unstable, and spatially isolated (Halpin 1987; Stapp 1998). Topographic variation, tall vegetation, and areas of urban or agricultural development are important barriers to dispersal and expansion of colonies (Koford 1958), but other landscape features such as roads and trails may facilitate movement (Garrett and Franklin 1988; Knowles 1986).

We used a series of microsatellite markers to estimate genetic variation within and among prairie dog colonies in northern Colorado. Highly variable microsatellite markers are well suited for studies of local dispersal and metapopulation structure (Goldstein and Pollock 1997). Our objectives were to evaluate whether landscape features such as roads and drainages functioned as dispersal corridors for black-tailed prairie dogs and to determine the influence of colonization and extinction on genetic differentiation among colonies.

Materials and Methods

Study area.—Thirteen colonies of black-tailed prairie dogs were studied within a 264-km^2 area of the Central Plains Experimental Range and the Pawnee National Grasslands in Weld County, Colorado (Fig. 1). Both areas are administered by the United States Department of Agriculture (Pawnee National Grasslands, Forest Service; Central Plains Experimental Range, Agricultural Research Service). Distribution of colonies was restricted by topography and other barriers, including tall vegetation, watercourses, and roads (Koford 1958). Prairie dog colonies were typically in low-lying areas, such as swales and broad lowland drainages, where vegetation is primarily short perennial bunchgrasses (*Bouteloua gracilis* and *Buchloe dactyloides*) and annual forbs. Upland areas separating prairie dog colonies also were dominated by these bunchgrasses but had greater cover of shrubs (*Artemesia frigida, Atriplex canescens, Eriogonum efusum, Gutierrezia sarothrae*—Bonham and Lerwick 1976).

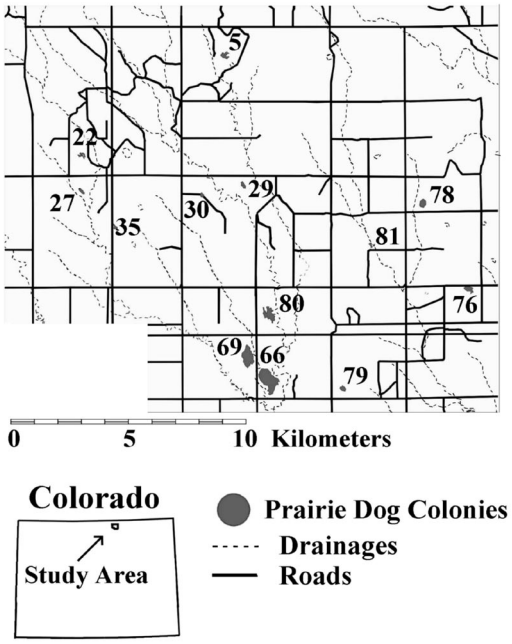

FIG. 1.—Distribution of 13 colonies of *Cynomys ludovicianus* (represented by numbers) in short-grass prairie of north-central Colorado (40°35′N, 104°45′W) from July 1997 to January 1998. The Central Plains Experimental Range comprised the northwestern portion of the area and included colonies 5–35. The remainder of the study area was the Pawnee National Grasslands, interspersed with Colorado public land and private land.

The Forest Service has monitored prairie dogs on Pawnee National Grasslands intermittently since 1967. Those surveys recorded location and active area of a colony, time since establishment, periods of inactivity (extinction), and time since recolonization after periods of inactivity (M. Ball, in litt.). The historic record of colonies on the Central Plains Experimental Range before 1997 was limited to presence or absence of prairie dog activity and 1 study (M. Ashby, pers. comm.; Koford 1958). Active area for each colony was estimated in 1997 by calculating the area bounded by active burrows along the colony edge. Sight or sound of prairie dogs, presence of fresh feces, active diggings, tracks, and clipping of adjacent vegetation distinguished active burrows. Locations of active burrows were recorded using global positioning satellites.

