

BREEDING GROUPS AND GENE DYNAMICS IN A SOCIALLY STRUCTURED POPULATION OF PRAIRIE DOGS

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Genetic substructuring of a colony of black-tailed prairie dogs (*Cynomys ludovicianus*) was examined using three different sources of information: allozyme alleles, pedigrees, and demography (a "breeding-group" model based on mating and dispersal patterns). Prairie dogs and their social breeding groups (called "coteries") were studied under natural conditions during a 15-year period. Prairie-dog coteries exhibited substantial genetic differentiation, with 15–20% of the genetic variation occurring among coteries. Mating patterns within the colony approximated random mating, and, thus, mates tended to originate from different coteries. Social groups of black-tailed prairie dogs resulted in genetic substructuring of the colony, a conclusion that was supported by estimates from allozyme alleles and colony pedigrees. Predictions of the breeding-group model also were consistent with and supported by estimates from allozyme and pedigree data. Some methodological problems were revealed during analyses. Although individuals of all ages usually are pooled for biochemical estimates of among-group genetic differentiation, our estimates of among-coterie variation from allozyme data were somewhat higher for young than for older prairie dogs, perhaps due to sampling effects caused by mating patterns and infanticide of offspring. Pedigree estimates of among-coterie genetic differentiation were significantly positive for young prairie dogs, adult females, and adult males. Those estimates were always more accurate for the offspring generation, however, because pedigree data were always more complete for young and genetic differences among coteries were diluted by virtually complete dispersal of males away from their natal coteries.

Key words: allozymes, breeding groups, demography, gene dynamics, pedigrees, black-tailed prairie dogs

Social behaviors that influence breeding patterns may have substantial influences on gene dynamics within populations (Chesser, 1991a, 1991b; Chesser et al., 1993; Sugg and Chesser, 1994; Sugg et al., 1996). In particular, social breeding groups of many mammalian species are composed of close relatives and, thus, should exhibit genetic substructuring due to kinship. In these species, females are often philopatric (Dobson, 1982; Greenwood, 1980), and philopatry leads to two related processes that enhance genetic similarity of individuals in social

breeding groups. First, females that remain in their natal home range may often be sisters or other close kin. Second, when females occur in local breeding groups, they are more likely to mate with the same male, because individual males should monopolize matings whenever possible (Emlen and Oring, 1977). Thus, offspring in social breeding groups are likely to exhibit a high degree of kinship because they have the same father and mothers are closely related. A breeding group, therefore, may differ genetically from other breeding groups.

Theoretical models suggest the likelihood of genetic substructuring of mammalian populations through social breeding groups (Chesser, 1991a, 1991b; Chesser et al., 1993; Sugg and Chesser, 1994), although empirical demonstrations are few (cf. Long, 1986; Patton and Feder, 1981; Pope, 1992; Schwartz and Armitage, 1980; Sugg et al., 1996). Three methods of estimation of the genetic composition of populations may be used to examine the influence of social breeding groups. First, biochemical markers such as allozyme alleles, DNA restriction fragments, or DNA sequences may be examined to indicate genetic similarities within and among breeding groups, following similar methods to those used for spatially separated populations (Chesser, 1983; Daly and Patton, 1990; Packer and Pusey, 1993; Patton and Feder, 1981). Second, pedigrees describe breeding history within populations (Wright, 1969) and, thus, may be used to indicate genetic structuring via patterns of kinship within and among social breeding groups. Finally, genetic structure of populations can be inferred from demographic "breeding-group" models that predict gene dynamics, under assumptions of particular patterns of mating and dispersal (Chesser, 1991a, 1991b; Chesser et al., 1993; Sugg and Chesser, 1994; Sugg et al., 1996).

Previous investigators have not been able to compare the three methods of estimating gene dynamics with data from the same population. Thus, compatibility of methods and problems involved with their application are virtually unknown. Our purpose was to examine gene dynamics of a highly social mammalian species, the black-tailed prairie dog (*Cynomys ludovicianus*). Prairie dogs live in social breeding groups called coterie (Hoogland, 1995; King, 1955). Several coterie together form semi-isolated aggregations called wards and largely isolated subpopulations called colonies (of one to several wards). Colonies are patchily distributed across a regional landscape of short-grass prairie. Prairie dogs exhibit a

variety of social behaviors, such as cooperative defense of coterie territories (Hoogland, 1981), vocal predator alarm warning (Hoogland, 1983), allogrooming (Hoogland, 1995), and even alloparenting (Hoogland et al., 1989). Prairie dog coterie usually are composed of two to four philopatric adult female kin, one or two adult males (sometimes coterie males also are relatives—Hoogland, 1995), and yearling and young offspring. Coterie may exhibit significant differentiation of allozyme alleles, although accurate identification of coterie membership is critical to estimation of genetic substructure of prairie dog colonies (Chesser, 1991b). Taken together, this evidence indicates that the black-tailed prairie dog is an appropriate species for testing the importance of social breeding groups on gene dynamics.

