

GENETIC EVIDENCE OF OUTBREEDING IN THE BLACK-TAILED PRAIRIE DOG (*CYNOMYS LUDOVICIANUS*)

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Received August 31, 1981. Revised May 24, 1982

The study of mating systems and the effect of social behavior on the genetic structure of animal populations is an important topic in evolutionary biology. The theoretical approaches of Wright (1978 and references therein) and Malecot (1969) have been extended by many other researchers, including Cockerham (1973), Jacquard (1974), Smith (1974) and Nei (1977). Two methods have been used to study mating systems in natural populations. The more usual approach is to assay the genetic structure by collecting a population sample and determining allele and genotype frequencies at one or more polymorphic loci. The number of such studies has increased rapidly in recent years, due to the now-routine application of gel electrophoresis in population biology. Previous research on the genetic structure of rodent populations includes that of Petras (1967), Selander (1970), Birdsall and Nash (1973), Myers (1974), Schwartz and Armitage (1980, 1981), Foltz (1981), Hanken and Sherman (1981) and Patton and Feder (1981). A second approach involves the analysis of pedigrees obtained by long-term study of populations whose members are individually marked. Because of the obvious difficulties in obtaining this information for natural populations, such studies are relatively rare. Exceptions include the work of Howard (1949), Bulmer (1973), Missakian (1973), Greenwood et al. (1978) and Brown and Brown (1981).

We here report on the genetic structure of the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*), as determined by electrophoretic study of four variable blood proteins and by pedigree analysis. There are several advantages to collecting electrophoretic and pedigree data from the same population. First, the electrophoretic data can be used to confirm the pedigree structure through paternity analysis. This part of our research is described elsewhere (Foltz and Hoogland, 1981). Second, analysis of several types of data from a single population may provide a better understanding of the underlying factors affecting its genetic structure than analysis of only one type of data (see, for example, Thompson and Roberts, 1980). In this paper, we calculate two measures of population structure: Wright's (1978) genotype fixation index, F_{IS} , and Allen's (1965) coefficient of nonrandom mating, F_n . The mean fixation index is negative in each year of the study, indicating an overall excess of heterozygotes. The coefficient of nonrandom mating is also negative each year, indicating an avoidance of consanguineous matings. This result is consistent with previous behavioral research on this species (Hoogland, 1982). We conclude that the mating pattern can explain some, but not all, of the heterozygote excess.

MATERIALS AND METHODS

The Study Colony.—The main study colony occupies an area of 6.6 hectares in Wind Cave National Park, Custer County, South Dakota. Within the colony, individuals live in social groups known as

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coterie, which are composed of one or two adult males, one to six adult females, and several yearlings and juveniles of both sexes (King, 1955; Hoogland, 1981b). Each year, the approximately 130 adults (animals older than one year) and yearlings in the colony are organized into approximately 25 coterie (Hoogland, 1981a). Since 1975, all residents in the study colony have been ear-tagged for permanent identification and marked with fur dye for visual identification (Hoogland, 1979, 1981b). Coterie compositions and mother-offspring relationships are determined from behavioral observations (King, 1955; Hoogland, 1981b). Mating occurs in February and March, and weaned offspring first appear above ground in May and June. Males and females generally first breed when two years old. However, in 1981 six yearling females weaned litters; in the five previous years, a total of only four yearling females had weaned litters. Also in 1981, five yearling males left their natal coterie and defended breeding coterie; defense of a breeding coterie by a yearling male was seen only once before at the study colony. In this paper, the term "reproductive female" refers to any female that successfully weaned a litter, regardless of her age.

Electrophoretic Analysis.—From 1979 through 1981, blood samples were collected from all prairie dogs in the study colony (Foltz and Hoogland, 1981). In 1981, blood samples were obtained from 17 individuals living in "Ward A" of the Shirttail Canyon colony (King, 1955), 10 km distant from the study colony; these 17 animals represented approximately 75% of the ward population. The procedure for horizontal starch-gel electrophoresis (Electrostarch lot 307 and Connaught starch lot 368-2) followed that given by Selander et al. (1971) and Harris and Hopkinson (1976). At least 50 prairie dogs, mostly adults, were examined for each biochemical locus. For monomorphic loci, the upper 95% confidence limit for the frequency of an undetected rare allele was 0.03.