Tissue collection, DNA extraction, and micro-

satellite genotype scoring.—Between June 1997 and January 1998, we live trapped prairie dogs from each of 13 colonies. We recorded sex, age (juvenile, adult), reproductive status, and body mass of each captured animal. We collected the distal 8–10 mm of the tail from each individual for genetic analysis. After tissue collection, prairie dogs were marked with ear tags and released. Samples from live trapped individuals were supplemented with tissues collected from 20 carcasses of recently shot prairie dogs. We collected tissue samples of 3–16 individuals per colony, for a total of 155 samples. On average, 35 trap days were required to obtain samples from each colony. Trap success (individuals/trap day $\times$ 100) was greater for colonies on the Central Plains Experimental Range (5.1%) than for colonies on the Pawnee National Grasslands (1.7%), which we attributed to absence of recreational shooting on the Central Plains Experimental Range and timing of trapping (Roach 1999). We were only able to capture 3 individuals from colony 81 because about 6 prairie dogs inhabited the colony. We recognize that we sampled a greater proportion of smaller colonies than larger ones, but we were not able estimate the percentage of individuals sampled per colony.

Tissue samples were placed in an isotonic saline buffer (1$\times$ SSC: 0.15 M NaCl, 15 mM sodium citrate, 1 mM ethylenediamine tetraacetic acid) and stored at -80°C for DNA extraction. DNA was isolated from tail tissue by the hexadecyltrimethylammonium bromide procedure (Black and DuTeau 1997). Primers for microsatellite analysis (IGS-1, IGS-6, CGS-14, CGS-17, CGS-22, CGS-25, and CGS-26) were developed by May et al. (1997) and Stevens et al. (1997). We surveyed additional microsatellite markers (IGS-110b, IGS-BP1, CGS-12, CGS-20, and CGS-34), but those were excluded because they failed to amplify, were monomorphic, or produced too many stutter bands for accurate scoring.

Polymerase chain reaction amplification was performed with an M. J. Research PTC-100 thermocycler (MJ Research, Inc., Watertown, Massachusetts) in 25-μl volumes containing $\approx$30 ng DNA. Amplification conditions and procedures were modified slightly from those described in May et al. (1997) and Stevens et al. (1997); details were provided in Roach (1999). Amplified samples were separated by electrophoresis at 45 W for 2–7 h, depending on the length of the fragment, in 8% denaturing polyacrylamide gels (Sambrook et al. 1989). Each gel was fixed for 20 min in 2 l of 10% glacial acetic acid, and DNA was visualized with silver stain (Black and DuTeau 1997). Individuals were assigned genotypes based on banding patterns from the silver-stained gels.

Population genetic structure.—Observed genotype frequencies were tested for departures from Hardy–Weinberg equilibrium at each locus within each colony using both Levene's correction (Levene 1949) for small sample and the exact probabilities options in BIOSYS-1 (Swofford and Selander 1989). We compared observed heterozygosity of newly founded colonies (1–2 years) and older colonies (4–10 years) using the Mann–Whitney *U*-test, with each colony weighted equally. Genetic differentiation among colonies and levels of inbreeding within colonies were estimated using FSTAT 2.9.1 (http://www.unil.ch/izea/softwares/fstat.html) updated from Goudet (1995). The program used the procedure of Weir and Cockerham (1984) for multilocus estimates, which were weighted by sample size within colonies and were related to the *F*-statistics of Wright (1965) as $F = F_{IT}$ (the overall inbreeding coefficient), $\Theta = F_{ST}$ (differentiation among colonies), and $f = F_{IS}$ (the within-colony inbreeding coefficient). The 95% confidence intervals (*CI*) around *F*-statistics were estimated by bootstrapping.

We also conducted assignment tests of each individual (Cornuet et al. 1999). Assignment tests, which place each individual by maximum likelihood into a colony of origin based upon its multilocus genotype, can be used to identify immigrants within colonies (Rannala and Mountain 1997). In that analysis, we knew where an individual was captured, and called that the individual's colony of capture. We inferred each individual's colony of origin based upon similarity of its multilocus genotype to genotypes found in each colony in the study. A useful statistic for determining population structure was the proportion of individuals assigned to their colony of capture. We assigned individuals to colonies using Bayesian probabilities, using the computer program GeneClass (Cornuet et al. 1999). Simulations were also conducted to assess the probability of exclusion of each individual from each colony. Colonies with probabilities of exclusion below a threshold were excluded as colony of

origin of that individual. We used 2 threshold probabilities for excluding colonies as the origin for each individual: 1/13 = 0.077, assuming each colony was a random draw from those sampled, and 1/155 = 0.0065, where each individual was randomly drawn from the 155 samples. The stricter threshold (1/155) increased the probability of excluding the true colony of origin, while the less strict threshold (1/13) increased the probability of falsely identifying a colony as the origin of an individual.