We examined if dispersal and mating patterns of prairie dogs resulted in significant substructuring of a large colony into genetically distinct coterie. Our study colony was one of the most extensively researched populations of any mammalian species and was observed during 15 years under natural field conditions (Hoogland, 1995). In addition to a wealth of information on behavior and natural history, this intensive long-term field study gathered data appropriate to biochemical (from allozyme alleles), pedigree, and breeding-group model estimates of gene dynamics. Thus, we used all three methods to estimate genetic substructuring of the prairie dog colony. We examined fixation indices (F -statistics—Wright, 1965, 1969) and predicted that they would reveal significant genetic differentiation among coterie. Further, we compared the three methods of estimation of gene dynamics. Because the breeding-group model predicts asymptotic fixation indices under ideal conditions that are probably seldom met in the field, we tested model predictions against estimated gene dynamics from allozyme alleles and pedigrees. Finally, we identified general problems and recommended procedures for future applications

of the three methods of estimating gene dynamics of social breeding groups.

MATERIALS AND METHODS

Black-tailed prairie dogs were studied in the field from 1975 through 1989 at Wind Cave National Park, Hot Springs, Custer Co., South Dakota (Hoogland, 1995). The study colony (1,300 m above sea level, ca. 1 km southwest of Rankin Ridge) occupied ca. 6.6 ha of meadowland surrounded by coniferous woodland and additional meadow and measured ca. 500 m (N–S) by 130 m (E–W). Numbers of adult and yearling prairie dogs in the colony during May of each year averaged 123 and ranged from 92 to 143. The annual number of juveniles weaned in the colony averaged 88 and ranged from 41 to 133. Black-tailed prairie dogs are diurnally active, and, unlike most other marmotine rodents, they do not hibernate. Males and females usually begin reproducing at 2 years of age, but females occasionally breed as yearlings. Mating occurs during February and March, and weaning of offspring occurs shortly after emergence of juveniles from natal burrows ca. 76 days later in May and June.

Fieldwork was conducted by J. L. Hoogland and 112 field assistants. Adult prairie dogs were captured in live traps baited with whole oats, and juveniles were captured in unbaited traps. Every prairie dog at the study colony was captured at least once each year. Shortly after capture, individuals were weighed, examined for sexual condition and ectoparasites, fitted with numbered metal ear tags for permanent recognition, given distinctive dye-markings to aid behavioral observations, and released at the point of capture. Subsequently, marked prairie dogs were observed from towers at the edge of the study colony. Evidence of underground matings suggested possible fathers, and paternity was confirmed by subsequent likelihood of paternity analyses using electrophoretic data from all mothers, juveniles, and possible fathers (Foltz and Hoogland, 1981; Hoogland and Foltz, 1982). Virtually all litters that survived until emergence from the natal burrow could be assigned unambiguously to their mother with behavioral observations.

Blood samples were collected from all of the prairie dogs in the colony between 1979 and 1988 ($n = 10$ years). Horizontal starch-gel electrophoresis was performed (Harris and Hopkin-

son, 1976; Selander et al., 1971), with staining for four polymorphic loci that were examined throughout the 10 years: transferrin (three alleles); nucleoside phosphorylase (three alleles, ECN 2.4.2.1); 6-phosphogluconate dehydrogenase (two alleles, ECN 1.1.1.44); phosphoglucomutase-2 (four alleles, ECN 2.7.5.1). In 1979, however, only transferrin and nucleoside phosphorylase had sufficient sample sizes for analyses. F -statistics were calculated for each electrophoretic locus using standard methods (Nei, 1977; Wright, 1965, 1978). Coterie were used as population subdivisions, so that F -statistics were calculated relative to breeding groups. This procedure yields results from standard F -statistics procedures (that produce estimates of F_{IS} , F_{IT} , and F_{ST}) that correspond to breeding-group F -statistics (hereafter designated F_{IL} , F_{IS} , and F_{LS} , respectively). These fixation indices are related by the formula:

$$(1 - F_{IS}) = (1 - F_{LS})(1 - F_{IL}) \quad (1)$$

Pedigrees were used to estimate average correlation of genes for offspring in each year: within individuals (the mean degree of inbreeding = F), between different individuals in the same coterie (coancestry within coterie = θ), and between different individuals from different coterie (α). Each individual captured from the population was assigned a unique identification number, year born, and coterie designation for each year alive. Identification number of the sire and dam was noted for each progeny born. If the sire or dam was unknown, as for immigrants and for individuals which were already present in the population at the beginning of the study (1975), that sire or dam was assigned a value of zero with other colony residents. The coancestry between any pair i, j of individuals was determined as:

