LEVELS OF INBREEDING AMONG PRAIRIE DOGS

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Abstract.—Because inbreeding and outbreeding both involve distinct benefits, some optimal level of inbreeding-outbreeding should result under natural conditions. Testing this hypothesis has been difficult, mainly because the detailed pedigrees necessary for defining levels of inbreeding have been unavailable for animals other than humans. A 14-yr study of black-tailed prairie dogs (Cynomys ludovicianus) has shown that individuals avoid extreme inbreeding with close kin such as parents, offspring, and full and half siblings, but they regularly inbreed with more distant kin such as full and half first cousins, full and half first cousins once removed, full and half second cousins, and so on. Previous research with other wild animals has not documented such a high frequency of moderate inbreeding. An examination of five measures of reproductive success failed to reveal inbreeding depression.

Advantages of outbreeding include reduced exposure of deleterious recessive alleles, increased overdominance or heterosis, and maximization of the advantages of sexuality itself, such as increased resistance to diseases, parasites, and drastic environmental changes (Ford 1964; Williams 1975; Falconer 1981; Hamilton and Zuk 1982; Mitton and Grant 1984; Stearns 1987; Michod and Levin 1988; O'Brien and Evermann 1988; Charlesworth 1989; Kirkpatrick and Jenkins 1989; Pomiankowski 1989; Tooby and Cosmides 1990). However, inbreeding also has advantages, such as increased maintenance of coadapted gene complexes and greater ease and safety in finding mates (Dobzhansky 1951; Ghiselin 1969; Alexander 1977; Bateson 1978, 1980, 1983; Price and Waser 1979; Shields 1982, 1993; Partridge 1983; Keane 1990; Rowley et al. 1993; Smith 1993). Natural selection should thus favor individuals that balance the costs and benefits of inbreeding and outbreeding, and some optimal level of inbreeding-outbreeding should result. Previous long-term studies have shown that individuals in numerous species usually copulate with members of the same local population (i.e., do not maximally outbreed with members of other populations) but avoid inbreeding with close kin (Woolfenden and Fitzpatrick 1984; Brown 1987; Koenig and Mumme 1987). However, mainly because of the difficulties of assigning paternities and tracking genealogies over an extended period of time, precise quantification of inbreeding-outbreeding under natural conditions is unavailable for animals other than humans. Using information from a 14-yr study, I report here that black-tailed prairie dogs (Sciuridae: Cynomys ludovicianus) systematically avoid copulating with close kin such as parents, offspring, and full and half siblings. However, prairie

dogs regularly inbreed with more distant kin such as full and half first cousins, full and half first cousins once removed, full and half second cousins, and so on.

METHODS

What, exactly, do the terms inbreeding and outbreeding mean? The terms are relative, of course, and mean different things to different investigators (Alexander 1979; Shields 1982, 1993; Bateson 1983; Partridge 1983; van den Berghe 1983). Here I define extreme inbreeding as copulation with an individual with whom the coefficient of genetic relatedness, r, is greater than or equal to 0.2500. Extreme inbreeding thus includes copulations that involve father and daughter ($r = 0.5000$), mother and son ($r = 0.5000$), full siblings ($r = 0.5000$), grandmother and grandson ($r = 0.2500$), grandfather and granddaughter ($r = 0.2500$), half siblings ($r = 0.2500$), full aunt and full nephew ($r = 0.2500$), and full uncle and full niece ($r = 0.2500$). I define moderate inbreeding as copulation with an individual for which $0.2500 > r \geq 0.0078$. Moderate inbreeding thus includes copulations that involve more distant kin such as full and half great uncle and full and half great niece ($r = 0.1250$ and $r = 0.0625$), full and half great aunt and full and half great nephew ($r = 0.1250$ and $r = 0.0625$), full and half first cousins ($r = 0.1250$ and $r = 0.0625$), full and half first cousins once removed ($r = 0.0625$ and $r = 0.0313$), full and half first cousins twice removed ($r = 0.0313$ and $r = 0.0156$), full and half second cousins ($r = 0.0313$ and $r = 0.0156$), full and half second cousins once removed ($r = 0.0156$ and $r = 0.0078$), full second cousins twice removed ($r = 0.0078$), and full third cousins ($r = 0.0078$). Finally, I define outbreeding as copulation with an individual for which $0.0078 > r \geq 0.0000$. Outbreeding thus includes copulations with distant kin such as half third cousins ($r = 0.0039$), full and half third cousins once removed ($r = 0.0039$ and $r = 0.0020$), full and half fourth cousins ($r = 0.0020$ and $r = 0.0010$), and so on, as well as all copulations for which there was no known kinship ($r = 0.0000$).