Statistical Analyses.—The data collect-

ed in each year of the study were analyzed separately. However, we did pool some test statistics and degrees of freedom across years and across loci, to increase the power of the tests. Using the electrophoretic data for offspring born each year, we calculated the within-population fixation index

$$F_{IS} = 1 - H_o/H_e \quad (1)$$

for each polymorphic locus, where H_o is the observed proportion of heterozygotes and H_e is the expected (Hardy-Weinberg) proportion, determined by Levene's (1949) unbiased formula. At least four factors other than avoidance of consanguineous matings can affect genotype proportions within populations. First, an excess of heterozygotes is expected when the sample consists of groups of siblings (Rasmussen, 1979). We avoided this source of bias by randomly sorting all the animals born each year into four or five subsamples, with at most one offspring from each litter per subsample. A fixation index was calculated for each subsample, and these values, weighted by expected numbers of heterozygotes (Kirby, 1975), were averaged to give a mean fixation index per locus, F_{IS} . Although, as used here, F_{IS} is a mean fixation index (across subsamples), we reserve the notation \bar{F}_{IS} for the mean fixation index across loci. Second, an excess of heterozygotes may occur if there are allele frequency differences between male and female parents (Robertson, 1965). This situation is particularly likely in a polygynous population because of the small number of breeding males. Similarly, Prout (1981) has shown that heterozygote excess may also result if there is sex-dependent migration between populations. The expected excess in a randomly-mating population due to sex-related allele frequency differences is

$$F_{exp} = 1 - \left(\sum_{i \neq j} p_i^{\circ} p_j^{\delta} \right) / \left(\sum_{i \neq j} \bar{p}_i \bar{p}_j \right) \quad (2)$$

where p° is the allele frequency among reproductive females, p^{δ} is the average allele frequency among adult males,

weighted by the number of litters fathered by each male, and \bar{p} is the overall (pooled) allele frequency. The expected value, based on parental allele frequencies, can then be compared to the observed value obtained from the offspring data. Third, heterozygotes may be in excess if selection acts before the offspring are censused, or if there are differences in fertility among the parents (Purser, 1966). The possible effects of selection on genotype proportions among the offspring are discussed later in this paper. A fourth factor, assortative mating, is assumed to be unimportant in the present study and will not be discussed further.

Adult animals were classified by several criteria (sex, reproductive condition, colony) and tested for heterogeneity in allele frequency by the "G" statistic (Sokal and Rohlf, 1969). Heterogeneity between colonies was measured by Wright's (1978) F_{ST} statistic:

$$F_{ST} = \frac{\sum_{i=1}^L \sum_{j=1}^2 (p_{ij} - \bar{p}_i)^2}{2 \sum_{i=1}^L \bar{p}_i(1 - \bar{p}_i)} \quad (3)$$

where p_{ij} is the frequency of the i th allele ($i = 1, \dots, L$) in the j th colony ($j = 1, 2$), and \bar{p}_i is the weighted mean frequency of the i th allele.

We also obtained several measures of population structure by pedigree analysis. Since 1975, the mother and probable father of each litter born at the study colony have been determined from behavioral observations (Hoogland, 1982), and starting in 1979, paternities have been confirmed by electrophoretic data (Foltz and Hoogland, 1981). Pedigrees for 126 adult animals were analyzed; 73% of the pedigrees included at least one parent, and 24% included at least one grandparent. In 27% of the cases, the adult either was an immigrant to the study colony or had been a resident since the first year that behavioral observations were taken. Allen (1965) suggested that the inbreeding coefficient obtained by pedigree analysis (F) could be

partitioned into a random component (F_r) and a nonrandom component (F_n), where

$$F_n = \frac{F - F_r}{1 - F_r} \quad (4)$$

(compare Thompson and Roberts, 1980 p. 449). Allen (1965 p. 195) noted that F_n "is negative when actual matings show avoidance of inbreeding. . . . F_n appears to be the proper quantity, rather than F , for use in any formula that involves deviation of genotype frequencies from those expected under random mating." However, F_n cannot be estimated directly from pedigree data. Instead, we calculated F_r by the following formula

$$F_r = \frac{\sum_{i=1}^N \sum_{j=1}^M \phi_{ij}}{NM} \quad (5)$$

where M is the number of adult males, N is the number of reproductive females and ϕ_{ij} is the coefficient of kinship (Jacquard, 1974) between the i th female and j th male. Thus, F and F_r are both average coefficients; F measures the average inbreeding observed in the population and F_r measures the average inbreeding expected if matings were at random.