$$\theta_{ij} = \frac{1}{4}(\theta_{s_i s_j} + \theta_{s_i d_j} + \theta_{s_j d_i} + \theta_{d_i d_j}), \quad (2)$$

where subscripts S and D denoted sire and dam, respectively, for the i th and j th individual. This expression was used to describe the way in which coancestry accumulates over the generations. The inbreeding coefficient of a progeny was equal to the coancestry of its parents calculated as:

$$F_i = \theta_{s_i d_i} \quad (3)$$

The weighted average coancestry within co-

teries each year was determined by the summed pair-wise values from the pedigree for each coterie multiplied by the size of the i th coterie (N_i) relative to the total size of the population (N_T) (c.f. Chesser, 1991a, 1991b; Cockerham, 1967, 1969, 1973):

$$\bar{\theta} = \sum_{i=1}^s \frac{N_i}{N_T} \sum_{j=1}^{N_i-1} \sum_{k=j+1}^{N_i} \theta_{j,k} \quad (4)$$

Similarly, average correlation of gene frequencies among groups (α) was determined from the mean coancestry of all individuals in different coteries:

$$\bar{\alpha} = \frac{\sum_{i=1}^{s-1} \sum_{j=1}^{N_i} \sum_{k=i+1}^s \sum_{m=1}^{N_k} \theta_{j,m}}{\sum_{i=1}^{s-1} \sum_{k=i+1}^s N_i N_k} \quad (5)$$

In this calculation, s was the number of coteries (i.e., breeding groups) in the colony. Lastly, the average inbreeding coefficient was determined over all individuals observed in the population (N_T) for a given year and was calculated as:

$$\bar{F} = \frac{1}{N_T} \sum_{i=1}^{N_T} F_i \quad (6)$$

Average values of gene correlations in each year were substituted from equations 4, 5, and 6 into the following equations to determine F -statistics for the rates of inbreeding of individuals with respect to the coterie (F_{IL}), individuals relative to the colony (F_{IS}), and coteries relative to the colony (F_{LS}) for each year from 1979 to 1988 (Chesser, 1991a, 1991b; Chesser et al., 1993; Sugg and Chesser, 1994):

$$F_{IL} = \frac{F - \theta}{1 - \theta} \quad F_{IS} = \frac{F - \alpha}{1 - \alpha}$$

$$F_{LS} = \frac{\theta - \alpha}{1 - \alpha} \quad (7)$$

We used the breeding-group model of Sugg and Chesser (1994) for making demographic predictions of fixation indices because that model allowed for multiple paternity within litters and among litters of individual females in different years. The model required estimates of several variables. Number of coteries (s) and numbers of adult males (m) and females (n) in a coterie were averaged over all years of the study. Other variables were based only on the lifetime of individuals that produced progeny that, in turn, survived to reproduce. Because the

life span of adult female prairie dogs is ca. 5 years and most do not mate until they are 2 years old, data from the last 2 years of the study (1987 and 1988) were not used. We estimated the mean (k) and variance (σ_k^2) of the number of progeny that survived to maturity that were produced by females, the mean (b) and variance (σ_b^2) of the number of females mated by each male that produced surviving progeny, the mean (p) and variance (σ_p^2) of the number of surviving progeny of a female sired by a single male, and the average number of successful males mated by each female (ℓ). Finally, dispersal of males (d_m) and females (d_f) was calculated as the proportion of individuals that moved from their natal coterie and successfully reproduced in other coterie. Dispersal within the colony was estimated using all years of data for individuals of known natal location.

Estimated variables were used to calculate breeding parameters (Chesser et al., 1993; Sugg and Chesser, 1994). The first parameter (ϕ_m) defined the probability that two randomly chosen progeny in the same breeding group (coterie) were sired by the same male. That parameter estimated the genetic polygyny of the average breeding group and was calculated as:

$$\phi_m = \frac{m[\sigma_b^2 + b(b-1)]}{\ell n(n-1)} \quad (8)$$

The second parameter (ϕ_i) defined the probability that two randomly chosen progeny in a coterie shared the same mother and may be termed the probability of shared maternity. That parameter was:

$$\phi_i = \frac{\sigma_k^2 + k(k-1)}{k(kn-1)} \quad (9)$$

The final breeding parameter (ϕ_w) estimated the probability that two randomly chosen progeny, produced during the entire lifetime of a female, were sired by the same male. That parameter indicated the probability of single paternity over a female's lifetime reproductive success (in the case of prairie dogs, multiple paternity primarily resulted from mating with different males in different years), calculated as:

$$\phi_w = \frac{\ell[\sigma_p^2 + p(p-1)]}{k(k-1)} \quad (10)$$

Breeding parameters, numbers of adults, and dispersal data were used in a series of transition equations to determine the expected change in

gene correlations between generations (for transition equations—Chesser, 1991a, 1991b; Chesser et al., 1993; Sugg and Chesser, 1994). The general approach of the transition equations was to use matrix multiplication to predict gene correlations within and among offspring from those of their parents, given patterns of demography and dispersal that commonly occur. The transition equation took the form: $V_{t+1} = TV_t + C$. In this equation, V_{t+1} and V_t are vectors of gene correlations at times $t+1$ and t , T is a matrix that incorporates the information about numbers of adult males and females, mating and survival patterns (from the previous ϕ values), and dispersal, and C is a vector of constants.

