DO BLACK-TAILED PRAIRIE DOGS MINIMIZE INBREEDING?

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Abstract.—Considerable controversy surrounds the importance of inbreeding in natural populations. The rate of natural inbreeding and the influences of behavioral mechanisms that serve to promote or minimize inbreeding (e.g., philopatry vs. dispersal) are poorly understood. We studied inbreeding and social structuring of a population of black-tailed prairie dogs (*Cynomys ludovicianus*) to assess the influence of dispersal and mating behavior on patterns of genetic variation. We examined 15 years of data on prairie dogs, including survival and reproduction, social behavior, pedigrees, and allozyme alleles. Pedigrees revealed mean inbreeding coefficients (F) of 1–2%. A breeding-group model that incorporated details of prairie dog behavior and demography was used to estimate values of fixation indices (F-statistics). Model predictions were consistent with the minimization of inbreeding within breeding groups ("coteries," asymptotic $F_{IL} = -0.18$) and random mating within the subpopulation ("colony," asymptotic $F_{IS} = 0.00$). Estimates from pedigrees (mean $F_{IL} = -0.23$, mean $F_{IS} = 0.00$) and allozyme data (mean $F_{IL} = -0.21$, mean $F_{IS} = -0.01$) were consistent with predictions of the model. The breeding-group model, pedigrees, and allozyme data showed remarkably congruent results, and indicated strong genetic structuring within the colony ($F_{LS} = 0.16$, 0.19, and 0.17, respectively). We concluded that although inbreeding occurred in the colony, the rate of inbreeding was strongly minimized at the level of breeding groups, but not at the subpopulation level. The behavioral mechanisms most important to the minimization of inbreeding appeared to be patterns of male-biased dispersal of both subadults and adults, associated with strong philopatry of females. Incest avoidance also occurred, associated with recognition of close kin via direct social learning within the breeding groups.

Key words.—*Cynomys*, *F*-statistics, gene diversity, gene dynamics, inbreeding, social behavior.

Because virtually all individuals within natural populations of diploid, sexual individuals are related to one another with some degree of kinship, inbreeding is undoubtedly widespread. The degree of inbreeding commonly displayed in natural populations, however, is a controversial topic (e.g., Ralls et al. 1986; Shields 1993; additional reviews in Thornhill 1993). Among different populations or species, the mean rate of inbreeding might vary along a continuum, from frequent matings among close relatives such as siblings, to virtually all matings among extremely distant kin. The position of a population or species along this continuum may often depend on behavioral and ecological characteristics, such as dispersal behavior and whether individuals live solitarily or in social breeding groups (Chesser 1991a,b).

Considerable debate has focused on the role of behavioral mechanisms in minimizing or promoting inbreeding. For example, sex-biased dispersal patterns of species of birds and mammals have often been explained as a behavioral mechanism that serves to minimize inbreeding (e.g., Dobson 1979, 1982; Greenwood 1980; Dobson and Jones 1985; Pusey 1987; Smith 1993). Under this scenario, sex-biased dispersal and associated mating patterns lower the likelihood that close relatives such as siblings or parents and offspring mate (Chesser and Ryman 1986). Matings between close relatives could lead to lower evolutionary fitness through the increased pro-

duction of deleterious or lethal homozygous alleles in offspring (e.g., Ralls et al. 1988; Mitton 1993; Pusey and Wolf 1996). Alternatively, a high rate of inbreeding might ultimately improve the fitness of offspring through the formation of complexes of homozygous alleles that are advantageous in the local environment (e.g., reviews by Shields 1982, 1987, 1993; Waser 1993a,b). This second scenario argues that behavioral mechanisms such as philopatry and assortative mating should promote inbreeding.

Sewell Wright (1965) developed several indices that estimate the influence of inbreeding on gene dynamics. The inbreeding coefficient (F) is the mean correlation of genes within individuals. In an ideal population (with equal and constant numbers of diploid, sexual individuals that mate randomly, with no migration, mutation, or overlap of generations), F increases consistently over time as the total effect of inbreeding accumulates, so that the value of F depends on both the rate of inbreeding and the number of generations that have passed since the founding of the population. Fixation indices (F-statistics, after Wright 1965) estimate deviation of gene dynamics from those expected in an ideal population. The value of F_{IS} indicates deviation in the rate of inbreeding in a genetic neighborhood or subpopulation from the rate of inbreeding expected under random mating in an ideal subpopulation. The value of F_{IT} likewise indicates

deviation of inbreeding from that expected in a randomly mating total population. The value of F_{ST} indicates the amount of genetic variation in the total population that is partitioned among subpopulations, or the deviation of population subunits from the expectation of a randomly mating total population. When F_{IS} and F_{IT} differ strongly from zero, then promotion (high positive values) or minimization (high negative values) of inbreeding relative to the subpopulation or total population may be indicated. Although fixation indices are based on patterns of matings, F-statistics are most often estimated from biochemical data (e.g., Patton and Feder 1981; Chesser 1983; Foltz and Hoogland 1983; Daly and Patton 1990; Sugg et al. 1990; Dobson 1994).