Genetic distance and landscape effects.—Genetic distances between pairs of colonies were calculated using 3 distance measurements. First, we calculated the proportion of alleles shared between colonies (D_A—Bowcock et al. 1994). Second, chord distance (D_C) of Cavalli-Sforza and Edwards (1967) was calculated using BIOSYS-1. Takezaki and Nei (1996) found that there was a higher probability of obtaining correct tree topologies for microsatellites under the stepwise mutation model using D_C than other distance measurements. Last, we used the ratio $F_{ST}/(1 - F_{ST})$ (D_F—Rousset 1997) provided by the program GENEPOP (Raymond and Rousset 1995). This measurement has been shown to behave well in describing two-dimensional isolation by distance over relatively short spatial scales (Rousset 1997).

We compared pairwise genetic distances to pairwise geographic distances between colonies, a widely used method for describing isolation by distance among populations (Slatkin 1993). To determine whether landscape elements that facilitate dispersal better predict genetic similarity among colonies than does linear distance alone, we incorporated landscape structure into geographic distances. Those measurements included distances along drainages and along roads, because both were thought to act as potential dispersal corridors for black-tailed prairie dogs (Garrett and Franklin 1988; Garrett et al. 1982; Knowles 1985, 1986). The 4 geographic distance measurements were: linear distance, the shortest straight line between colonies; drainage distance, the shortest distance between colonies following water courses and swales only; road distance, the shortest distance given the restriction that prairie dogs must follow roads; drainage–road distance, the shortest distance given the constraint that prairie dogs must follow the shortest route on roads or drainages. The relationships between each of the 3 measurements of genetic distance (D_A, D_C, or D_F), and each of the 4 geographic distance matrices were determined using Mantel's general regression test (Manly 1991). The statistical significance of the observed Mantel correlations was determined by 10,000 random permutations of the geographic distance matrix. Significance levels were designated as the proportion of permutations in which the simulated correlation coefficient was equal to or greater than the observed value and were adjusted for multiple testing by the Bonferroni procedure for 12 tests (Sokal and Rohlf 1995).

This analysis was extended to incorporate colony age, which may have explained additional variation in the genetic distance between colonies. We calculated mean age of each pair of colonies and then included colony age in multivariate models. Genetic distance served as the dependent variable, with geographic distance and colony age as independent (predictor) variables. Models were constructed separately for each genetic distance measurement (D_A, D_C, and D_F). Model selection was carried out in a manner similar to stepwise regression, based on Akaike's Information Criterion (AIC—Akaike 1973; Burnham and Anderson 1998; Lebreton et al. 1992). This method used information theory (Burnham and Anderson 1998) and measured the relative expected difference between competing models and empirical observations. A set of candidate models was selected a priori, knowing that reality was not among them, and the model with the lowest AIC value was estimated to be closest to reality. Model selection by AIC was not a test of a hypothesis in that no null hypothesis (i.e., model) was evaluated at an arbitrary α level. Rather, AIC provided a theoretical basis for selecting the best model among a number of alternatives (Akaike 1981; Burnham and Anderson 1998).

Adjusted R^2-statistics were used to determine the degree to which landscape factors and colony age explained variation in genetic similarity among colonies. Adjusted R^2-statistic was the coefficient of determination adjusted for the number of model parameters estimated from the data (SAS Institute Inc. 1989). The best model weighed parsimony against models with more parameters (dependent variables). Calculations of AIC, AIC_c, and Akaike weights are described by Burnham and Anderson (1998). AIC-values were calculated from least squares regressions

TABLE 1.—Area, age (years since recolonization), nearest-neighbor distances, and estimates of genetic variability for each of 13 colonies of *Cynomys ludovicianus* on Central Plains Experimental Range (CPER: colonies 5–35) and the Pawnee National Grassland (PNG: colonies 66–81) in short-grass prairie of north-central Colorado. Colony statistics: n_t = sample size per population, n_s = mean sample size per locus, n_a = mean number of alleles per locus; *SE* in parentheses.