RESULTS

As described previously (Foltz and Hoogland, 1981), four loci were polymorphic in the study colony: transferrin (Trf) was polymorphic for three alleles, esterase-1 ($Est-1$) for two alleles, nucleoside phosphorylase (Np) for three alleles, and 6-phosphogluconate dehydrogenase ($6-Pgd$) for two alleles. In addition, 21 loci were monomorphic or nearly monomorphic (rare alleles being undetected in samples of 50 or more animals): albumin, postalbumin, sorbitol dehydrogenase, lactate dehydrogenase-1, lactate dehydrogenase-2, malate dehydrogenase, glucose-6-phosphate dehydrogenase, glyceraldehyde-phosphate dehydrogenase, NADH diaphorase, indophenol oxidase, creatine kinase, adenylate kinase, phosphoglucomutase, esterase-2, peptidase-1, peptidase-2, leucine aminopeptidase, adenosine deaminase,

TABLE 1. Allele frequencies for black-tailed prairie dogs in South Dakota for 6-phosphogluconate dehydrogenase (6-Pgd), nucleoside phosphorylase (Np), esterase-1 (Est-1) and transferrin (Trf). Superscripts a, b and c designate different alleles; N denotes sample size. The data for 6-Pgd in 1979 are incomplete (due to denaturation of some samples) and have been omitted.

Year	Category	N	6-Pgd ^a	6-Pgd ^b	Np ^a	Np ^b	Np ^c	Est-1 ^a	Est-1 ^b	Trf ^a	Trf ^b	Trf ^c
1979	Total adults	99			.192	.414	.394	.286	.714	.858	.061	.081
	Reproductive females	22			.205	.409	.386	.318	.682	.795	.091	.114
	Reproductive males	22			.159	.409	.432	.477	.523	.636	.205	.159
1980	Total adults	91	.256	.744	.170	.506	.324	.275	.725	.857	.061	.082
	Reproductive females	30	.267	.733	.233	.450	.317	.233	.767	.900	.033	.067
	Reproductive males	30	.300	.700	.117	.633	.250	.267	.733	.750	.117	.133
1981	Total adults	83	.247	.753	.193	.422	.385	.283	.717	.825	.109	.066
	Reproductive females	37	.324	.676	.203	.459	.338	.284	.716	.838	.095	.067
	Reproductive males	37	.189	.811	.176	.432	.392	.297	.703	.703	.176	.121
1981	Shirttail Canyon	17	.147	.853	.206	.235	.559	.412	.588	.941	.059	.000

fumarase, mannose phosphate isomerase and phosphoglucose isomerase. The proportion of loci that were polymorphic was 0.160, and the average number of alleles per locus was 1.240. Based on all adult animals alive in 1980, the mean observed heterozygosity per individual per locus was 0.068, and the expected heterozygosity was 0.066.

Estimates of allele frequencies for each locus are shown in Table 1 for each year of the study. The total allele frequency estimates are based on all adults alive at the main study colony in a given year. Separate estimates are also given for two categories of adults: reproductive females and reproductive males. These estimates correspond, respectively, to p° and p^{δ} in expression (2). There was little heterogeneity in allele frequency between the sexes or among years for any locus. Table 1 also gives estimates of allele frequencies for all polymorphic loci in the Shirttail Canyon sample. None of these values was significantly different from the corresponding value for the study colony in 1981, when tested by the G statistic. However, the pooled G statistic was significant (13.93, 6 *d.f.*, $P < .03$), indicating moderate heterogeneity between colonies. The mean F_{ST} value between colonies for the four loci was .028 (range: .020-.037).

Genotype frequencies and estimates of within-population fixation indices for offspring born in the main study colony are

presented in Table 2. Nine of the 11 indices were negative, indicating an excess of heterozygotes, but different loci exhibited different patterns. *Est-1* consistently exhibited the greatest excess of heterozygotes, whereas *Np* showed either a slight excess of heterozygotes or a deficiency (in 1981). *Trf* exhibited a moderate excess of heterozygotes in all years. The \bar{F}_{IS} values for 1979, 1980 and 1981 were $-.085$, $-.075$ and $-.022$, respectively; the grand mean was $-.058$. None of the 11 fixation indices was significantly different from 0, when tested by the G statistic. However, the 95% confidence interval for the grand mean ($-.097$, $-.018$) did not include zero, suggesting an overall tendency for genotype proportions to depart from the Hardy-Weinberg expectations in the direction of heterozygote excess. To determine if the F_{IS} values were homogeneous across loci and across years, we performed a two-way analysis of variance on the fixation indices calculated for the various subsamples, using the approach of Neel and Ward (1972). The F_{IS} values were homogeneous across years but not across loci; the interaction term was nonsignificant (Table 3).

The significant heterogeneity in F_{IS} values across loci suggested a possible role for selection, and prompted a more detailed examination of the genetic structure of the main study colony. We examined the potential effect of selection on genotype proportions in two ways. First, we counted

TABLE 2. Genotype frequencies, F_{IS} values and G statistics for fit to Hardy-Weinberg proportions among offspring born in a black-tailed prairie dog colony. Expected F_{IS} values, from expression (2), are shown in parentheses. d.f. denotes degrees of freedom; other notation as in Table 1.