Prairie dogs are large (500–1,000 g for adults), diurnal, herbivorous, colonial rodents that live in cooperative, territorial, harem-polygynous family groups called coteries (King 1955). Coteries typically contain one adult (≥ 2 yr old) male, three to four adult females, and several yearling and juvenile offspring (Hoogland 1985). My study colony in Wind Cave National Park, South Dakota, occupied 6.6 ha and each year contained approximately 125 adults and yearlings, 80 juveniles, and 22 coteries (Hoogland 1986). For 14 consecutive years (1975–1988), I ear-tagged and color marked all adult, yearling, immigrant, and juvenile prairie dogs at the study colony (Hoogland et al. 1988, 1989). Maternal and sibling genetic relationships were easy to determine because single females associated with isolated litters for approximately 6 wk until the first emergence of juveniles from the natal burrow (King 1955; Hoogland 1985).

Paternity inferred from patterns of pairing can be misleading in studies of inbreeding (Greenwood et al. 1978; Koenig et al. 1984; Rowley et al. 1986; Craig and Jamieson 1988; Gibbs and Grant 1989), because females "paired" to one male frequently copulate with, and are inseminated by, a different male (Wrege and Emlen 1987; Brown and Brown 1988; Sherman and Morton 1988). I assigned

paternities necessary for determining precise prairie dog pedigrees from a combination of (a) detailed behavioral observations of the male(s) that copulated with each female during her single 3–4-h period of estrus each year (1978–1988) and (b) electrophoretic analyses of blood samples from all possible parents and all but one of the 981 juveniles from 278 litters weaned at the study colony from 1978 through 1988 (Hoogland and Foltz 1982; J. L. Hoogland, unpublished manuscript).

I used conventional analysis of pedigrees (Crow and Kimura 1970; Falconer 1981; Shields 1982) to calculate the value of r for the male and female of each copulating pair, who sometimes had more than one common ancestor. Coefficients were available for 770 copulations by 557 estrous females. The number of known generations per pedigree (mean ± SD) was 3.96 ± 1.33. The number of different copulating males per estrous female (mean ± SD) was 1.38 ± 0.60 (range = 1–4). When $r > 0.0000$, r ranged from 0.0020 to 0.5039. Of the 770 copulations, 234 (30%) involved inbreeding at some level (i.e., $r \geq 0.0078$), and 194 of 557 estrous females (35%) copulated with at least one male relative of $r \geq 0.0078$.

RESULTS AND DISCUSSION

Early in my research I learned that prairie dogs systematically avoid extreme inbreeding by four different mechanisms (Hoogland 1982; Foltz and Hoogland 1983). First, young males depart from the natal coterie territory before sexual maturity whereas females usually remain there for their entire lifetimes. Second, older males usually do not remain in the same breeding coterie territory for more than 2 consecutive years and consequently have dispersed to a new breeding coterie territory before their daughters reach sexual maturity at the usual age of 2 yr. Third, father-daughter inbreeding is unlikely for another reason: females sometimes first copulate as yearlings, but a yearling female is significantly less likely to come into estrus when her father is still in her natal coterie territory. Fourth, when related sexually mature prairie dogs of the opposite sex end up in the same coterie territory in spite of the first three mechanisms, estrous females frequently refuse to copulate with close male kin but rather solicit copulations from unrelated males of other coteries.

These four mechanisms worked well, but not perfectly: 36 of 770 copulations (5%) involved a sexual partner of $r \geq 0.2500$. However, coupled with these 36 copulations were three intriguing lines of evidence indicating that the females tried to avoid extreme inbreeding (Hoogland 1982; J. L. Hoogland, unpublished manuscript). (a) The behavioral observations sometimes indicated such a struggle. For example, females R70 and R78 were yearling full sisters whose father was still in their natal coterie territory. Both females came into estrus on the same day in 1986, when they repeatedly left the home coterie territory and tried to copulate with either of the two breeding males in the adjacent multimale coterie territory. However, both females were repelled by the females of the adjacent territory. Neither female was able to copulate with an unrelated male, and each ended up copulating at the end of the day with her father. (b) Females that copulated with a closely related male were significantly more likely to copulate

