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Authors: Manno, Theodore G., Dobson, F. Stephen, Hoogland, John L., and Foltz, David W.

Source: Journal of Mammalogy, 88(2) : 448-456

Published By: American Society of Mammalogists

URL: <https://doi.org/10.1644/06-MAMM-A-099R1.1>

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SOCIAL GROUP FISSION AND GENE DYNAMICS AMONG BLACK-TAILED PRAIRIE DOGS (*CYNOMYS LUDOVICIANUS*)

THEODORE G. MANNO,* F. STEPHEN DOBSON, JOHN L. HOOGLAND, AND DAVID W. FOLTZ

Department of Biological Sciences, Auburn University, Auburn, AL 36849, USA (TGM, FSD)

Appalachian Laboratory, University of Maryland Center for Environmental Studies, Frostburg, MD 21532, USA (JLH)

Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA (DWF)

Social groups of philopatric female kin coupled with male-biased dispersal characterize many mammalian species. Such groups exhibit genetic properties, or gene dynamics (i.e., changes in genetic correlations), that potentially facilitate the evolution of group cohesion and cooperation. When groups fission, changes in gene dynamics occur that might affect cooperation. The distribution of females among coalitions newly formed via fission also may promote reproductive success by alleviating intraspecific competition. Families of black-tailed prairie dogs (*Cynomys ludovicianus*), called coterie, were observed during a 15-year study at Wind Cave National Park, South Dakota, and pedigrees of individuals were determined from livetrapping and electrophoretic analyses of paternity. We investigated the importance of coterie size, coterie density, and coancestry on the probability of fission; the effect of fissions on survivorship and territorial boundaries of coterie; and gene dynamics during and after fissions. Most new coterie occupied a subsection of the original territory. New coterie that contained a single female became extinct after about 1 year and their territories were usurped by adjacent coterie. Large coterie were more likely than smaller coterie to fission, but female coancestry within coterie usually did not influence the likelihood of fission, or the individuals that banded together in new groups. Members of new coterie interacted hostilely in the year after fission, but 1 or 2 generations elapsed before the new coterie became genetically distinct. We conclude that fission is probably driven by intraspecific competition within coterie rather than coancestry, and that coancestry does not explain the abrupt cessation of cooperation between individuals of the new coterie that result from fission.

Key words: coancestry, competition, cooperation, *Cynomys ludovicianus*, dispersal, fission, gene dynamics, kinship, philopatry, prairie dogs

The evolution of cooperation most commonly occurs within groups of close kin (Brown 1987; Chesser 1998; Hamilton 1964; Wilson 1975). Thus, patterns of philopatry and dispersal might influence the evolution of sociality (Dobson, in press). Long-term studies of mammals yield numerous examples of groups that are based on philopatric female kin in combination with male-biased dispersal (e.g., Dobson 1982; Greenwood 1980). In some species, groups split and females redistribute among several new groups near their natal area (e.g., Chepko-Sade and Sade 1979; Cords and Rowell 1986; Melnick and Kidd 1983). These “fissions” are important for 3 reasons. First, individuals that split from the original group and settle other

areas can improve their reproductive success, and thereby will promote gene flow (Armitage 1991; Chesser 1983; Halpin 1987; Templeton 1980). Second, fission can elevate coancestry (the average genetic correlation between members of a group—Sugg et al. 1996; Wright 1922) if close kin band together in the formation of new groups (e.g., Chepko-Sade et al. 1989; de Ruiter and Geffen 1998; Nash 1976; but see Harris and Murie 1984). Third, fission can alleviate competition by splitting groups that exceed some optimal size (e.g., Armitage 1987; Aviles 2000; Franks 1989; Oi 1988; Packer et al. 1990).