We first assumed that the population started with unrelated individuals (i.e., that F , θ , and α were initially zero), and expected gene correlations were obtained for generations subsequent to the initial generation until genetic equilibrium was approximated. In turn, gene correlations were used to determine asymptotic fixation indices of F_{IL} , F_{IS} , and F_{LS} from equations 7. To indicate variation due to demographic changes over the years, fixation indices were estimated for each year using annual values of numbers of adult males, adult females, and coteries from 1977 through 1988 ($n = 12$ years) with the study-long average values of mating patterns and dispersal.

RESULTS

For young black-tailed prairie dogs, significant genetic differentiation in allozyme alleles occurred among coteries in all years and averaged 25.0% ($F_{LS}-t = 19.2$, $n = 10$ years, number of young = 38 in 1988 to 133 in 1986, $P < 0.0001$, Fig. 1a). Older prairie dogs exhibited somewhat lower among-coterie allelic differentiation, averaging 16.3% over the 10 years ($F_{LS}-t = 27.6$, $n = 10$ years, number of individuals = 98 in 1985 to 145 in 1983, $P < 0.0001$). The difference between young and older prairie dogs was significant (Wilcoxon $z = 2.68$, $n = 10$, $P < 0.01$). We pooled allozyme data over all prairie dogs and years and found that allelic differentiation among coteries averaged 16.6%, similar to the pattern for older, but not young prairie dogs ($F_{LS}-t = 21.3$, $n = 10$ years, number of

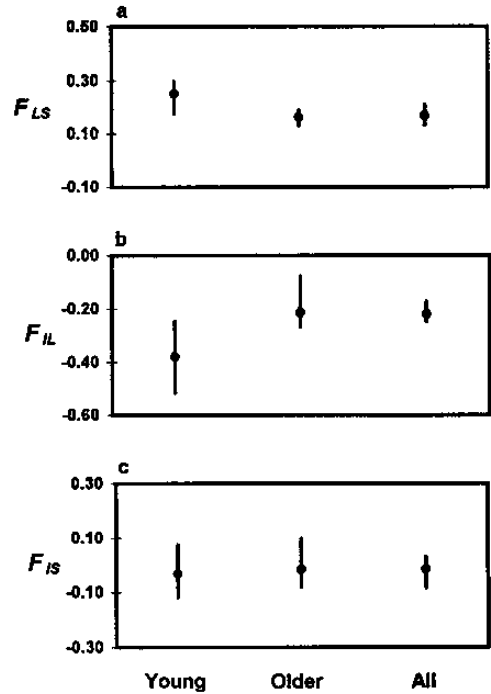


FIG. 1—Means and ranges (of annual estimates from 1979 to 1988) of fixation indices from allozyme data that were gathered on young, older, and all (pooled) black-tailed prairie dogs (coterie were nested within a colony that was studied during 1979 to 1988). a) F_{LS} , b) F_{IL} , and c) F_{IS} .

individuals = 158 in 1988 to 258 in 1981, $P < 0.0001$).

Means of F_{IL} over the 10 years of the study were -0.380 for young prairie dogs, -0.213 for older individuals, and -0.218 for all prairie dogs combined ($t = 13.0$, 12.2 , and 29.9 , respectively, all $P < 0.0001$, Fig. 1b). The difference between young and older prairie dogs was significant (Wilcoxon $z = 2.78$, $n = 10$, $P < 0.01$). Ranges of annual values of young and older individuals were greater than that for the pooled samples. Values of F_{IS} were slightly negative for young, older, and the pooled sample of prairie dogs ($\bar{X} = -0.032$, -0.015 , and -0.014 , respectively, all $P > 0.05$, Fig. 1c). Because individuals of all ages commonly are pooled in allozyme studies (Chesser, 1983; Dobson, 1994; Hoogland and Foltz,