TABLE 1

Observed versus Expected Frequencies of Inbreeding in 1988

Coefficient of Genetic Relatedness (r) between Male and Female of Copulating Pair	Observed Number of These Copulatory Pairs	Expected Number of These Copulatory Pairs
$r \geq 0.2500$	6	6*
$0.2500 > r \geq 0.1250$	4	5
$0.1250 > r \geq 0.0625$	18	10
$0.0625 > r \geq 0.0313$	12	12
$0.0313 > r \geq 0.0156$	10	11
$0.0156 > r \geq 0.0078$	3	7
$0.0078 > r \geq 0.0000$	8	8
No known kinship ($r = 0.0000$)	8	10
Total	69	69

Note.—For the 44 estrous females and 17 sexually active males in 1988 (18 coteries), I computed the $44 \times 17 = 748$ r-values for all possible copulatory pairs. I then used these r-values to calculate the expected value for each type of inbreeding if choice of mates was unrelated to r. For example, 131 of 748 possible pairings (18%) included a male and female for which $0.0625 > r \geq 0.0313$. The expected number of copulations for which $0.0625 > r \geq 0.0313$ was therefore $18\% \times 69 = 12$. Observed values did not differ from expected values, which indicates that choice of mates was independent of r ($P = .227$, chi-square goodness-of-fit test, df = 7).

* Five of these six cases of extreme inbreeding involved a pair of 2-yr-old full brothers who moved into a breeding coterie containing females sired by their father. The males had not associated with the females during much of their first year and probably did not recognize them as their half sisters (see text).

with a second (unrelated) male as well. Copulation with a second male would, of course, mean that resulting offspring might be sired by the unrelated rather than the related sexual partner. (c) Females were significantly more likely to avoid copulating with male close kin with whom they had continuously associated since first juvenile emergence. Most of the cases of extreme inbreeding resulted after the related pair had lived in different coterie territories for a year or more, which suggests that unbroken familiarity with genetic relatives in the home coterie territory is crucial for the avoidance of extreme inbreeding. For example, five of the six cases of extreme inbreeding in 1988 involved consanguineous sexual partners who had been living in different coterie territories for most of the first year (see below and table 1).

After learning that prairie dogs systematically avoid extreme inbreeding, I wondered whether they also avoid less extreme inbreeding with more distant kin. As time passed and the prairie dog pedigrees became more complete, I was in a unique position to investigate this important question. Figure 1 provides the answer: although they avoided extreme inbreeding, prairie dogs regularly practiced less extreme, moderate inbreeding with distant kin such as full and half first cousins, full and half first cousins once removed, full and half second cousins, and so on. More specifically, 198 of 770 copulations (26%) involved moderate inbreeding, and 161 of 557 estrous females (29%) copulated with at least one male
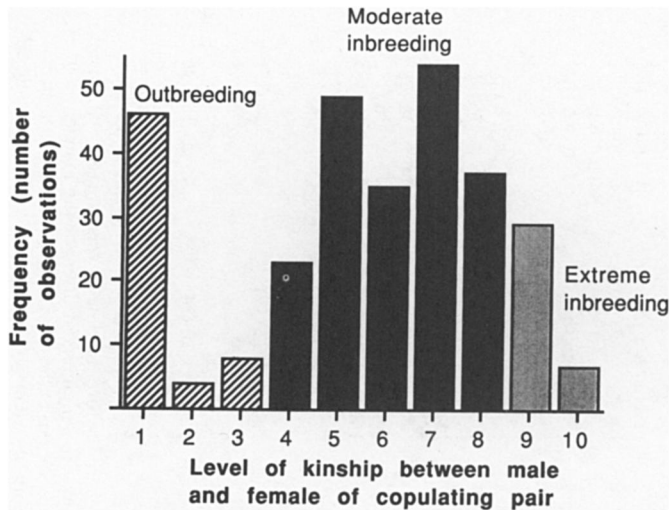
FIG. 1.—Frequencies of different levels of inbreeding in a natural population of prairie dogs. Maternal and sibling genetic relationships resulted from the marking of entire litters associated with single mothers from 1975 through 1988 (Hoogland 1986). Paternal genetic relationships resulted from detailed behavioral observations of copulations in combination with electrophoretic analyses of blood samples from all possible parents and 980 juveniles (Hoogland and Foltz 1982). Not shown here are data from 478 copulations with no known kinship between the male and female. For level 1 of kinship, $0.5000 > r > 0.0000$ but the exact value of r was unknown; for most cases of level 1, r was probably less than 0.0625. For level 2, $0.0039 > r > 0.0000$. For level 3, $0.0078 > r \geq 0.0039$. For level 4, $0.0156 > r \geq 0.0078$. For level 5, $0.0313 > r \geq 0.0156$. For level 6, $0.0625 > r \geq 0.0313$. For level 7, $0.1250 > r \geq 0.0625$. For level 8, $0.2500 > r \geq 0.1250$. For level 9, $0.5000 > r \geq 0.2500$. For level 10, $1.0000 > r \geq 0.5000$.

relative for which $0.2500 > r \geq 0.0078$ (fig. 1). Other researchers have documented inbreeding at various levels within natural populations (Shields 1982; Ralls et al. 1986; Chepko-Sade and Halpin 1987; Gibbs and Grant 1989) but not at such a high frequency.