Black-tailed prairie dogs (*Cynomys ludovicianus*; hereafter, simply “prairie dogs”) are colonial, diurnal, and herbivorous ground-dwelling squirrels that are active all year except during severe winter weather (Hoogland 1995; King 1955; Lehmer et al. 2001). Within colonies, individuals live in territorial breeding groups called coterie (King 1955) that typically contain 1 breeding adult (> 2 years old) male, 2–4 breeding adult females, and 1 or 2 nonbreeding yearlings of both sexes; the generation

* Correspondent: mannotg@auburn.edu

time for prairie dogs is usually about 3 years (Dobson et al. 2004). The area and configuration of the home coterie territory usually remain constant across years despite substantial fluctuations in coterie size (King 1955). Males usually disperse from the natal coterie before sexual maturation, but females commonly remain in the natal territory for life (Garrett and Franklin 1988; Halpin 1987; Hoogland 1995). Consequently, females within a coterie invariably exhibit high levels of coancestry, and coterie exhibit significant genetic differentiation (e.g., Dobson 2007; Dobson and Zinner 2003; Dobson et al. 1997, 1998, 2004; Sugg et al. 1996). Interactions between members of different coterie usually involve fights, chases, or territorial disputes. Interactions among coterie members, by contrast, are usually amicable, except when pregnant and lactating females are defending nursery burrows (Hoogland 1995).

From a 15-year study of black-tailed prairie dogs, Hoogland (1995) found that fissions are rare events that affect only 4% of coterie; large coterie are more likely than smaller coterie to show fission; and close kin may or may not band together within the new coterie that result from fission. We examined coterie fission further in 3 ways. First, we investigated the effect of fissions on boundaries of coterie territories and on the survival of individuals in new coterie. Second, using a multivariate approach, we examined the effects of coterie size, coterie density, and coancestry on likelihood of fission. Third, we investigated genetic patterns associated with fissions to identify the potential for kin selection to influence cooperation within and between the new coterie that result from fission. Although coterie may be typified by high coancestry among females, Chesser (1998) predicted that social group formation should not depend on coancestry alone, but that coancestry might influence the evolution of cooperation once groups form for other reasons. This idea runs counter to the intuitive hypothesis of fission into cooperative coalitions of female kin (e.g., Chepko-Sade et al. 1989). From Chesser's (1998) hypothesis, we predicted that new coterie might form without high degrees of coancestry among same-coterie females, and that individuals of high coancestry that live in adjacent new coterie might not interact amicably after fission. Coterie fissions gave us an opportunity to test these predictions for the formation of social groups.

MATERIALS AND METHODS

Behavioral observations.—One of us (JLH) studied prairie dogs from 1975 through 1989 at the Rankin Ridge Colony in Wind Cave National Park, South Dakota (Hoogland 1995). The study colony (elevation 1,300 m) occupied 6.6 ha of meadowland surrounded mostly by coniferous woodland, and measured about 500 m (north–south) by 130 m (east–west). The numbers of adult and yearling prairie dogs at the study 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; and the number of coterie averaged 21 and ranged from 15 to 26.

We captured all adult, yearling, and juvenile prairie dogs at the study colony at least once each year. Shortly after capture,

individuals were weighed, examined for sexual condition and ectoparasites, fitted with numbered metal fingerling ear tags (National Band and Tag Co., Newport, Kentucky) for permanent recognition, given distinctive markers with Nyanzol dye (Greenville Colorants, Clifton, New Jersey) for visual identification from a distance, and released at the point of capture. We observed marked prairie dogs from 5-m-high towers on the edge of the colony.

To age individuals, we calculated the time since the 1st emergence as a juvenile from the natal burrow. Juveniles were individuals that 1st emerged from their natal burrow within the last 8 months. Yearlings had 1st emerged from the natal burrow within the last 8–20 months, and adults had 1st emerged >20 months previously. Males and females usually 1st copulate at 2 years of age, but females occasionally copulate as yearlings (Hoogland 1995). Matings occur in mid-February through March, pregnancy lasts about 5 weeks, lactation lasts another 5–6 weeks, and nearly weaned young 1st emerge from their nursery burrows in May and June (Hoogland 1995). Coterie size is the number of adults and yearlings that live in the same territory; coterie density is the number of adults and yearlings per hectare.

We determined maternity and sibling–sibling relationships from observations and from capturing juveniles shortly after they 1st appeared aboveground. We determined paternity from behavioral observations of mating in combination with electrophoretic analyses of blood samples from mothers, juveniles, and all possible sires (Hoogland 1995; Hoogland and Foltz 1982). JLH followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) for animal care and use, and field methods were approved by the Institutional Animal Care and Use Committees at Princeton University and the University of Maryland.