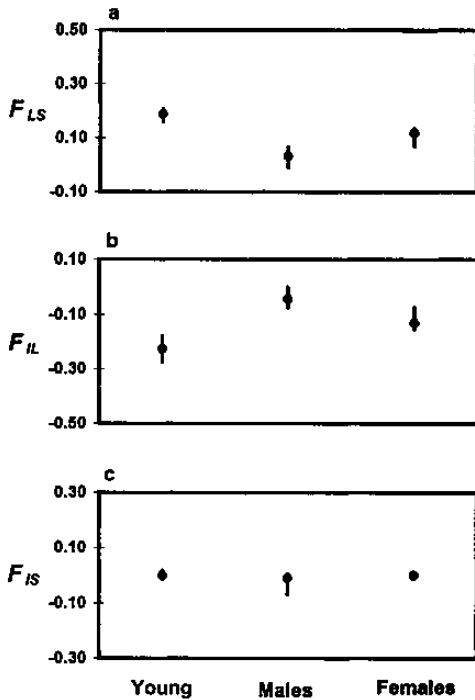


FIG. 2—Means and ranges (of annual estimates from 1979 to 1988) of fixation indices from pedigree data that were gathered on young, adult male (labeled “males”), and adult female (labeled “females”) black-tailed prairie dogs. a) F_{LS} , b) F_{IL} , and c) F_{IS} .

1983), further comparisons of results were made with samples from combined young and older prairie dogs within each year of the study. The estimate of among-coterie genetic differentiation was conservative with respect to the null hypothesis of no genetic difference among coterie (Fig. 1).

Pedigree analyses also indicated substantial genetic differentiation among prairie dog coterie (Fig. 2a). Mean genetic differentiation during the study averaged 18.7% for young prairie dogs, 3.1% for adult males, and 11.8% for adult females ($t = 33.3, 4.7, \text{ and } 17.5, P < 0.0001, 0.01, \text{ and } 0.0001$, respectively). Adult males were defined as those older than yearlings; adult females were defined as those older than young, because over one third of yearling females mate. Values of F_{IL} averaged -0.226 for young prairie dogs, -0.042 for

adult males, and -0.132 for adult females during the study ($t = 25.5, 5.9, \text{ and } 16.7, P < 0.0001, 0.001, \text{ and } 0.0001$, respectively, Fig. 2b). Values of F_{IS} averaged 0.000 for young, -0.010 for adult males, and 0.001 for adult females ($P > 0.05$, Fig. 2c). Combining pedigree data from breeding and nonbreeding adults with offspring was expected to dilute the magnitude of fixation indices (Chesser, 1991a; Spielman et al., 1977), so further comparisons of results were made from pedigrees of offspring.

Adult females practiced infanticide within their home coterie against the offspring of their reproductive female kin (Hoogland, 1985, 1995). The proportion of litters that were victimized completely by this type of infanticide varied from 5 to 26% among the years when infanticide by coterie females was studied (1981–1988). In years when complete litters were killed by marauders, relatedness among coterie offspring was expected to increase because a higher proportion of offspring would be siblings. This conjecture was supported by significant associations between the annual frequency of complete infanticide of litters and annual estimates of F_{LS} from allozyme and pedigree data ($r_s = 0.738$ and 0.857 , respectively, $n = 8$ years, $P = 0.04$ and < 0.01). In addition, similar but negative associations of complete litter infanticide and annual estimates of F_{IL} from allozyme and pedigree data approached significance ($r_s = -0.714$ and -0.667 , respectively, $n = 8$ years, $P = 0.05$ and 0.07).

Between 1976 (when pedigrees began to develop)–1988, there was an average of 20.83 coterie (s) and the number of coterie ranged from 15 to 26. Between 1977 (after the first year)–1988, there was an average of 2.65 adult females (n) and 1.38 adult males (m) in each of the coterie. Mean values of n ranged from a yearly maximum of 3.09 (1977) to a yearly minimum of 2.24 (1982). Mean values of m ranged from a maximum of 2.21 (1983) to a minimum of 0.74 (1988). The mean number of progeny produced by a female (k) was 2.00 (range = 1–4), and the

variance in this number (σ_k^2) was 1.44. Mean (b) and variance (σ_b^2) in the number of females mated by a male were 1.68 (range = 1–3) and 0.66, respectively. Average number of successful mates a female had (ℓ) was 1.25 (range = 1–3). The average number of progeny produced by a female that shared the same father (p) may be estimated as k/ℓ and was 1.60, with a variance (σ_p^2) of 0.64. Finally, the male (d_m) and female (d_f) dispersal rates were 1.00 and 0.02, respectively. Using those estimates, the degree of genetic polygyny (ϕ_m) was 0.46, the probability of shared maternity (ϕ_f) was 0.40, and the probability of single paternity (ϕ_w) was 1.00.