Although F-statistics have traditionally been applied to subpopulations and populations, several levels of population substructuring are possible (e.g., Chesser 1983). In particular, social breeding groups may strongly influence gene dynamics in populations of social animals, for example, some mammalian species (e.g., Long 1986; Pope 1992; Sugg et al. 1996). Complete understanding of the effects of inbreeding and of influences of behavioral mechanisms on gene dynamics requires information about the levels of genetic structure in populations. Especially informative are F-statistics that include the lowest level of genetic structure where breeding occurs (Chesser 1991a,b; Chesser et al. 1993a). If a level of genetic structure is ignored, such as the level of social breeding groups, then F_{IS} may be mistakenly interpreted as a test for promotion or minimization of inbreeding within subpopulations (i.e., by combining social subunits of a population, an unintentional Wahlund [1928] effect is produced, reviewed by Sugg et al. 1996). Because inbreeding may still be influential at the lower level of genetic structure, a proper test must include evaluation of gene dynamics of social breeding groups.

Perhaps the most controversial example of F-statistics and inbreeding is the case of black-tailed prairie dogs (*Cynomys ludovicianus*). Prairie dogs live in social breeding groups called "coteries," usually composed of about four adults and their juvenile and subadult offspring (King 1955; Hoogland 1995). In typical habitat, several coteries occur together in "colonies" that form in patches of suitable habitat in the local and regional landscape. Male prairie dogs usually disperse from their natal coterie as subadults, and also usually disperse after breeding in a coterie for two years (often coincident with maturation of their daughters), but dispersal among colonies is much less common than within a colony (Garrett and Franklin 1988; Hoogland 1995). When they occur in a coterie together, maturing daughters generally avoid mating with their fathers (Hoogland 1982, 1995). Patterns of male dispersal and female mate choice appear to preclude most matings between prairie dogs that are genetically related by about a quarter or more (e.g., full and half siblings or parents and offspring), but more distantly related kin mate about as often as expected at random (Hoogland 1992).

The influence of behavioral mechanisms on the gene dynamics of black-tailed prairie dogs is unclear, and whether prairie dogs are relatively inbred or outbred remains an open question (Smith 1993). Foltz and Hoogland (1983) derived a slightly negative but statistically significant inbreeding coefficient (F_{IS}) with allozyme data from a single colony, and

concluded that prairie dogs were relatively outbred. For several colonies in the same local region, Daley (1992) obtained a slightly negative estimate of F_{IS} that was not significantly different from zero. Thus, from Daley's estimate we might conclude that inbreeding within prairie dog colonies was neither promoted nor minimized. In a different geographic region, Chesser (1983) documented significantly positive inbreeding coefficients (F_{IS}), also from allozyme data, and suggested either strong inbreeding or high relatedness among adult female prairie dogs. Only the latter study attempted to examine the effects of inbreeding with respect to coteries, the social breeding groups.

The purpose of the present study was to test for the promotion or minimization of inbreeding of prairie dogs at the levels of social breeding groups and subpopulations. With comparisons to earlier studies, we also examined the effect of inbreeding relative to local and regional populations. Finally, we inferred the possible influence of behavioral mechanisms, specifically dispersal and mating patterns, on the promotion or minimization of inbreeding at the different levels of population structure. As predicted by theoretical studies (e.g., Chesser 1991a,b; Chesser et al. 1993a), we expected that influences of behavioral mechanisms would be most apparent for social breeding groups (coteries), the lowest level of population structure. Our goals were accomplished using comparisons among three different methods of estimating fixation indices for prairie dogs.

Chesser (1991a,b), Chesser et al. (1993a), and Sugg and Chesser (1994) provided a theoretical framework of fixation indices for evaluating the effect of inbreeding of individuals relative to breeding groups (F_{IL}), of individuals relative to the local subpopulation (F_{IS}), and of breeding groups relative to the subpopulation (F_{LS}). These breeding-group F-statistics have been designed to incorporate influences of philopatry and dispersal, mating systems, and even details of mating systems like multiple paternity. We used the breeding-group model to estimate fixation indices from behavioral and demographic data (after Sugg et al. 1996). We also estimated F-statistics from allozyme data, using Wright's (1978; see also Nei 1977) basic method except that coteries were used as the unit of population subdivision. Finally, the inbreeding coefficient (F) and F-statistics were estimated from pedigrees. Pedigrees potentially give the most accurate estimates of inbreeding because they reflect actual breeding structure (e.g., Wright 1969; Long 1986), although accuracy of estimated fixation indices depends upon the completeness of pedigrees.

MATERIALS AND METHODS

Field and Laboratory

Black-tailed prairie dogs were studied in the field from 1975 through 1989 at Wind Cave National Park, Hot Springs, Custer County, South Dakota (Hoogland 1995). The study colony (1300 m elevation, about 1 km southwest of Rankin Ridge) occupied about 6.6 ha of meadowland surrounded by coniferous woodland and additional meadow and measured roughly 500 m (N-S) by 130 m (E-W). The nearest other colonies were about 1 km and 2 km away, and at least a dozen colonies occur within or are adjacent to Wind Cave

National Park. The number 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.