Colony no. (CPER or PNG)	Age (year)	Area (ha)	Distance to nearest colony (km)	n_t	n_s	n_a	Heterozygosity	
							Observed	Expected
81 PNG	1	1.0	2.9	3	3.0 (0.0)	3.1 (0.3)	0.52 (0.14)	0.66 (0.08)
29 CPER	1	3.1	1.8	16	15.3 (0.4)	5.1 (0.6)	0.67 (0.05)	0.70 (0.05)
22 CPER	1	3.8	1.5	11	10.6 (0.4)	4.1 (0.6)	0.56 (0.07)	0.66 (0.05)
30 CPER	2	2.2	1.8	10	10.0 (0.0)	4.3 (0.5)	0.69 (0.11)	0.61 (0.07)
35 CPER	2	2.4	2.2	15	14.9 (0.1)	3.6 (0.7)	0.52 (0.07)	0.50 (0.06)
27 CPER	2	2.8	1.5	14	13.9 (0.1)	3.0 (0.2)	0.50 (0.10)	0.51 (0.07)
5 CPER	2	6.1	5.7	15	14.9 (0.1)	3.7 (0.4)	0.59 (0.06)	0.56 (0.05)
79 PNG	4	4.0	4.3	15	14.9 (0.1)	3.9 (0.7)	0.63 (0.09)	0.61 (0.08)
76 PNG	4	7.6	4.2	12	11.9 (0.1)	3.0 (0.8)	0.39 (0.10)	0.40 (0.09)
78 PNG	4	7.9	4.2	10	9.7 (0.3)	4.4 (0.6)	0.51 (0.09)	0.63 (0.06)
80 PNG	4	18.0	2.0	8	7.9 (0.1)	4.1 (0.7)	0.65 (0.08)	0.68 (0.08)
69 PNG	8	31.9	1.4	11	10.7 (0.3)	4.1 (0.6)	0.65 (0.10)	0.66 (0.06)
66 PNG	10	52.0	1.4	15	14.7 (0.2)	4.1 (0.3)	0.71 (0.06)	0.65 (0.04)

with normally distributed errors from the equation

$$AIC_i = n \log(\sigma^2) + 2K,$$

where $\sigma^2 = \Sigma\varepsilon_i^2/n$ and ε_i were estimated residuals for a candidate model and K was the number of parameters. To adjust for small sample, we calculated each AIC_c (Hurvich and Tsai 1989) by

$$AIC_{ci} = AIC_i + [2K(K + 1)/(d - K - 1)],$$

where d was the number of pairwise distance measurements (d = 78). Smaller AIC_c-values indicate better models. Because AIC and AIC_c were on a relative scale, Burnham and Anderson (1998) recommend computing AIC differences (Δ),

$$\Delta_i = AIC_{ci} - \min AIC_{ci},$$

for each of the candidate models. As a general guideline, Δ_i-values differing by ≤ 2 had substantial support and should have received consideration in making inferences, whereas models with Δ_i-values of 4–7 had less support. Models with Δ_i-values >10 had almost no support and failed to explain substantial variation in the data.

Relative importance of various predictors was determined from estimates of Kullback–Leibler information (Burnham and Anderson 1998). This information–theoretical approach allowed estimates of the formal likelihood of each model ($\pounds[model_1 \mid x_i]$) given the data ($x_i$). Normalizing likelihoods allowed them to sum to 1 and obtain an Akaike weight for each of the fitted models. The weight of a given model is calculated as:

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

Weights were summed for all models containing a particular independent variable to provide ''strength of evidence'' for that variable. All estimates, test statistics, and AIC-values were computed using SAS (SAS Institute Inc. 1989).

RESULTS

Characteristics of colonies.—In 1997–1998, active area of the 13 colonies was 2.4–52 ha. Nearest-neighbor distances were 1.4–5.7 km, and maximum pairwise colony distance was 24 km (Table 1). Seven of the colonies had been recolonized within the

previous 1–2 years and 6 had been active the previous 4–10 years (Table 1). Colony age was correlated with colony size; colonies that were established recently were smaller in area (Pearson correlation, $r = 0.89$). Prairie dogs were intermittently seen on Pawnee National Grasslands between 1967 and 1981 but were absent at the time when regular monitoring began in 1981. Colony 66 was recolonized in 1988, and other sites on Pawnee National Grasslands were recolonized during subsequent years. On the Central Plains Experimental Range, prairie dog colonies were active between 1990 and 1993, after which all colonies became extinct because of either poisoning or plague epidemics (M. Ashby, pers. comm.). Central Plains Experimental Range colonies were recolonized in 1994–1996. In addition, 3 of the largest Pawnee National Grasslands colonies (numbers 66, 69, and 80) became extinct as a result of plague after samples were collected in 1998.