Designation of coterie and fissions.—We assigned individuals to the same coterie if they participated in the defense of the same territory and if they spent the night in burrows located within the same territory (Hoogland 1995). We determined territorial boundaries by mapping territorial disputes between individuals within different coterie, and from interactions and feeding sites of individuals of the same coterie (Hoogland 1995). Behavioral interactions also helped us identify members of the same coterie, because, as noted above, intracoterie interactions were more amicable than intercoterie interactions.

We tracked the longevity of all new coterie until they disappeared or until research at the study colony concluded in 1989. For example, if a territory had the same boundaries for 3 consecutive years, and then subdivided into 2 smaller territories whose boundaries remained the same for 2 years, then we scored 3 longevities (1 of 3 years and 2 of 2 years). When 1 or more individuals moved into an adjacent territory or began to defend a subsection of the original home territory, we called this a fission. When a fission occurred, we named the fission with a letter (e.g., “fission A”). We then used the letter to designate the “original coterie” (e.g., A) during the year of the fission and the resultant groups as “new coterie” (e.g., A-1 and A-2). We designated coterie that showed no fission as “stable coterie.”

Pedigree estimates.—To examine the effect of coancestry on fission, we constructed pedigrees from estimates of maternity, paternity, and sibships (Hoogland 1995; Hoogland and Foltz 1982). We studied the gene dynamics among the females at the study colony by using pedigrees to estimate the average correlations of genes between the parents of individuals (mean inbreeding coefficient = F), for different individuals in the same coterie (coancestry within coterie = θ), and between individuals from different coterie (α —Chesser 1991). To calculate gene correlations, we used the methods of Sugg et al. (1996). We assigned each individual a unique identification number, and specified its sire and dam. If the sire or dam was unknown (as for immigrants or individuals already present in the population at the beginning of the study in 1975), then we assigned that sire or dam a gene correlation of zero with other colony residents. Because several years of data were needed to build pedigrees, we were only able to calculate the pedigrees for all individuals involved in fissions occurring after 1979 ($n = 17$ new coterie, $n = 8$ fissions).

The coancestry (θ) between any pair (i, j) of individuals was determined as:

$$\theta_{i,j} = 1/4(\theta_{SiSj} + \theta_{SiDj} + \theta_{SjDi} + \theta_{DiDj}), \quad (1)$$

where S and D denote the sire and dam, respectively, of the i th and j th individuals. This expression can be used to describe the way in which coancestry accumulates over the generations. The coancestry of an individual to itself is:

$$\theta_{i,i} = (1 + F_i)/2, \quad (2)$$

and the inbreeding coefficient of the progeny is equal to the coancestry of its parents:

$$F_i = \theta_{SiDi}. \quad (3)$$

The weighted average coancestry within coterie for each year was estimated by the summed pairwise values from the pedigree within the i th coterie, divided by the number of dyads in the i th coterie [$N_i(N_i - 1)/2$] (where N is the number of individuals), averaged across coterie (s) in the population (Chesser 1991; Cockerham 1967, 1969, 1973):

$$\bar{\theta} = \frac{1}{s} \sum_{i=1}^s \frac{2}{(N_i N_i - 1)} \sum_{j=1}^{N_i-1} \sum_{k=j+1}^{N_i} \theta_{i,j,k}. \quad (4)$$

Similarly, the mean correlation of gene frequencies among groups (α) for each year during 1980–1989 was determined from the mean coancestry of all dyads of individuals in different coterie:

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

In this calculation, s was again the number of coterie in the colony. To determine α for new coterie resulting from the same fission, we used this formula with s as the number of new coterie.

Statistical analysis.—We calculated all F , $\theta_{i,j}$, α , and their weighted averages and confidence intervals. Most matriline and coterie territories persisted across years, but the number of

adults and yearlings of both sexes (i.e., coterie size) varied substantially over time (Hoogland 1995). We therefore considered coterie in different years to be statistically independent ($n = 142$ coterie). For all analyses we tested for normality by using Kolmogorov–Smirnov tests, and then used nonparametric tests if the data did not meet the assumptions of normality for parametric analyses.