Fieldwork was conducted by J. L. Hoogland and 112 field assistants. Adult prairie dogs were captured in live traps baited with whole oats (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 matings (matings occurred underground) 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; Hoogland 1995). Through behavioral observations, virtually all litters that survived until emergence from the natal burrow could be unambiguously assigned to their mother.

On average, the study colony contained about 21 coteries, and over the years the number of coteries ranged from 15 to 26 (Hoogland 1995). Coteries generally contained one or two adult males, two to four adult females, and several yearlings and young of the year. Black-tailed prairie dogs are diurnally active, and, unlike most other marmotine rodents, they do not hibernate. Males and females usually began reproducing at about two years of age, but occasionally yearling females bred. Generation time was 2.8 years for males and 3.0 years for females. Mating occurs during February and March, and weaning of offspring occurs shortly after emergence of juveniles from natal burrows, about 76 days later, in May and June.

The Breeding-Group Model

The breeding-group model used characteristics of natural history (e.g., mating systems, dispersal patterns, and social structure) to produce estimates of F-statistics. To estimate gene correlations (F, θ, and α, see below) for the breeding-group model, it was necessary to obtain means and variances for several model parameters. The number of coteries (s) was averaged from 1976 to 1988. Mean numbers of adult males (m) and females (n) per coterie were averaged from 1977 to 1988. The remaining parameters served to define reproductive success and were based only on the lifetime of individuals that produced progeny that, in turn, survived to reproduce. Because the life span of the prairie dog was approximately five years, and most did not mate until they were two years old, data from individuals born in the last few years of the study (1987–1989) were not used for estimating these parameters. The remaining parameters are the mean (k) and variance (σ^2_k) of the number of progeny that survive to maturity that were produced by females, the mean (b) and variance (σ^2_b) of the number of females mated by each male that produce surviving progeny, the mean (p) and variance (σ^2_p) of the number of surviving progeny of a female that were

sired by a single male, and the average number of 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 coteries and successfully reproduced in other coteries. These last two parameters were estimated using all years of data for individuals of known parentage.

The above parameters were used to calculate breeding parameters for the model developed by Chesser et al. (1993a) and Sugg and Chesser (1994). The first parameter (ϕ_m) defines the probability that two randomly chosen progeny in the same breeding group (coterie) are sired by the same male. This parameter estimates the genetic polygyny of the average breeding group and is calculated with the following formula:

$$\phi_m = \frac{m[\sigma^2_b + b(b - 1)]}{ln(n - 1)}. \tag{1}$$

The second parameter (ϕ_f) defines the probability that two randomly chosen progeny in a coterie share the same mother and may be termed the probability of shared maternity. This parameter is calculated as:

$$\phi_f = \frac{\sigma^2_k + k(k - 1)}{k(kn - 1)}. \tag{2}$$

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

$$\phi_w = \frac{l[\sigma^2_p + p(p - 1)]}{k(k - 1)}. \tag{3}$$

The breeding parameters and ecological data can be used in a series of transition equations to determine the expected change in gene correlations between generations (for transition equations, see Chesser 1991a,b; Chesser et al. 1993a; Sugg and Chesser 1994). Gene correlations may be defined within individuals (F), within coteries (θ), and within the colony (α). We began by assuming that the population starts with unrelated individuals (i.e., that F, θ, and α were zero), and expected gene correlations were obtained for generations subsequent to the initial generation until genetic equilibrium was reached. In turn, the gene correlations were used to determine the fixation indices at a given time by the following equations (Cockerham 1967, 1969, 1973; Chesser et al. 1993a):

$$F_{IL} = \frac{F - \theta}{1 - \theta}, \qquad F_{IS} = \frac{F - \alpha}{1 - \alpha}, \qquad F_{LS} = \frac{\theta - \alpha}{1 - \alpha}. \tag{4}$$

The breeding-group model assumes that generations do not overlap, an assumption that was clearly violated. This assumption, however, affects the time required to reach genetic equilibrium, but not the asymptotic values (Hill 1979). Since we were only interested in the asymptotic values, the assumption of nonoverlapping generations was not onerous. The model could be adapted to the annual breeding cycle of prairie dogs, and with sufficient samples model, estimates of

F-statistics could be calculated for each generation (at least three generations for the years 1979–1988). For our preliminary examination of the breeding-group model, however, samples were most appropriate for average estimates of gene correlations and F-statistics over the duration of the study.