Of the 129 individuals whose sex and age could be determined at the time of sample collection, 30 were adult females, 32 were adult males, 38 were juvenile females, and 29 were juvenile males.

Population genetic structure.—The number of alleles per locus ranged from 4 to 13 for the 7 microsatellite loci. We found no evidence of deviations from Hardy–Weinberg equilibrium within colonies, and because we did not find heterozygote deficiencies in any of the colonies, it was unlikely that null alleles segregate at high frequency at the microsatellite loci surveyed in those colonies (cf. Pemberton et al. 1995).

Observed heterozygosity within colonies ranged 0.386–0.705 (Table 1) but did not differ between old and young colonies (mean heterozygosity for young and old colonies = 0.577 and 0.587, respectively; Mann–Whitney $U = 0.214$, $P = 0.830$). Hierarchical genetic analysis showed little, if any, inbreeding within colonies ($f = 0.017$) with a lower 95% *CI* below zero (Table 2). On the other hand, Θ-values revealed moderate genetic differentiation among colonies (mean $\Theta = 0.118$), with 95% *CI* well above zero.

TABLE 2.—*F*-statistics of Weir and Cockerham (1984) for each microsatellite locus from 13 colonies of *Cynomys ludovicianus* in shortgrass prairie of north-central Colorado; significance tested by bootstrapped 95% *CI*. *F* is analogous to F_{IT}, *f* is analogous to F_{IS}, Θ is analogous to F_{ST}.

Locus	*F*	*f*	Θ
IGS-1	0.070	−0.025	0.092
IGS-6	0.177	0.057	0.127
CGS-14	0.250	0.110	0.157
CGS-17	0.148	0.030	0.122
CGS-22	0.125	0.004	0.121
CGS-25	−0.032	−0.105	0.066
CGS-26	0.125	0.008	0.118
Mean	0.133	0.017	0.118
95% *CI*	0.065–0.188	−0.034–0.060	0.096–0.135

Assignment tests reflected a similar and moderate level of genetic differentiation. Using Bayesian probabilities (Cornuet et al. 1999), 95 of 155 individuals (61.3%) were assigned to their colony of capture. With greater genetic differentiation, a higher number of individuals would be assigned in this way. We determined age and sex of 129 individuals. Of those, the proportion assigned to the colony of capture did not differ between adult females (21/30), adult males (19/32), juvenile females (23/38), and juvenile males (23/29; $\chi^2 = 3.64$, *d.f.* = 3, $P > 0.10$). Exclusion analysis, in which individuals could be statistically excluded from colonies, showed similar results. At the strict threshold of exclusion (probability of exclusion of a colony ≥ 1/155 = 0.0065), only 27 individuals were excluded from all colonies except their colony of capture. Ninety-nine individuals could not be excluded from either the colony of capture or several other colonies. Fifteen individuals were excluded from the colony of capture, but not from other colonies. Fourteen individuals were excluded from all colonies, implying they migrated into the area from colonies that had not

TABLE 3.—Mantel correlations between each of 3 pairwise estimates of genetic distance and each of 4 measurements of geographic distance for colonies of *Cynomys ludovicianus*. D_A denotes the proportion of alleles shared between colonies, D_C denotes Cavalli-Sforza and Edwards' chord distance between colonies, and D_F denotes $F_{ST}/(1 - F_{ST})$ distance measurement between colonies.

Genetic distance index	Mantel correlation			
	Drainage distance	Road distance	Drainage-road distance	Linear distance
D_A	0.36**	0.14	0.25**	0.16
D_C	0.41**	0.23**	0.23**	0.20*
D_F	0.43**	0.22*	0.24**	0.22*

* $P \leq 0.05$, ** $P \leq 0.002$.

been sampled. At the less strict threshold of exclusion (probability of exclusion $\geq 1/13 = 0.077$), 38 individuals were excluded from all colonies other than the colony of capture. Fifty-nine individuals could not be excluded from either the colony of capture or several other colonies. Twenty-four individuals were excluded from the colony of capture, but not from other colonies. Thirty-four individuals were excluded from all of the sampled colonies. With greater differentiation and less gene flow, it should have been possible to exclude all other colonies, other than the colony of capture, as the origin of each individual.