To investigate whether new coterie resulting from fission contained individuals that had greater coancestry than expected from chance, we calculated the average $\theta_{i,j}$ for individuals in the new coterie for the year after the fission. We then compared these values to the average $\theta_{i,j}$ for their respective original groups with Mann–Whitney U -tests. We also used 2-sample t -tests (assuming equal variances) to compare the average $\theta_{i,j}$ for coterie that fissioned against the average $\theta_{i,j}$ for all coterie that were stable. To determine if coterie density, coterie size, or mean coancestry within a coterie were predictors of fission, we conducted a binary logistic regression analysis; for this analysis, the dependent variable was the presence or absence of fission.

To determine the magnitude of genetic differences among new coterie that resulted from fission, we calculated α for the individuals in the new coterie for each year subsequent to the fission, and then used Mann–Whitney U -tests to compare the values to the mean α for all stable coterie. We determined the year in which the new coterie from the same fission were significantly different (i.e., had approximately the same α as we observed among stable coterie) using linear regression. If necessary, we extrapolated the regression line for the new coterie through the regression line for stable coterie to determine when this should have occurred. To test for equality of these slopes, we used 1-way analysis of covariance (ANCOVA), which allowed us to determine whether α degenerated significantly over time for stable coterie or for new coterie that resulted from fission (Damon and Harvey 1987).

We used Excel 2005 (Microsoft, Redmond, Washington) and Statistical Analysis Software (SAS Institute Inc. 2005) for statistical tests. Numbers shown in the text are means ± 1 SE. Standard errors indicate the number of coterie rather than the number of dyads (a conservative procedure). P values result from 2-tailed tests.

RESULTS

Dispersal and persistence of new coterie.—For the 142 coterie at the study colony from 1980 through 1989, 8 fissions occurred (5.6%). Four fissions occurred from 1975 through 1979, but we did not use these fissions for our analyses because they occurred early in the research before we had good information about coancestry. From 1980 through 1989, 7 coterie split into 2 smaller coterie in the following year, and 1 other split into 3 smaller coterie (Table 1). In 5 cases the larger of the new coterie that resulted from fission defended the larger subdivided area, and in 3 cases the larger new coterie defended the smaller area. Occasionally, prairie dogs invaded a territory, evicted all the residents there, and then continued to live there ($n = 3$). In other cases, the invading

TABLE 1.—Changes in territories of new coterie of black-tailed prairie dogs at Wind Cave National Park, South Dakota, from 1980 through 1989 (see also Hoogland 1995:table 6.1). The sum of the new coterie sizes usually differs from the original coterie size for 3 reasons: we scored juveniles in 1 year as yearlings in the following year, individuals sometimes died or disappeared shortly after a fission, and coterie sometimes contained varying numbers of breeding males before and after fission because of the transitory relationship of males with coterie.

New coterie	Year of fission	Number of females	Number of prairie dogs	Changes in original coterie territory (i.e., after fission)	Longevity of new coterie after fission
A-1 and A-2	1980	2, 5	3, 12	Both defended approximately equal subsections of the original territory	A-2 persisted until the end of the study; A-1 fissioned in 1987
B-1 and B-2	1981	5, 1	8, 2	B-1 defended a larger section of the original territory than B-2; the territory of B-2 was usurped by an adjacent coterie	B-2 became extinct in 1985 after usurpation of territory by adjacent coterie; B-1 fissioned in 1983
C-1 and C-2	1983	6, 2	7, 5	C-2 defended a larger section of the original territory than C-1; C-1 usurped an adjacent coterie territory several years later	C-2 persisted until the end of the study; C-1 fissioned in 1987
D-1, D-2, and D-3	1983	3, 5, 1	4, 16, 2	D-2 and D-1 defended larger sections of the original territory than D-3	D-1 and D-3 became extinct in 1985 after females disappeared; D-2 persisted until the end of the study
E-1 and E-2	1985	7, 1	15, 1	E-1 retained the entire original territory; E-2 usurped part of an adjacent coterie territory	E-2 became extinct in 1986 after the lone female disappeared; E-1 fissioned in 1987
F-1 and F-2	1987	5, 1	12, 3	F-1 defended most of the original territory; F-2 dispersed to the edge of the colony and defended territory; the rest of the original territory was usurped by an adjacent coterie	F-2 became extinct in 1988 after the lone female disappeared; F-1 persisted until the end of the study
G-1 and G-2	1987	7, 1	9, 3	G-1 retained the entire original territory; G-2 usurped part of an adjacent coterie territory	G-2 became extinct in 1988 after the lone female disappeared; G-1 persisted until the end of the study
H-1 and H-2	1987	8, 2	10, 4	H-2 defended a larger section of the original territory than H-1	Both H-1 and H-2 persisted until the end of the study

prairie dogs continued to live in the new territory, but allowed 1 or 2 of the original residents to remain, without evicting them ($n = 2$).