Pedigree Estimates

Pedigrees were constructed from field observations of mothers and offspring and assignment of paternity from field observations combined with maximum-likelihood analyses of allozyme data (Foltz and Hoogland 1981; Hoogland and Foltz 1982). Gene correlations necessary for estimation of F-statistics (F, θ, α, eqs. 4) were determined directly from the pedigrees. Each individual captured from the population was assigned a year born, coterie designation for each year alive, and unique identification number. The sire and dam identification number was noted for each progeny. If the sire or dam was unknown, as for immigrants and for individuals that were already present in the population at the beginning of the study, then that sire or dam was assigned gene correlations of zero with other colony residents. The coancestry (θ) between any pair (i, j) of individuals was determined as:

$$\theta_{i,j} = \frac{1}{4}(\theta_{S_iS_j} + \theta_{S_iD_j} + \theta_{S_jD_i} + \theta_{D_iD_j}),\qquad(5)$$

where subscripts S and D denote sire and dam, respectively, for the ith and jth individual. This expression can be used to describe the way in which coancestry accumulates over the generations. The coancestry of an individual to itself is: $\theta_{i,i} = (1 + F_i)/2$. The inbreeding coefficient of a progeny is equal to the coancestry of its parents, calculated as:

$$F_i = \theta_{S_iD_i}.\qquad(6)$$

The weighted average coancestry within coteries each year was determined by the summed pairwise values from the pedigree for each coterie multiplied by the size of the ith coterie (N_i) relative to the total size of the population (N_T) (c.f., Cockerham 1969, 1973; Chesser 1991b):

$$\bar{\theta} = \sum_{i=1}^{s} \frac{N_i}{N_T} \sum_{j=1}^{N_i-1} \sum_{k=j+1}^{N_i} \theta_{j,k}.\qquad(7)$$

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

$$\bar{\alpha} = \frac{\sum_{i=1}^{s-1} \sum_{j=1}^{N_i} \sum_{k=i+1}^{s} \sum_{m=1}^{N_k} \theta_{j,m}}{\sum_{i=1}^{s-1} \sum_{k=i+1}^{s} N_i N_k}.\qquad(8)$$

Lastly, the average inbreeding coefficient was determined over all individuals observed in the population (N_T) for a given year, and was calculated as:

$$\bar{F} = \frac{1}{N_T} \sum_{i=1}^{N_T} F_i.\qquad(9)$$

Average values from equations (7, 8, 9) were used in equations (4) to determine the F-statistics. Mean values of coancestries were calculated for several years of study (1979–

TABLE 1. Parameters (means and variances) that describe reproduction and dispersal of black-tailed prairie dogs. The parameters were used to calculate F-statistics from the breeding-group model of Sugg and Chesser (1994). Details of calculation and years of data included are given in the text.

Characteristic	Symbol	Mean/variance
Number of coteries	s	20.83
Number of adult males/coterie	m	1.38
Number of adult females/coterie	n	2.65
Number of surviving progeny/female	k	2.00
Variance in surviving progeny	σ_k^2	1.44
Number of females mated/male	b	1.68
Variance in females mated/male	σ_b^2	0.66
Progeny of a female with the same father	p	1.60
Variance in progeny with the same father	σ_p^2	0.64
Number of successful mates/female	l	1.25
Male dispersal from natal coterie	d_m	1.00
Female dispersal from natal coterie	d_f	0.02

1988), and each yearly mean was compared to estimates from previous years to ensure accuracy. Subsets of data for both progeny born in a particular year and for adults in that year were determined by the above methods.

Allozyme Estimates

Blood samples were collected from all of the prairie dogs in the colony between 1979 and 1988 ($n = 10$ years), except for a few emergent juveniles that disappeared before they could be captured (Hoogland 1985, 1995). Horizontal starch gel electrophoresis was performed (by the methods of Selander et al. 1971; Harris and Hopkinson 1976), with staining for four polymorphic loci: transferrin (three alleles), nucleoside phosphorylase (three alleles), 6-phosphogluconate dehydrogenase (two alleles), and phosphoglucomutase-2 (four alleles). Only transferrin and nucleoside phosphorylase had sufficient sample sizes for analyses in 1979, but all four loci were analyzed for the years 1980–1988.

F-statistics were calculated for each allozyme locus using standard methods from Wright (1978; see also Nei 1977). Corrections for small sample sizes (e.g., Nei and Chesser 1983; Weir and Cockerham 1984) were not applied because blood was collected and analyzed from virtually all individuals in the colony, and thus the coteries and colony were not subject to population sampling error (loci, however, *were* sampled). Coteries were used as population subdivisions, so that the 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).

RESULTS

Breeding-Group Model Predictions

From the demographic and reproductive parameters of the prairie dogs (Table 1), we calculated the degree of genetic polygyny (ϕ_m) at 0.46, the probability of shared maternity (ϕ_f) at 0.40, and the probability of single paternity (ϕ_w) at
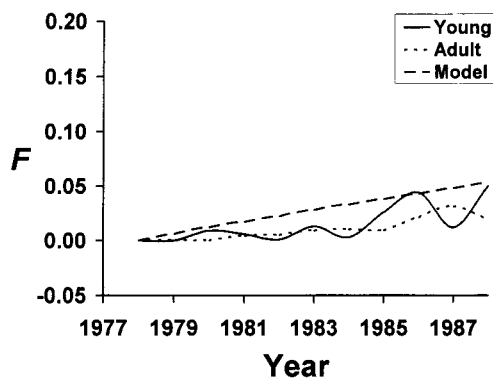
FIG. 1. Estimates of F, the average inbreeding coefficient per individual, for prairie dogs in the study colony. The predicted values from the breeding-group model (for 10 years, 1979–1988) and estimates from analyses of offspring and adult pedigrees are plotted with smoothed curves connecting yearly points. Initial values were assumed to be zero in 1978.