Despite the high observed frequency of moderate inbreeding (fig. 1), estrous females might have actively solicited the males with whom the coefficient of genetic relatedness was lowest, such that the observed frequency was lower than the expected frequency. In other words, prairie dogs might have tried to avoid moderate as well as extreme inbreeding whenever possible. For example, individuals might have systematically solicited immigrants who were presumably more outbred than individuals born and reared at the study colony. Alternatively, individuals might have been like white-footed mice (*Peromyscus leucopus;* Keane 1990) that promote moderate inbreeding by systematically choosing mates for which $0.2500 > r \geq 0.0078$. To investigate these important issues, I would have preferred to compare r-values for members of all observed copulating pairs ($N = 770$) and all possible copulating pairs ($N = 13,847$) for 1978–1988. However, I was deterred by the herculean task of computing so many r-values for possible

TABLE 2

REPRODUCTIVE SUCCESS OF INBRED AND OUTBRED PRAIRIE DOG LITTERS

Coefficient of Genetic Relatedness (r) between Male and Female of Copulating Pair	Probability of Producing Emergent Litter	Litter Size at First Juvenile Emergence	Juvenile Weight at First Juvenile Emergence	Number of Emergent Young That Survive through the First Year	Proportion of Emergent Young That Survive through the First Year
1.0000 > r ≥ 0.5000	.500 (6)	3.00 ± 1.73 (3)	148 ± 27.5 (4)	1.33 ± 1.16 (3)	.67 ± .58 (3)
0.5000 > r ≥ 0.2500	.615 (26)	3.25 ± .97 (12)	151 ± 20.5 (12)	1.78 ± 1.39 (9)	.48 ± .38 (9)
0.2500 > r ≥ 0.1250	.484 (31)	3.11 ± 1.05 (9)	143 ± 31.5 (9)	1.78 ± 1.20 (9)	.61 ± .33 (9)
0.1250 > r ≥ 0.0625	.460 (50)	3.35 ± 1.11 (17)	154 ± 25.9 (17)	2.00 ± .97 (16)	.64 ± .32 (16)
0.0625 > r ≥ 0.0313	.533 (30)	3.08 ± 1.12 (13)	153 ± 19.7 (13)	.57 ± .79 (7)	.24 ± .38 (7)
0.0313 > r ≥ 0.0156	.559 (34)	3.11 ± .83 (18)	149 ± 21.7 (18)	1.41 ± 1.06 (17)	.47 ± .36 (17)
0.0156 > r ≥ 0.0078	.500 (16)	3.78 ± .44 (9)	160 ± 20.4 (9)	1.86 ± 1.21 (7)	.49 ± .31 (7)
0.0078 > r ≥ 0.0039	.500 (4)	. . . (0)	. . . (0)	. . . (0)	. . . (0)
0.0039 > r ≥ 0.0010	.000 (1)	. . . (0)	. . . (0)	. . . (0)	. . . (0)
r > 0.0000 but exact value of r unknown	.368 (38)	2.75 ± 1.18 (16)	167 ± 40.2 (17)	1.88 ± 1.22 (17)	.69 ± .36 (17)
No known kinship, but copulation did not involve immigrant (r = 0.0000)	.510 (253)	3.16 ± 1.08 (147)	152 ± 33.4 (148)	1.53 ± 1.30 (146)	.49 ± .38 (146)
Copulation with immigrant (r = 0.0000)	.484 (64*)	3.00 ± 1.15 (33)	151 ± 41.4 (32)	1.86 ± 1.46 (29)	.62 ± .43 (29)

NOTE.—Numbers are means ± 1 SD. I excluded those cases in which the copulating female disappeared before the time of weaning ($N = 4$). Sample sizes in parentheses indicate either the number of females that copulated (for the probability of producing an emergent litter) or the number of litters that emerged from the natal burrow (for the other four measures of reproductive success). For juvenile weight at first emergence from the natal burrow, I used a single mean weight for the entire litter for all statistical analyses. In cases of no known kinship ($r = 0.0000$) that did not involve an immigrant, I could always trace genealogies back at least one full generation. All pairwise and multivariate analyses were statistically insignificant ($P > .050$ for all), which suggests that prairie dogs under natural conditions do not experience inbreeding depression.