Finally, exclusion of individuals from their colony of capture did not differ between adult females, adult males, juvenile females, or juvenile males at either the strict threshold ($\chi^2 = 1.54$, *d.f.* = 3, $P > 0.50$) or the less strict threshold ($\chi^2 = 3.21$, *d.f.* = 3, $P > 0.10$).

Genetic distance and landscape effects.—Mantel correlations between estimates of pairwise genetic distances and pairwise geographic distances were positive, indicating isolation by distance between colonies. Correlations were greater for drainage distance than for the other 3 geographic distances (Table 3). AIC model selection for chord distance between colonies indicated that age and drainage are important predictors of genetic distance. The AIC model that included drainage distance and age had the highest R^2, lowest AIC_c, and the highest weight (w_i), and thus was selected as the best model (Table 4). Detailed results for chord distance (D_C) are presented; results using other genetic distance measures (D_A, D_F) were similar but are not reported. Comparison of AIC_c weights (w_i) for the 5 predictor variables for all genetic distances highlighted the importance of colony age and drainage distance as predictor variables and provided weak support for linear, road,

TABLE 4.—Results of model selection based on Akaike's Information Criterion (AIC) for isolation by distance of colonies of *Cynomys ludovicianus* in short-grass prairie of north-central Colorado as a function of Cavalli-Sforza and Edwards' chord distance. K = number of parameters, AIC_c = Akaike's Information Criterion, Δ_i = differences in AIC_c-values, w_i = AIC_c weights. Other genetic distance measures (D_A, D_F) showed similar results.

Model parameters	K	Adjusted R^2	AIC_c	Δ_i	w_i
Drainage distance and age	2	0.159	−455.14	0	0.529
Age	1	0.12	−452.87	2.33	0.17
Road distance and age	2	0.13	−452.17	2.97	0.12
Linear distance and age	2	0.12	−451.55	3.59	0.09
Drainage–road distance and age	2	0.12	−451.29	3.85	0.08
Drainage distance	1	0.05	−446.86	8.29	0.01
Road distance	1	0.02	−444.02	11.12	0.00
Linear distance	1	0.00	−442.78	12.36	0.00
Drainage–road distance	1	0.00	−442.76	12.39	0.00

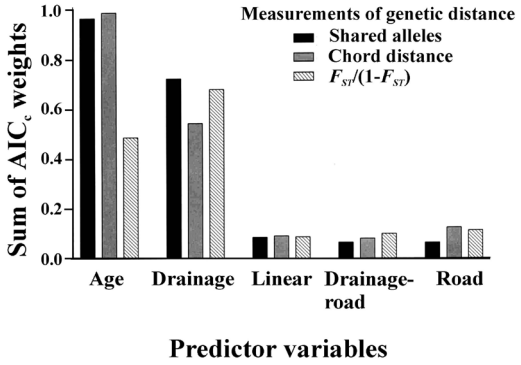

FIG. 2.—Relative importance of 5 predictors of 3 different measurements of genetic distance (proportion of shared alleles, Cavalli-Sforza and Edwards' chord distance, $F_{ST}/[1 - F_{ST}]$) between colonies of *Cynomys ludovicianus* in short-grass prairie of north-central Colorado. Relative importance was measured as the sum of Akaike's Information Criterion weights.

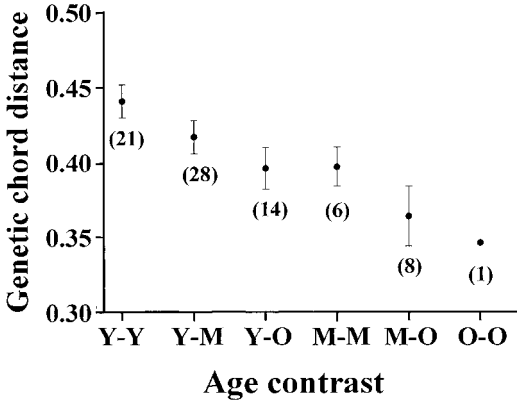

FIG. 3.—Mean (±*SE*) of Cavalli-Sforza and Edwards' genetic chord distance D_C between pairs of colonies of *Cynomys ludovicianus* characterized as young (Y), medium (M) or old (O). Y = colony age < 2 years; M = colony age of 4 years; O = colony age > 8 years. Values in parentheses indicate the number of pairwise comparisons for each mean.

and drainage–road distances as predictors of genetic distance (Fig. 2).