1.00. These latter parameter estimates were entered into the transition equations of Chesser et al. (1993a) and Sugg and Chesser (1994). In the breeding-group model, F exhibited a constant increase that reflected continual loss of genetic variation in the population, a similar pattern to the more variable empirical values from pedigrees (Fig. 1). Because natural-history parameters were averaged across the entire period of study, only a single asymptotic value of each F-statistic was produced: F_{IL} was estimated at -0.184, F_{IS} at 0.002, and F_{LS} at 0.157 (Fig. 2). The breeding-group model did not take immigration from other colonies into account, and from 1979 to 1988 there were 12 males and four females that immigrated and successfully bred in the colony.

Pedigree Estimates

For each year of the study from 1979 to 1988, the colony was divided into those individuals that were part of the adult population (individuals older than yearlings, and thus potential parents) and offspring (young of the year). Over the 10 years, the mean value of F (the inbreeding coefficient) was 0.016 for offspring and 0.011 for adults (Fig. 1). Estimates of F among years were not significantly different between offspring and adults ($t_{18} = 0.77$, $P = 0.45$). Estimates of fixation indices from pedigrees of prairie dogs, however, were very different for offspring compared to the adult portion of the population (Fig. 3). F_{IL} averaged -0.226 for offspring and -0.082 for adults, a significant difference ($t_{18} = 14.45$, $P < 0.0001$). F_{IS} averaged 0.000 for offspring and 0.002 for adults ($t_{18} = 0.75$, $P = 0.46$). Finally, F_{LS} averaged 0.187 for offspring and 0.075 for adults, another highly significant difference ($t_{18} = 16.15$, $P < 0.0001$).

Within each year, the parental population exhibited F_{IL}- and F_{LS}-values that were much closer to zero than the values for the offspring (Fig. 3). F_{IS} values were more similar between the parent and offspring divisions of the population, although values for offspring were lower in most years. Inclusion of breeding and nonbreeding adults with offspring were expected to dilute the magnitude of the fixation indices (Spielman et al. 1977; Chesser 1991a). Pedigrees for offspring were always one generation more complete than those

for adults, so we chose to compare the pedigree values from the offspring with other estimates of F-statistics. Estimates of F-statistics from pedigree analysis of offspring varied among the 10 years of the study (Figs. 1, 2), probably due to annual changes in such characteristics as sex ratio, dispersal rates, mating patterns, number of coteries, and population size.

Allozyme Estimates

Fixation indices were estimated from the allozyme data for each year of study, and reflected the past history of the population (e.g., Slatkin 1985, 1987). As is common among studies of allozyme variation (e.g., Patton and Feder 1981; Chesser 1983; Sugg et al. 1990; Dobson 1994), we pooled breeding adults, nonbreeding adults, subadults, and young for analyses. Among 10 years for all the individuals in the prairie dog colony, F_{IL} averaged -0.213, F_{IS} averaged -0.012, and F_{LS} averaged 0.166. F_{LS}, averaged across loci, was significantly greater than zero (χ^2-test, $P < 0.001$) in all years. Estimates of all of the F-statistics from allozyme data varied over the 10 years of study (Fig. 2).

DISCUSSION

The Breeding-Group Approach

Studies of genic data such as allozyme alleles frequently estimate F-statistics, and then discuss the sorts of breeding and dispersal patterns that would produce the fixation indices (e.g., Patton and Feder 1981; Chesser 1983; Foltz and Hoogland 1983; Sugg et al. 1990; Dobson 1994). It is our contention that it may often be more worthwhile to examine breeding and dispersal patterns, and then estimate the gene dynamics that should result (e.g., Fleischer 1983; Daly and Patton 1990; Waser and Elliot 1991; Pope 1992; Sugg et al. 1996). The breeding-group model predicted gene dynamics from behavioral and reproductive data (see also Sugg et al. 1996). We compared results from the breeding-group model to pedigree and allozyme estimates of breeding-group fixation indices, to examine the efficacy of the model.