Those parameters were entered into transition equations of Sugg and Chesser (1994). Because natural-history parameters were averaged across the entire period of study, a single asymptotic value of each fixation index was produced: the breeding-group model predicted F_{LS} at 0.157 indicating ca. 16% genic differentiation among coterries, F_{IL} at -0.184, and F_{IS} at 0.002 (Fig. 3). Ranges of annual model values that were based on annual demographic patterns were similar to estimates from allozyme data and pedigrees for F_{LS} and F_{IL} , but not F_{IS} , which exhibited little variation. Overall asymptotic model values of F_{LS} , F_{IL} , and F_{IS} were somewhat more conservative (closer to zero) than means of allozyme and pedigree estimates (Fig. 3), although all values of F_{IS} were close to zero.

DISCUSSION

Our primary purpose was to examine if social breeding groups, as represented by coterries of black-tailed prairie dogs, created genetic substructuring within the population. Before this question could be examined, however, we had to decide which results to compare. Although we had an extremely large sample of hundreds of prairie dogs, it was spread over 10 years of sampling and an average of ca. 21 coterries/year. Thus, some variation in results might be expected. In addition, each method of estimation of fixation indices was based on dif-

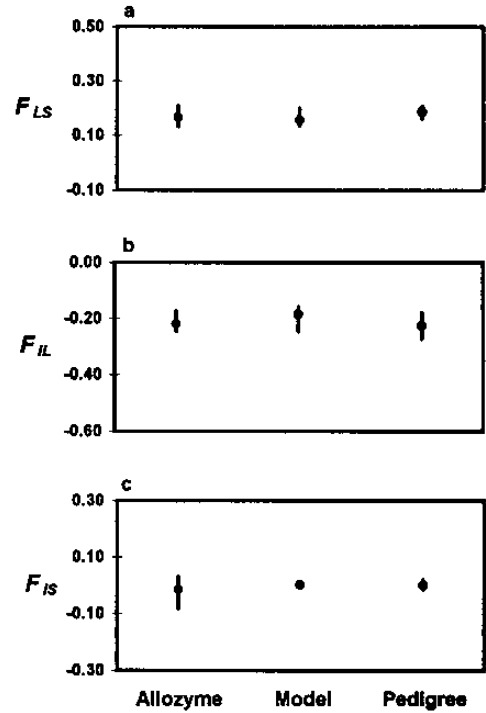


FIG. 3.—Means and ranges (of annual estimates from 1979 to 1988) of fixation indices from allozyme, pedigree, and demographic (breeding-group model) data that were gathered on black-tailed prairie dogs. a) F_{LS} , b) F_{IL} , and c) F_{IS} .

ferent sources of data and, thus, different underlying assumptions.

Allozyme data reflect events in the history of a population (Slatkin, 1985, 1987) and, thus, are retrospective. The primary assumption was that alleles were selectively neutral, and we had no evidence to the contrary (evidence for rejection of neutrality—Slatkin, 1987). Means of F_{LS} from allozyme alleles were somewhat greater for young than older prairie dogs (Fig. 1a). Estimates of F_{LS} for young should reflect a random assortment of parental alleles, and, thus, young and adults might not be expected to differ greatly in gene dynamics. Offspring, however, were nested within litters and may not reflect equal contribution from all adults in each coterie. In addition, infanticide within coterries may have inflated further the estimate of F_{LS} for offspring because fewer adults success-

fully bred when complete litters were killed. Allozyme studies generally have examined either adult individuals or both young and adults (Chesser, 1983; Dobson, 1994; Pope, 1992; Schwartz and Armitage, 1980). Because our estimates for those two groups were similar, we used the total sample of individuals in comparisons with other estimates of fixation indices.

Estimates of genetic differentiation among coteries from pedigrees also exhibited variable patterns among age and sex groupings (Fig. 2a). Unlike allozyme data, pedigrees can be used to predict genetic composition of offspring (Wright, 1969), and, thus, pedigrees are prospective. Two factors may have promoted accuracy of estimates of fixation indices from pedigrees of young offspring. First, and perhaps most important, pedigrees were always "one step" more complete for young than for their parents, although pedigree information became more complete as the study progressed and more kin relationships were known. Second, migration of males away from their natal areas, immigration of males and females to the colony, and occasional fissions of coteries (Hoogland, 1982, 1992, 1995) may have resulted in some homogenization of kin among coteries. Naturally, selective infanticide of coterie offspring by resident reproductive females also could inflate fixation indices, and infanticide in some years likely had a substantial influence on colony gene dynamics. Coterie young, and secondarily adult females, reflected most accurately both processes that promoted genetic differences among coteries: philopatry of females and increased kinship via predominant polygyny of single males within coteries (Fig. 2; Chesser, 1991a, 1991b).