Year	N	6-Pgd					Np							
		a/a	a/b	b/b	F_{IS}	G (1 d.f.)	a/a	a/b	b/b	a/c	b/c	c/c	F_{IS}	G (3 d.f.)
1979	58						.052	.086	.207	.121	.431	.103	-.018 (-.002)	4.73
1980	82	.049	.415	.536	-.079 (-.001)	.58	.012	.244	.280	.110	.256	.098	-.001 (-.021)	3.23
1981	117*	.068	.385	.547	-.006 (-.024)	.01	.061	.112	.233	.172	.293	.129	.087 (-.002)	5.99
Year	N	Est-1					Tpf							
		a/a	a/b	b/b	F_{IS}	G (1 d.f.)	a/a	a/b	b/b	a/c	b/c	c/c	F_{IS}	G (3 d.f.)
1979	55**	.091	.564	.345	-.170 (-.026)	2.19	.463	.296	.000	.148	.074	.019	-.067 (-.023)	4.84
1980	82	.024	.415	.561	-.138 (-.002)	2.36	.756	.098	.000	.146	.000	.000	-.080 (-.028)	2.65
1981	117*	.060	.466	.474	-.111 (-.001)	1.72	.513	.325	.000	.110	.026	.026	-.070 (-.018)	12.54

* 116 for Np and Est-1.
 ** 54 for Tpf.

TABLE 3. Analysis of variance of F_{IS} values among offspring born in a black-tailed prairie dog colony. Notation as in Table 2.

Source of variation	d.f.	Mean square	F-value
Within	41	.01823	
Locus	3	.06687	3.67*
Year	2	.02802	1.54
Locus \times year	5	.00707	.39

* $P < .02$.

the numbers of heterozygous and homozygous offspring born to heterozygous females. For a two-allele system, heterozygous females are expected to produce 50% heterozygous offspring if there are no selective differences among genotypes. This expectation does not depend on the paternal genotype(s) or on the mating system (e.g., multiple paternity, inbreeding), and is thus fairly robust. Unfortunately, this test does not generalize to systems of more than two alleles. Therefore, in applying the test we combined rare alleles as necessary to reduce each polymorphic locus to two alleles. Analysis of segregation ratios among offspring born to heterozygous females revealed a significant excess of heterozygotes ($P < .05$) in one of 11 cases (*Est-1* in 1981); however, the pooled G statistic was not significant (9.88, 11 d.f., $P > .5$). In six cases there was a deficiency of heterozygous offspring and in five cases heterozygotes were in excess. In general, there was no tendency for heterozygous females to produce an excess of heterozygous offspring. Second, for each locus we performed a one-way analysis of variance on the square-root transformed litter sizes classified according to maternal genotype; significant differences in mean litter size would suggest possible selective differences among genotypes. For all loci tested, we observed no significant effect of maternal genotype on mean litter size in any of the three years.

Only in 1981 was a probable case of inbreeding (father-daughter) observed which resulted in offspring. Because 37 females in the main study colony produced litters that year, the observed inbreeding

coefficient (F) was .25/37 or .007. In all other years of this study, the observed inbreeding coefficient was 0. In each year, however, the number of observed cases of inbreeding was less than the number expected under random mating. Therefore, F_n was negative, indicating avoidance of consanguineous matings. For 1979, 1980 and 1981, the values of F_n were $-.004$, $-.006$ and $-.003$, respectively.

DISCUSSION

From behavioral observations, Hoogland (1982) reported that prairie dogs at the study colony avoid close inbreeding, despite the small number of adults (fewer than 100 in each year of the study). Several aspects of the social system contribute to the avoidance of consanguineous matings (Hoogland, 1982). First, males usually disperse from their natal coterie territories as yearlings (thus avoiding mother-son and sister-brother matings), whereas females are more sedentary. Second, breeding males usually change their coterie of residence after one or two years (thus avoiding father-daughter matings). Third, yearling females are more likely to come into estrus when their fathers are no longer present in the home coterie than when their fathers are still present. Fourth, when adult male relatives are present in the home coterie, estrous females usually avoid them and mate with other males. However, the probable occurrence of one father-daughter mating in 1981 demonstrates that avoidance of close inbreeding in the black-tailed prairie dog is not absolute. Reports of inbreeding avoidance in other vertebrates have been reviewed by Greenwood (1980), Hoogland (1982) and Shields (1982).