We calculated the mean (±*SE*) of chord distance (D_C) between pairs of colonies of different ages and found that younger colonies were more genetically distant than older colonies (Fig. 3). Differences in genetic distance between small young colonies likely reflected the sampling process of recolonization by a small number of dispersers, and as colonies became older, they became more genetically similar because dispersers genetically homogenized colonies after the time they were established.

DISCUSSION

Population genetic structure.—The level of genetic differentiation in our study (Θ = 0.118) is similar to those reported in other population genetic studies of black-tailed prairie dogs (Chesser 1983; Daley 1992; Foltz and Hoogland 1983), other prairie dog species (McCullough and Chesser 1987; Travis et al. 1997), and several other social sciurids of North America (Dobson 1994; Gavin et al. 1999; Schwartz and Armitage 1980). This level of genetic differentiation, both within and between colonies of social ground squirrels, has been attributed to effects of matrilineal social structure (Chesser 1991). Concordance of estimates between previous prairie dog studies and ours are surprising, given that previous estimates were from areas where plague epizootics had not yet been recorded (New Mexico—Chesser 1983) or have never been recorded (South Dakota—Daley 1992; Foltz and Hoogland 1983). This suggests that extinction and recolonization of colonies over the last 10 years has not increased genetic differentiation among colonies on the Pawnee National Grasslands or Central Plains Experimental Range of north-central Colorado. However, this also underscores a critical aspect of expected genetic differentiation within metapopulations; increased differentiation is only expected in metapopulations when initial colonization is much different than subsequent dispersal (Barton and Whitlock 1997; Wade and McCauley 1988).

Our data suggest that dispersal occurs on a regular basis among prairie dog colonies after initial colonization. First, we found few unique alleles within colonies, despite

the large number of alleles identified at each of the 7 microsatellite loci. Second, no evidence was obtained in support of founder effects or genetic drift within small new colonies; observed heterozygosity did not differ between old and young populations. Heterozygosity estimates from small samples like these have large standard errors, and larger samples may detect genetic effects of bottlenecks. Third, assignment and exclusion tests showed that >30% of individuals were immigrants or the offspring of immigrants, and probability of assignment to the colony of capture did not differ between males and females or juveniles and adults. Finally, continuous dispersal among colonies can explain the relationship between colony age and genetic distance (Fig. 3). Recently colonized populations are more genetically distant from each other because they are not in migration-drift equilibrium. With high dispersal after initial recolonization, alleles will continue to arrive, so that over time, prairie dog colonies will become more genetically similar, both in terms of which alleles are present and frequencies of those alleles. Taken together, these results suggest that colonies of black-tailed prairie dog are spatially isolated and genetically differentiated but dispersal between colonies continues after initial colonization.

Landscape effects.—Overall, the best-fitting isolation by distance model explained relatively small amounts of the total variance in genetic distance ($R^2 \approx 0.16$), indicating that some unmeasured features of either prairie dogs or their habitats may increase predictability of dispersal between colonies. Prairie dog dispersal distances also may be more skewed than we have assumed in these models, meaning that the relationship between predictor variables and genetic distance may not be linear. Models fitting polynomial (curvilinear) predictors or genetic distances may provide better fits (higher R^2), but our data are not sufficient to adequately test those models. Regardless, AIC analysis shows that 2 geographic distance measurements, linear distance and road distance between colonies, have no explanatory power (Fig. 2). Isolation by distance via linear distance assumes that habitat matrix between colonies is homogeneous and that distance between colonies is the only cost associated with dispersal (Wiens 1996). Also, little evidence supports the contention that roads act as primary dispersal corridors, which seems to contradict other studies that report the importance of roads for prairie dog dispersal (Knowles 1985, 1986; Koford 1958). Prairie dogs traveling along roadways likely suffer appreciable mortality by automobiles (Reading and Matchett 1997) and high numbers of predators. However, researchers typically travel on roads, so that their importance as corridors for dispersal may have been previously overestimated for prairie dogs.