Estimates of fixation indices from the breeding-group model incorporated a variety of information about coterie and colony composition, mating patterns, and dispersal among coteries (Chesser et al., 1993; Sugg and Chesser, 1994). Parameters of the model were used to describe mathematically the

same sorts of information that were represented in actual pedigrees. The model did not, however, incorporate observations of immigration into the colony or temporal changes in mating or dispersal patterns, and, thus, sensitivity of model predictions to changes in these parameters is unknown. Ranges of values produced by changing demographic parameters, however, indicated variation in model predictions on the same order of that of allozyme and pedigree data, except for the values of F_{IS} (Fig. 3). The breeding-group model assumed genetic equilibrium in the colony. Genetic equilibrium, however, was at best only approximated, as evidenced by the range of values of fixation indices from allozyme and pedigree estimates.

Social breeding groups appeared to produce significant substructuring of the prairie dog colony, with ca. 15–20% of the colony's total genetic variation among coteries in most years (Fig. 3a). This conclusion was corroborated by three types of information that are gathered in different ways: allozyme data from blood samples, pedigrees from behavioral observations and paternity exclusion, and breeding-group model predictions from demographic information about the prairie dogs. Although these data are not independent biologically and variations among estimates and predictions occurred, the basic conclusion of behavioral genetic substructuring of a prairie dog colony was supported. A case for genetic substructuring of mammalian populations due to social breeding groups has been made previously, with F_{LS} estimated at ca. 0.07 for a small sample of polygynous groups of yellow-bellied marmots (*Marmota flaviventris*—Schwartz and Armitage, 1980) and pocket gophers (*Thomomys bottae*—Patton and Feder, 1981), ca. 0.23 for 18 coteries of black-tailed prairie dogs in an earlier study (Chesser, 1983), and ca. 0.22 for 18 troops of red howling monkeys (*Alouatta seniculus*—Pope, 1992). These studies estimated F_{LS} from allozyme data and compared biochemical results with evidence of

likely mating combinations and observations of dispersal.

In addition to F_{IS} , we estimated F_{IL} and F_{IS} from allozyme data, pedigrees, and the breeding-group model. These latter fixation indices can be used to indicate deviations from random mating (Foltz and Hoogland, 1983). In a randomly mating (viz., ideal) coterie and colony, respective values of F_{IL} and F_{IS} should be close to zero. Strongly negative values reflect minimization of opportunities for inbreeding, and positive values indicate promotion of consanguineous matings in coterie and the colony. Substantially negative values of F_{IL} from allozyme data, pedigrees of young and adult females, and the breeding-group model indicated that mating was nonrandom within coterie and biased against consanguineous matings (Dobson et al., 1997). Because of ubiquitous dispersal of male prairie dogs from their natal coterie, pedigree estimates of F_{IL} for adult males were closer to zero than those of adult females and young offspring, although they were still negative (Fig. 2b).

Estimates of F_{IS} were generally close to zero, indicating random mating within the colony. Of course, matings were not truly random because females within coterie mated preferentially with coterie males. Virtually complete dispersal of males from their natal coterie, however, produced a mix of mating partners that closely approximated random mating within the colony. Estimates of F_{IS} from allozyme data and pedigrees of adult males were slightly negative, perhaps reflecting immigration into the colony of adult males ($n = 12$) and females ($n = 4$) that produced offspring during 1979–1988. While the estimate of F_{IS} from the demographic model ignored immigration and was virtually zero, it was not greatly different from other estimates. Thus, the assumption of no immigration to the colony did not appear to create a substantive bias in the breeding-group model (Fig. 3c).

The demographic “breeding-group” approach was developed in a series of mod-

eling efforts (Chesser, 1991a, 1991b; Chesser et al., 1993; Sugg and Chesser, 1994) and was applied to preliminary data on black-tailed prairie dogs (mainly from Hoogland, 1995) to indicate its facility of calculation from data collected in studies of behavioral ecology and natural history (Sugg et al., 1996). Efficacy of the breeding-group model, however, has not been subjected previously to empirical tests. We found that values of fixation indices predicted by our breeding-group model were similar to estimates from allozyme and pedigree data and, thus, were corroborated strongly (Fig. 3). The breeding-group model provided accurate estimates of gene dynamics of black-tailed prairie dogs and also might prove extremely effective for predicting gene dynamics in other species of highly social mammals.