* These 64 copulations involved three different female immigrants and 15 different male immigrants.

combinations over an 11-yr period. I therefore chose a more manageable data set and analyzed copulations from 1988 only and compared the r-values for the 69 observed copulations and the 44 (number of estrous females) $\times$ 17 (number of sexually active males) = 748 possible copulations. Table 1 shows a close agreement between the observed frequencies and the expected frequencies if choice of mates was independent of r. Like other animals (Read and Harvey 1989), prairie dogs neither avoided nor promoted moderate inbreeding. Moderate inbreeding was nonetheless common simply because possible mates for which $0.2500 > r \geq 0.0078$ were so common.

Figure 1 and table 2 include data both from early years of the study (when the known pedigree for each individual was short, sometimes extending back only one generation) and from later years (when pedigrees were longer) and therefore underestimate the frequency of different levels of inbreeding among prairie dogs. Many of the cases with $r = 0.0000$ (no known kinship) in table 2, for example, were from early years and probably involved undetected low levels of inbreeding. In 1988, when genealogies were most complete—sometimes including pedigrees that went back as far as six generations—every one of the 44 estrous females (100%) copulated with at least one male with whom she shared at least one known common ancestor. Of the 69 copulations in 1988 by these 44 estrous females, eight (12%) involved pairs with no known common ancestor, eight (12%) involved a distant male kin for which $0.0078 > r > 0.0000$, 47 (68%) involved moderate inbreeding, and six (9%) involved extreme inbreeding.

The most common type of extreme inbreeding involved half siblings ($N = 13$), but six cases resulted when fathers copulated with their daughters. Most cases of moderate inbreeding resulted from movements of male relatives into the female's home coterie territory. Matings involving full first cousins resulted, for example, when female A's full brother dispersed into a breeding coterie territory and produced a son who then dispersed back into female A's coterie territory and copulated with female A's philopatric daughters. Because individuals of both sexes typically remain in the natal coterie territory for at least the first 11 mo after first juvenile emergence from the natal burrow (King 1955; Hoogland 1985, 1986), familiarity probably would make it easy for prairie dogs to learn to recognize close kin such as parents, offspring, full and half siblings, full aunts, and so on, as members of the same home (natal or breeding) coterie. However, the recognition of genetic relatives born in different coteries would be more difficult and probably would require some sort of "kin recognition" in the absence of long-term familiarity (Holmes and Sherman 1982, 1983; Waldman et al. 1988), for which evidence from prairie dogs under natural conditions is lacking (Hoogland 1983, 1986). In proximate terms, then, the avoidance of extreme inbreeding coupled with the prevalence of moderate inbreeding may result because prairie dogs can easily learn to recognize and avoid close kin (as members of the home coterie) but cannot easily recognize and avoid more distant kin from different, nonhome coteries. In ultimate terms, the coupling probably results from the natural selection of individuals that strike a balance between maximal inbreeding and maximal outbreeding (Alexander 1977; Shields 1982; Bateson 1983; Partridge 1983; Keane 1990). If the avoidance of moderate as well as extreme inbreeding were important

to prairie dogs, then natural selection would presumably favor mechanisms that allow recognition of more distant kin in the absence of long-term familiarity.

Measuring levels of inbreeding under natural conditions is difficult, but measuring possible costs and benefits of inbreeding and outbreeding under natural conditions is even more difficult. As discussed below, I was able to examine two possible costs (inbreeding depression and lost mating opportunities) and two possible benefits (overdominance and ease of finding mates).

Inbreeding depression is the reduction in fitness of offspring due mainly to the increased exposure of deleterious recessive alleles in consanguineous matings (Crow and Kimura 1970; Falconer 1981; Ralls et al. 1986). Numerous investigators have demonstrated inbreeding depression in plants (Falconer 1981; Shields 1982) and in domestic, zoo, and laboratory populations of animals (Lasley 1978; Seal 1978; Connor and Belluchi 1979; Ralls et al. 1979, 1988; Warwick and Legates 1979). However, evidence from natural populations of nonhuman animals is almost nonexistent. Possible exceptions include the research on great tits (*Parus major*) by Greenwood et al. (1978) and van Noordwijk and Scharloo (1981), but paternities in these studies were precariously inferred from patterns of pairing.