One obvious limitation of our study is that consanguinity prior to 1975 was undetected in the pedigree analysis. As a result, both F and F_n increased in magnitude from year to year, reflecting the greater depth of the pedigrees in the later years of the study. Jacquard (1974 p. 171) noted that "an inbreeding coefficient cannot be regarded as an estimate of any real quantity, but is simply a measure of in-

formation." Therefore, we have not attempted to compare the inbreeding coefficients obtained by us to those reported for other species. Our results emphasize the amount of effort required to obtain information about consanguinity in a natural population. Although the data were collected over a seven-year period, the pedigrees were barely adequate to detect consanguinity.

Compared to pedigrees, electrophoretic data are easier to collect but more difficult to interpret. The mean fixation index (-0.058) was significantly different from 0, indicating an overall trend for genotype frequencies at polymorphic loci to depart from the Hardy-Weinberg expectations in the direction of heterozygote excess. The fixation indices obtained from the offspring born in the main study colony were significantly different across loci, but were homogeneous across years. This observation suggested that the heterozygote excess might be caused by selective differences among genotypes. However, there was no tendency for heterozygous females to produce more than 50% heterozygous offspring, which might have been expected if there were gametic or early zygotic selection at one or more loci. Although females heterozygous for *Est-1* produced a nominally significant excess of heterozygotes in 1981, the F_{IS} value for that locus was closer to 0 in that year than in the previous two years. Also, there were no genotype-dependent differences in average litter size, and hence no evidence for fertility or early zygotic selection. It would be interesting to repeat this analysis with a larger sample size, and to consider the effect of the male genotype on segregation ratios and litter sizes. A second explanation for differences in F_{IS} values across loci would be sex-related allele frequency differences. However, the "expected" F_{IS} values obtained from expression (2) were generally much closer to 0 than the observed values (Table 2), indicating that allele frequency differences between male and female parents can not explain all of the observed excess of heterozygotes. Per-

haps the best explanation for these results is simply that avoidance of consanguineous matings, selection and sex-related allele frequency differences are all involved in determining genotype frequencies in the offspring.

The suggestion that black-tailed prairie dogs are relatively "outbred" is supported by the high observed heterozygosity (compared to other rodents; see Smith et al., 1978) and by the moderate heterogeneity between the main study colony and the Shirttail Canyon colony. Also, rates of migration among colonies are relatively high. The average annual migration rate into the main study colony, expressed as the number of immigrants who reproduced divided by the total number of reproductively-active animals in the colony was .028 for females and .104 for males. Outbreeding may turn out to be a common explanation for heterozygote excess in natural populations, but this conclusion will require further research.

SUMMARY

The genetic structure of the black-tailed prairie dog (*Cynomys ludovicianus*) was studied by an electrophoretic analysis of four polymorphic blood proteins and by pedigree analysis. Only one probable case of close inbreeding (father-daughter) was observed in a three-year period; the average inbreeding coefficient was less than that expected if matings were at random. The evidence for nonrandom mating was consistent with behavioral observations taken at the main study colony. In nine of 11 instances, polymorphic loci exhibited an excess of heterozygotes (that is, negative fixation indices). The existence of locus-specific differences among fixation indices suggested that some factor in addition to the avoidance of close inbreeding was causing the excess of heterozygotes. Two possible explanations for this result are selective differences among genotypes and sex-related allele frequency differences. Additional evidence for outbreeding in the black-tailed prairie dog is (a) the relatively high heterozygosity within colonies, (b) the

relatively low genetic heterogeneity among colonies and (c) the high rate of male migration among colonies.

ACKNOWLEDGMENTS

We thank B. Balog, C. Bertsch, D. Boyd, K. Campbell, K. Clowser, W. Dolphin, C. Flory, P. Hardison, L. Holvenstot, J. G. Hoogland, M. Killebrew, V. Kraupa, I. Kroot, J. Little, P. McCarthy, D. Miller, L. Moore, M. Mulhollam, D. Olson, L. Reich, T. Welch, and W. Wong for field assistance and J. Gee and L. Whitcomb for laboratory assistance. We also thank M. R. Rose and E. Zouros for helpful discussions and R. K. Selander, P. W. Sherman, P. E. Smouse and three anonymous reviewers for comments on an earlier draft of this paper. Any remaining errors are, of course, our own. This research was supported by an NIH post-doctoral fellowship to Foltz and by National Geographic Society grants 78-1860 and 79-2063 and NSF grants BNS 77-15594 and BNS 79-24093 to Hoogland. Additional support was provided by the University of Minnesota and by the Whitehall Foundation of Princeton University.

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