Previous analyses of inbreeding coefficients and fixation indices for black-tailed prairie dogs have focused primarily on colonies (e.g., Foltz and Hoogland 1983; Daley 1992). These studies ignored the social structuring of the population that occurs at the level of the coteries, and thus must be interpreted carefully (Chesser 1983, 1991a; Sugg et al. 1996). In particular, estimates of the effects of inbreeding may be biased by an unintentional Wahlund (1928) effect if genetic substructures of a subpopulation are mistakenly ignored. Such a bias arose because colony subunits of genetic structure (coteries) that exhibit different patterns of genetic variation were pooled. A highly positive or negative fixation index (e.g., colony F_{IS} or coterie F_{IL}) might indicate that inbreeding was promoted or minimized. The influence of mechanisms that serve to minimize inbreeding, however, such as sex-biased dispersal (e.g., Greenwood 1980; Dobson 1982; Ralls et al. 1986), should be most evident at the lowest level of genetic structure (F_{IL}; Chesser 1991a,b; Chesser et al. 1993a). Thus, only examination of the coterie level of population
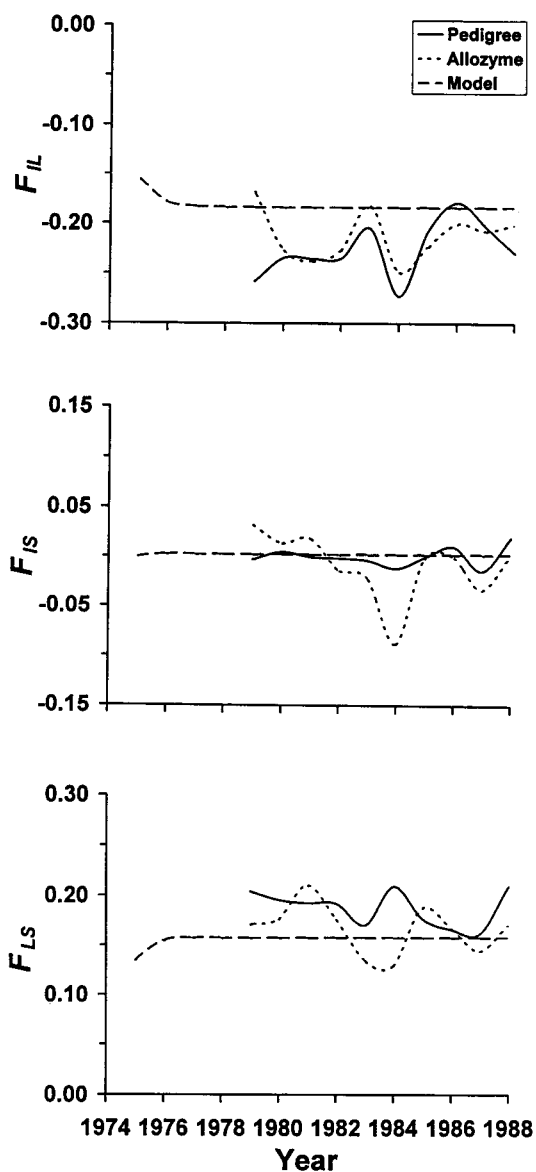
FIG. 2. Estimates of F_{IL}, F_{IS}, and F_{LS} (the average inbreeding coefficient of individuals relative to their coterie, the average inbreeding coefficient of individuals relative to the colony, and the average inbreeding coefficient of coteries relative to the colony, respectively) for prairie dogs in the study colony. The predicted values from the breeding-group model (for 14 years, 1975–1988) and estimates from analyses of offspring pedigrees and allozyme alleles (both for 10 years, 1979–1988) are plotted with smoothed curves connecting yearly points. Estimates of F_{LS} from allozyme alleles were significantly greater than zero in all years (loci pooled, χ^2-tests, $P < 0.001$).

FIG. 3. Pedigree estimates of F-statistics (F_{IL}, F_{IS}, F_{LS}) for adult and young (offspring) prairie dogs in the study colony during 10 years (1979–1988). Values are plotted with smoothed curves connecting yearly points. F_{IL} and F_{LS} were significantly different between adults and young (t-tests, $P < 0.0001$).

structure (F_{IL}) is a proper test of influences of behavioral mechanisms on inbreeding in prairie dogs.

Comparison of Three Methods

The inbreeding coefficient (F), calculated from the pedigree data and averaged over all individuals, was 1–2%. This result was not surprising, since Hoogland (1992, 1995) observed that prairie dogs frequently mated with moderately
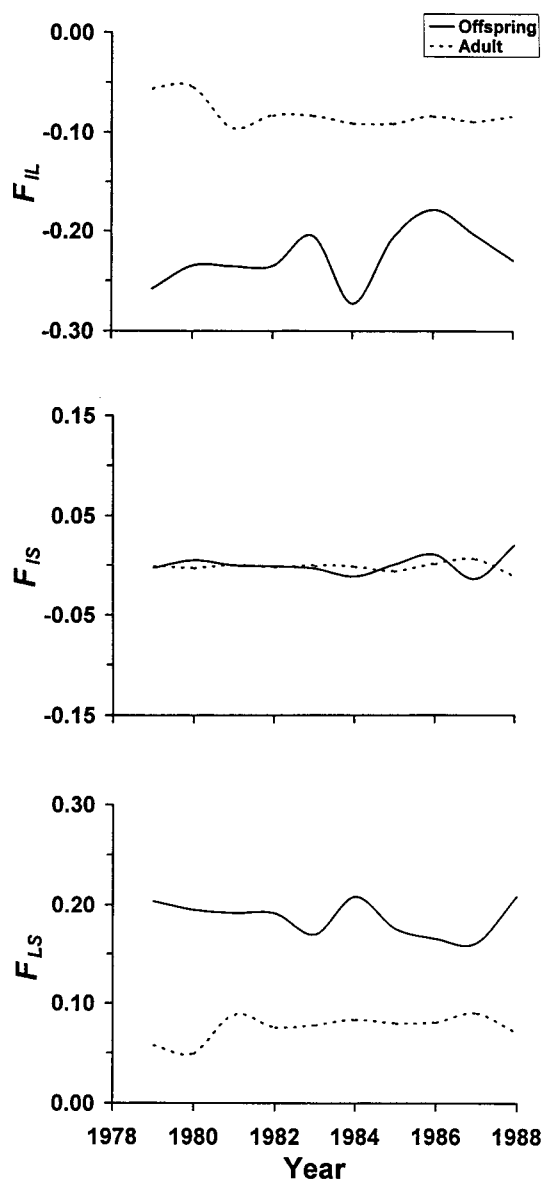
related kin such as aunts and uncles, nieces and nephews, and various levels of cousins. Thus, inbreeding accumulated over the generations for prairie dogs (Fig. 1). Matings between prairie dogs of moderate and distant kinship appear associated with the system of individual recognition, in which members of the home (natal) coterie are recognized as close relatives through a process of direct social learning (Hoogland 1995). In contrast, individuals born in adjacent coteries are not recognized as close relatives or according to relative degree of kinship. Yet, individuals in adjacent coteries may be fairly close kin, such as aunts, uncles, nieces, nephews, various levels of cousins, and even nonlittermate siblings. Such relatives bred together about as often as would be ex-