New coterie varied in their persistence over time. Of the 17 new coterie that were formed, 11 were still present at the end of the study in 1989. Four of these new coterie (A-1, B-1, C-1, and E-1) split a 2nd time. Six coterie (B-2, D-1, D-3, E-2, F-2, and G-2) were extinct by the end of the study ($n = 5$ female disappearances, $n = 1$ invasion by an adjacent coterie where the females of the invaded coterie were evicted and then disappeared). In 4 cases, extinction via female disappearance occurred in new coterie that contained only 1 female.

Extinction of coterie, usurpation of coterie territories, and new coterie splitting a second time sometimes led to a complex series of events (see also Halpin 1987). Fig. 1 shows that during 1981–1988, coterie 5B (from fission B) split 3 times and the resultant new coterie both gained and lost territory. Another interesting series occurred in 1985, when females from A-1 and A-2 lived separately and defended different burrows, but interacted amicably. This was the only year during the persistence of A-1 and A-2 during which the individuals interacted amicably. At the start of field season in 1986, individuals in A-1 and A-2 were mostly hostile toward each other, and defended separate coterie territories.

Coterie size and density.—Coterie that split had more females (8.1 ± 0.92 versus 3.6 ± 0.2 , $t = 6.2$, $df. = 140$, $P < 0.001$) and more members of both sexes (12.1 ± 2.1 versus

6.0 ± 0.3 , $t = 4.7$, $df. = 140$, $P < 0.001$) than did coterie that were stable. New coterie were not significantly smaller than stable coterie (3.3 ± 0.6 versus 4.8 ± 1.2 , $t = 0.42$, $df. = 149$, $P = 0.24$). Most fissions resulted in unequal divisions of the original coterie (Table 1). New coterie from the same original coterie contained significantly different numbers of members when considering adult and yearling females (smaller new coterie: 1.6 ± 0.3 ; other new coterie(s): 6.0 ± 0.6 , $t = 6.9$, $df. = 15$, $P < 0.001$) or adults and yearlings of both sexes (smaller new coterie: 3.1 ± 1.1 ; other new coterie(s): 11.1 ± 3.9 females, $t = 6.9$, $df. = 15$, $P < 0.001$).

Coterie had slightly (but not significantly) lower densities in the year preceding fission than coterie that did not split when we considered adult and yearling females (7.5 ± 3.2 versus 8.9 ± 0.6 females per hectare, $t = 0.52$, $df. = 140$, $P = 0.61$) and adults and yearlings of both sexes (10.0 ± 4.3 versus 14.0 ± 1.2 individuals per hectare, $t = 0.73$, $df. = 140$, $P = 0.47$). New coterie were significantly less dense than original coterie when considering adult and yearling females only (6.2 ± 1.3 versus 8.9 ± 0.6 females per hectare, $t = 2.2$, $df. = 23$, $P < 0.05$), but were not less dense when adults and yearlings of both sexes were included (8.8 ± 1.8 versus 9.7 ± 4.3 individuals per hectare, $t = 0.23$, $df. = 23$, $P = 0.84$).

We detected no maximal coterie size or coterie density above which all coterie split. In the year before fission, coterie varied widely in the number of females (range = 5–22). Coterie with numbers of females within this range encompassed 65 of