Inbreeding depression among prairie dogs would clarify the observed avoidance of extreme inbreeding, and I was fully expecting to find such depression. However, table 2 indicates that wild prairie dogs did not experience inbreeding depression. Any pairwise (comparing more and less extreme levels of inbreeding) or multivariate analysis failed to show a significant depression (at the level of $P \leq$ .050) for any of the five estimates of reproductive success. Evidence for depression was even absent in the comparisons involving immigrants, the most outbred of all possible mates for prairie dogs at the study colony ($P > .100$ for all). In view of the apparent absence of inbreeding depression, the avoidance of extreme inbreeding remains puzzling.

Even though the sample sizes in table 2 are among the largest ever reported for a natural population, inbreeding depression may still occur among prairie dogs in some fashion that I could not easily detect, for at least three reasons. (*a*) The severity of inbreeding depression usually varies directly with the intensity of inbreeding (Crow and Kimura 1970; Falconer 1981; Ralls et al. 1988). Thus, it may be that significant depression occurs only in the most extreme cases of inbreeding ($r \geq 0.5000$, e.g., for which sample sizes were small because of avoidance) but does not occur at lower levels of inbreeding ($0.5000 > r \geq 0.0078$, for which sample sizes were much larger). (*b*) Shooting and poisoning have probably reduced prairie dog numbers by over 90% during the last century (Clark 1979; Halpin 1987). Populations may have lost most deleterious recessive alleles while passing through this ''genetic bottleneck'' (Shields 1982; Templeton 1987), so that inbreeding depression in today's populations is not easily detectable. (*c*) Finally, the selective disadvantage of extreme inbreeding in prairie dogs may be only about 1%–2%, which probably would be sufficient to lead to the avoidance of extreme inbreeding but which would require huge sample sizes for detection under natural conditions (Fisher 1965; Falconer 1981).

As noted above, female prairie dogs usually refuse to copulate with closely related sexually mature males that are in the home coterie territory. Such discrim-

inating females sometimes are unable to copulate with unrelated males from other coteries and pay the cost of avoiding extreme inbreeding by losing a breeding season. For example, female R63 refused to copulate with the only adult male in her coterie, her father, when she was in estrus in 1986. Female R63 was unable to solicit a copulation from any of the males living in any of the adjacent coteries and therefore did not conceive in 1986.

For a variety of reasons (Dobzhansky 1951; Ford 1964; Mitton and Grant 1984; Zouros and Foltz 1987), heterozygosity at one or more loci sometimes results in increased survival and reproduction. When such overdominance (heterosis or heterozygote superiority) occurs, natural selection will favor outbreeding over inbreeding because the former is more likely to produce heterozygotes (Fisher 1965; Falconer 1981). Data from five polymorphic loci indicate that neither maternal nor juvenile heterozygosity affected survival or reproductive success among prairie dogs sampled over a 7-yr period (Foltz et al. 1988). The possibility remains, however, that overdominance may occur at other polymorphic loci that I could not score via electrophoresis.

When a prairie dog male successfully disperses, his new coterie territory is usually either adjacent to the former coterie territory or more distant but still within the boundaries of the same home colony (Hoogland 1982). Rarely, the new coterie territory is in a different colony that can be as far away as several kilometers (Garrett and Franklin 1988). Predation on males that attempt to move between colonies—away from burrows and scanning, alarm-calling conspecifics—is high (Hoogland 1981, 1983; Garrett and Franklin 1988)—much higher than the predation on those males that remain in the safety of the home colony and breed with distant kin. Thus, males that moderately inbreed within the home colony find mates more easily and safely and usually outreproduce those outbreeding males that risk dispersal away from the home colony.

Although the study colony was large when compared with colonies used in previous research (King 1955; Tileston and Lechleitner 1966; Halpin 1987; Garrett and Franklin 1988), it was small relative to most prairie dog colonies that contain thousands of residents. Before the recent reduction in prairie dogs, colonies sometimes contained hundreds of thousands, and even millions, of residents (McNulty 1971; Clark 1979; Hoogland 1981; Halpin 1987). In these larger colonies, males have more opportunities to disperse to distant coterie territories— sometimes as far as several kilometers away—while still remaining in the safety of the home colony. Consequently, levels of inbreeding at these larger colonies might be lower than those observed at my study colony. Additional studies are necessary for a better understanding of the levels of inbreeding under natural conditions.

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