pected from random mate selection within the colony (Hoogland 1992, 1995).

Estimates of the inbreeding coefficient do not indicate whether patterns of male-biased dispersal and incest avoidance served to minimize the degree of inbreeding. According to theory, gene dynamics within coteries should yield a strongly negative fixation index (F_{IL}), if consanguineous matings were minimized compared to the expectation under random mating in an "ideal" coterie (Wright 1969; Chesser 1983, 1991a,b; Long 1986; Sugg et al. 1996). The breeding-group model estimated F_{IL} as strongly negative (-0.18), and average estimates from offspring pedigrees and allozyme data were very similar (-0.23 and -0.21, respectively). Thus, our proper test using the breeding-group approach indicated strong minimization of the rate of inbreeding *at the coterie level* of population structure, rather than either random mating or promotion of inbreeding. The genetic consequences of inbreeding appeared to be minimized in coteries of prairie dogs, primarily due to the complete dispersal of young and old males from their natal or previous breeding coteries (as suggested by Hoogland's [1982, 1995] behavioral observations), but also partly due to behavioral incest avoidance.

The rate of inbreeding of individuals relative to that expected in an ideal colony was estimated by the value of F_{IS}. If mating were truly random within a colony of finite size, F_{IS} would be approximately zero (because inbreeding accumulates within individuals over the generations, the predicted value is actually slightly positive; see eqs. [4] for F_{IS}). From the pattern of immigrants to the colony that eventually produced offspring (1.6 immigrants/year, about 1% of the spring population; see also Garret and Franklin 1988; Hoogland 1995), a low but negative value of F_{IS} might be expected. The breeding-group model estimated F_{IS} at $+0.002$, and estimates from pedigrees of offspring and allozyme data were also close to zero. Thus, we could not discriminate the rate of inbreeding within the colony from the expectation of random mating within an ideal population of the same size. Inbreeding was neither minimized nor promoted *at the colony level* of population structure.

The fixation index F_{LS} estimates the proportion of the total genetic variation in the colony that is partitioned among the coteries. The breeding-group model estimated an F_{LS} of 0.16, similar to the offspring pedigree and allozyme estimates (0.19 and 0.17, respectively). Coteries thus exhibited substantial genetic differentiation, despite the universal dispersal of males from their natal coteries. Among-coterie genetic differentiation likely resulted from high relatedness of philopatric females and their progeny within coteries, and may contribute to the evolutionary maintenance of social groups (Chesser et al. 1993b). The pedigree estimate of F_{LS} for adults, however, averaged only 0.08, a much lower value. For adult prairie dogs, the pedigree F_{LS}-value, like the pedigree F_{IL}, may have been low in magnitude due to incompleteness of the pedigree compared to the more accurate pedigrees for offspring. In any case, the strong concordance of estimates of F_{LS} from the breeding-group model, offspring pedigrees, and allozyme data indicate significant genetic structuring within the colony due to social grouping and female philopatry within the coteries.

Fixation indices should approach equilibrium after several

generations (e.g., Chesser 1991a,b; Sugg and Chesser 1994), but demographic fluctuations likely cause deviations from equilibrium values. Variations in our estimates from pedigrees and allozyme data may have indicated that averaging over several years of data was necessary to describe the typical pattern of gene dynamics in the population. The breeding-group model, however, incorporated variations in behavioral and reproductive data that reflected salient aspects of pedigrees within the colony, and thus provided reasonable estimates of average gene dynamics. Our estimated fixation indices from the breeding-group model could be considered predictions that were strongly supported by the agreement of the estimated fixation indices from the pedigree and allozyme data. The concordance of results from the three different methods strengthens our conclusion that coterie social structure had a major influence on gene dynamics within the prairie dog colony.