Drainage distance between black-tailed prairie dog colonies is an important predictor of dispersal. The habitat between colonies is heterogeneous, and dispersal and gene flow will be related to both colony isolation and usable habitat between colonies in the landscape. Detectability of colonies by prairie dogs, proximity of a colony to favorable habitat, and possible habitat barriers might influence dispersal in black-tailed prairie dogs. Natural drainages may function as dispersal corridors because colonies typically are located in swales and seasonally wet lowlands. As a consequence, dispersing prairie dogs have a greater likelihood of encountering a colony along drainage systems (Garrett and Franklin 1988). The importance of drainages as dispersal corridors also could result from habitat selection based on vegetation, cover, and differential survival of dispersers in these habitats.

Implications for conservation.—A metapopulation can persist as long as rate of recolonization exceeds rate of extinction, even though no local population may survive continuously over time (McCullough 1996). Ability of prairie dogs to disperse

among colonies is critical because recolonization after local extinction is essential for regional persistence of metapopulations (Fahrig and Merriam 1994; Hanski 1999; Hanski and Simberloff 1997; Harrison and Taylor 1997). Our data suggest that potential dispersal corridors, such as drainages, should be maintained to ensure recolonization of unoccupied colonies and continual dispersal among colonies. In terms of genetics, extinction and recolonization of colonies will not increase genetic differentiation of colonies of black-tailed prairie dogs as long as dispersal and gene flow after recolonization remain high. Greater isolation and loss of dispersal corridors should increase genetic differentiation between colonies and decrease genetic diversity within colonies, including overall loss of alleles via genetic drift, and possibly, population declines caused by inbreeding depression (Hedrick and Kalinowski 2000).

For many species, it is assumed that smaller populations within a metapopulation are likely to disappear first, as suitable habitat is lost and isolation is increased. Longer persistence of large populations is expected (Hanski 1999), but this assumption does not consider effects of disease on metapopulation structure (Hess 1996). Recent studies in Oklahoma demonstrate that small and isolated colonies of prairie dogs are less likely to persist than large colonies when plague is absent (Lomolino and Smith 2001). When plague is present, however, persistence of both large and small colonies is reduced (Lomolino and Smith 2001). Thus, long-term persistence of prairie dog metapopulations will depend on the interplay between extinctions as a result of small colony size, loss of colonies of all sizes because of plague epidemics, and subsequent dispersal and recolonization. In the time since we sampled our study sites in Colorado in 1997–1998, 3 of the largest colonies have been decimated by plague (numbers 66, 69, and 80; Fig. 1); other colonies have persisted. This implies that large prairie dog colonies may be more susceptible to plague epidemics, which would be expected if high densities of prairie dogs lead to greater exchange of plague-infected fleas and increase rate of spread of plague (Barnes 1993). At present, however, it is difficult to predict which colonies will persist because we do not have a firm understanding of how plague is spread within and between colonies (Barnes 1993; Cully 1993; Koford 1958; Rayor 1985).

Management of black-tailed prairie dogs should be based on regional persistence of the species and not on a colony-by-colony basis. Management of individual colonies will also affect neighboring colonies. Because accurate predictions of persistence of any given prairie dog population is not currently possible, colonies must be connected by dispersal so that the negative impact of extinction may be counterbalanced by recolonization.

Our study provides empirical support for the metapopulation concept, which plays a pivotal role in strategies of conservation when anthropogenic habitat loss and fragmentation are substantial (Driscoll 1998; Harrison 1994; McCullough 1996). Moreover, dispersal between isolated colonies is not based on intercolony distance alone but is facilitated by dispersal corridors. Through grazing and burrowing activities, prairie dogs play a critical role in grassland ecosystems by altering vegetative structure, plant community dynamics, and nutrient cycling (Whicker and Detling 1988). Burrows constructed by prairie dogs provide habitat for other grassland animals, and prairie dogs themselves are major prey of many raptorial birds and carnivorous mammals, including the endangered black-footed ferret (*Mustela nigripes*—Kotliar et al. 1999; Stapp 1998). Understanding the dynamics of remaining prairie dog colonies, estimated to occupy $<10\%$ of their historic range (Anderson et al. 1986) in increasingly fragmented landscapes may be crucial not only for their survival but also for maintenance of biodiversity and functioning ecosystems in the grasslands.

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