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LITERATURE CITED

- CHESSER, R. K. 1983. Genetic variability within and among populations of the black-tailed prairie dog. *Evolution*, 37:320–331.
- . 1991a. Gene diversity and female philopatry. *Genetics*, 127:437–447.
- . 1991b. Influence of gene flow and breeding tactics on gene diversity within populations. *Genetics*, 129:573–583.
- CHESSER, R. K., O. E. RHODES, JR., D. W. SUGG, AND A. SCHNABEL. 1993. Effective sizes for subdivided populations. *Genetics*, 135:1221–1232.
- COCKERHAM, C. C. 1967. Group inbreeding and coancestry. *Genetics*, 56:89–104.
- . 1969. Variance of gene frequencies. *Evolution*, 23:72–84.
- . 1973. Analysis of gene frequencies. *Genetics*, 74:679–700.
- DALY, J. C., AND J. L. PATTON. 1980. Dispersal, gene flow, and allelic diversity between local populations of *Thomomys bottae* pocket gophers in the coastal ranges of California. *Evolution*, 44:1283–1294.
- DOBSON, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, 30:1183–1192.
- . 1994. Measures of gene flow in the Columbian ground squirrel. *Oecologia*, 100:190–195.
- 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.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, 197:215–223.
- FOLTZ, D. W., AND J. L. HOOGLAND. 1981. Analysis of the mating system in the black-tailed prairie dog (*Cynomys ludovicianus*) by likelihood of paternity. *Journal of Mammalogy*, 62:706–712.
- . 1983. Genetic evidence of outbreeding in the black-tailed prairie dog (*Cynomys ludovicianus*). *Evolution*, 37:273–281.
- GREENWOOD, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Animal Behaviour*, 28:1140–1162.
- HARRIS, H., AND D. A. HOPKINSON. 1976. *Handbook of enzyme electrophoresis in human genetics*. American Elsevier, Publishing Company, Inc., New York (chapters pagged separately).
- HOOGLAND, J. L. 1981. Nepotism and cooperative breeding in the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). 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.
- . 1983. Nepotism and alarm calling in the black-tailed prairie dog (*Cynomys ludovicianus*). *Animal Behaviour*, 31:472–479.
- . 1985. Infanticide in prairie dogs: lactating females kill offspring of close kin. *Science*, 230:1037–1040.
- . 1992. Levels of inbreeding among prairie dogs. *The American Naturalist*, 139:591–602.
- . 1995. *The black-tailed prairie dog*. The University of Chicago Press, Chicago, Illinois, 557 pp.
- HOOGLAND, J. L., AND D. W. FOLTZ. 1982. Variance in male and female reproductive success in a harem-polygynous mammal, the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). *Behavioral Ecology and Sociobiology*, 11:155–163.
- HOOGLAND, J. L., R. H. TAMARIN, AND C. K. LEVY. 1989. Communal nursing in prairie dogs. *Behavioral Ecology and Sociobiology*, 24:91–95.
- KING, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. *Contributions from the Laboratory of Vertebrate Biology, University of Michigan*, 67:1–123.
- LONG, J. C. 1986. The allelic correlation structure of Gainj- and Kalam-speaking people. I. The estimation and interpretation of Wright's *F*-statistics. *Genetics*, 112:629–647.
- NEI, M. 1977. *F*-statistics and analysis of gene diversity in subdivided populations. *Annals of Human Genetics*, 41:225–233.
- PACKER, C., AND A. E. PUSEY. 1993. Dispersal, kinship, and inbreeding in African lions. Pp. 375–391, in *The natural history of inbreeding and outbreeding* (N. W. Thornhill, ed.). The University of Chicago Press, Chicago, Illinois, 575 pp.
- Patton, J. L., and F. H. Feder. 1981. Microspatial genetic heterogeneity in pocket gophers: non-random breeding and drift. *Evolution*, 35:912–920.
- POPE, T. R. 1992. The influence of dispersal patterns and mating system on genetic differentiation within and between populations of the red howler monkey (*Alouatta seniculus*). *Evolution*, 46:1112–1128.
- SCHWARTZ, O. A., AND K. B. ARMITAGE. 1980. Genetic variation in social mammals: the marmot model. *Science*, 207:665–667.
- SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). University of Texas Publications, 7103:49–90.
- SLATKIN, M. 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics*, 16:393–430.
- . 1987. Gene flow and the geographic structure of natural populations. *Science*, 236:787–792.
- SPIELMAN, R. S., J. V. NEEL, AND F. H. F. LI. 1977. Inbreeding estimation from population data: models, procedures and implications. *Genetics*, 85:355–371.
- SUGG, D. W., AND R. K. CHESSER. 1994. Effective population sizes with multiple paternity. *Genetics*, 137:1147–1155.
- SUGG, D. W., R. K. CHESSER, F. S. DOBSON, AND J. L. HOOGLAND. 1996. Population genetics meets behavioral ecology. *Trends in Ecology and Evolution*, 11:338–342.
- WRIGHT, S. 1965. The interpretation of population structure by *F*-statistics with special regard to systems of mating. *Evolution*, 19:395–420.
- . 1969. *Evolution and the genetics of populations*. Volume 2, the theory of gene frequencies. The University of Chicago Press, Chicago, Illinois, 511 pp.
- . 1978. *Evolution and the genetics of populations*. Volume 4, variability within and among natural populations. The University of Chicago Press, Chicago, Illinois, 580 pp.