Comparisons with Earlier Studies

Foltz and Hoogland (1983) used pedigree analysis to estimate a mean F over three years of about 0.003, which is almost five times lower than our average over 10 years of about 0.014. This difference is likely explained by the fact that more complete pedigrees were available in later years of the study, and intermediate relatives such as various levels of cousins were included. Long-term studies may be required to accurately estimate F, due to fluctuations in gene correlations caused by annual changes in population demography. In addition, even the extensive 15 years of data on black-tailed prairie dogs were not sufficient to produce complete pedigrees. The value of F_{IL} among 18 coteries in New Mexico was estimated from allozyme data at $+0.11$ (Chesser 1983), a very different value from the -0.17, on average, that we found. As discussed by Chesser (1991b), the positive F_{IL} from New Mexico probably resulted from inaccurate identification of coterie members.

Previous estimates of F_{IS} from prairie dogs at Wind Cave National Park varied from -0.06 in one colony (Foltz and Hoogland 1983) to -0.02 averaged over eight colonies (Daley 1992). In the present study, F_{IS} was effectively zero (within a single colony), calculated from the same study colony but over a longer time period than Foltz and Hoogland's (1983) estimate. Positive values of F_{IR} from Wind Cave National Park (R defined as the regional population within and adjacent to the park, $F_{IR} = 0.09$, Daley 1992) and across New Mexico (R defined as the regional population within New Mexico, $F_{IR} = 0.40$, Chesser 1983) indicate considerable promotion of inbreeding of individuals relative to the assumption of random mating in these local and broader regional populations, respectively. At regional spatial scales, deviation from the expectation of random mating was likely due to geographic isolation of colonies relative to the limited dispersal capabilities of individual prairie dogs.

Our preliminary conclusion from present evidence is that as spatial scale is expanded from coterie F_{IL}, to colony F_{IS}, to regional F_{IR} (R defined to represent total genetic variation within a region), to broad geographic regional F_{IT} (the broadest region would include the entire species, with T defined as total genetic variation at the highest level), the rate of

inbreeding relative to that expected under random mating changes from negative, to zero, to positive. Note that as each level of population structure and spatial scale is added into consideration (represented by the gene correlations F, θ, α, and perhaps β and δ for the higher levels of spatial scale), the total genetic variation will increase due to the incorporation of a larger number of colonies, resulting in changes in allele frequencies and perhaps the inclusion of new alleles.

A previous estimate of F_{LS} of 0.20 was made by Sugg et al. (1996) from behavioral data gathered in the study colony and presented in Hoogland's (1995) book on black-tailed prairie dogs. Also, Chesser's (1983) allozyme study of 18 coteries within a single colony in New Mexico estimated F_{LS} at 0.23. These values are only slightly higher than the 0.16–0.19 that we found. The value calculated by Sugg et al. (1996) contained rough estimates of several parameters for the breeding-group model, and was only slightly higher than the model prediction from the actual data and the estimates from offspring pedigrees and allozyme data in the present study. Thus, the breeding-group approach appears fairly robust for field data on prairie dogs, and indicates substantial genetic differentiation among the coterie social groups.

In an allozyme study of eight distinct colonies at Wind Cave National Park, Daley (1992) estimated F_{ST} at 0.11, a value similar to Chesser's (1983) estimate of 0.10 for 21 more widely dispersed colonies of prairie dogs in New Mexico. We did not study regional population differentiation in the present study, but comparison with our values of F_{LS} (at about 0.17) proved interesting. It is important to remember that the amounts of genetic variation that were available at the colony and regional levels of scale were different, with greater genetic variation expected at the broadest regional level. Nonetheless, the degree of partitioning of available genetic variation within the colony was much greater than the partitioning of variation among colonies in the regional studies. This result supports our conclusion that the influence of dispersal, philopatry, and mating patterns on the partitioning of genetic variation among coteries was substantial.

Conclusions

Virtually all diploid, sexual species inbreed to some degree, simply because real populations are finite and dispersal distances are limited. Behavioral observations (Hoogland 1992, 1995) and estimates of F from pedigrees demonstrated and quantified limited inbreeding in black-tailed prairie dogs. The magnitude of the strongly negative F_{IL}-values from our study indicated that dispersal and mating patterns of prairie dogs served to minimize inbreeding within coteries, a result that was also supported by behavioral observations of a strongly male-biased dispersal pattern and a few daughters that avoided mating with their fathers (Hoogland 1982, 1995). At the coterie level, therefore, prairie dogs are relatively outbred, even though some inbreeding is evident. We also had strong evidence (from $F_{IS} \approx 0$ and from positive estimates of F_{IT} in the literature) that prairie dogs do not further minimize inbreeding at the colony level and are relatively inbred at higher spatial levels of population structure.

Chesser's (1991a,b) models of gene dynamics within social species that may be characterized by polygynous breeding groups demonstrated how gene dynamics could be directly calculated from behavioral and reproductive data that behavioral ecologists commonly collect. In the present study, we tested predictions of a breeding-group model (that incorporated the influence of multiple paternity; Sugg and Chesser 1994), and found that model predictions were strongly corroborated by analyses of pedigree and allozyme data. The breeding-group model provided an accurate assessment of gene dynamics because it incorporated mating and dispersal patterns (thus, reflecting important aspects of the pedigree), and focused on the lowest level of population structure where breeding actually occurs (Chesser 1991a,b; Chesser et al. 1993a).

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