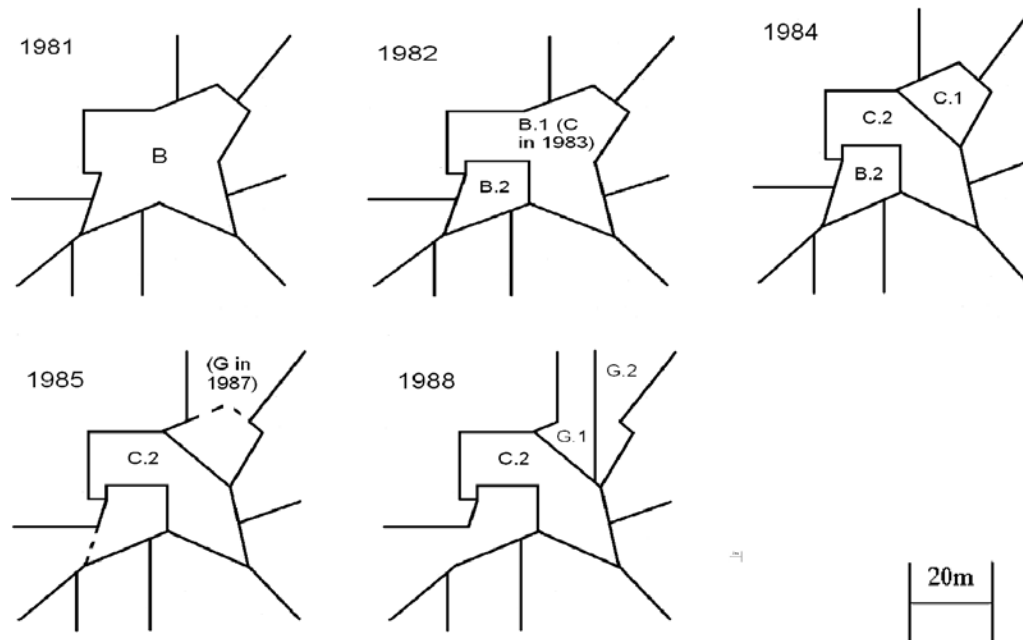


FIG. 1.—Changes in coterie territory configurations resulting from the fission of coterie 5B (fission B). The territories persisted, as shown here, but some of the new coterie territories that resulted from fission split again at a later date (e.g., fission C and fission G). Others became extinct. Solid lines indicate boundaries of coterie territories; dotted lines denote where coterie territory boundaries formerly existed.

the 142 coterie territories we analyzed, 57 (87.7%) of which did not fission. Coterie territories that split also varied widely in the number of adult and yearling females per hectare (range = 1.6–23) and adults and yearlings of both sexes per hectare (range = 1.9–32). Coterie territories with adult and yearling female densities in this range encompassed 126 of the 142 coterie territories we analyzed, 118 (93.7%) of which did not fission. Coterie territories with densities of adults and yearlings of both sexes in this range encompassed 132 of the 142 coterie territories we analyzed, 124 (93.9%) of which did not fission.

Coancestry.—Each new coterie ($n = 17$) contained a new breeding male in the year after fission, and all nonbreeding yearling males ($n = 13$) of new coterie territories either died or dispersed within a year after fission. Thus, we did not include males when determining the effect of relatedness on fission. In all cases ($n = 17$), males that were juveniles in splitting coterie territories remained with their closest living female kin (e.g., mother or sister) in the after year (when the males were yearlings).

Before fission, females in coterie territories that split exhibited slightly but not significantly lower coancestry than in coterie territories that were stable (fissioned: average $\theta_{i,j} = 0.12 \pm 0.03$, $n = 8$ coterie territories; stable: average $\theta_{i,j} = 0.15 \pm 0.04$, $n = 134$ coterie territories; $t = 1.7$, $d.f. = 140$, $P = 0.097$). Only 2 of the 8 fissions split such that coancestry among females in new coterie territories was higher than coancestry among females in the original coterie (Table 2).

Females within a coterie were invariably kin (Hoogland 1995), but some dyads had higher $\theta_{i,j}$ than others. Even though average coancestry among adult and yearling females was low in some coterie territories, particular dyads were sometimes highly related (i.e., $\theta_{i,j} \geq 0.25$). Fissions split these highly related dyads (all mother–daughter pairs) on 4 occasions (fissions A, B, C, and D). In these 4 instances, the coancestry among the females

in new groups would have been higher if the mother–daughter pairs had remained together after the fission. For instance, the average $\theta_{i,j}$ of individuals formerly in coterie A (in the new coterie A-1) increased to 0.16 ± 0.02 after the split; the average $\theta_{i,j}$ for the new coterie would have been 0.18 ± 0.01 after fission if the mother had followed her daughters. Another example was the fission of coterie B, where a mother and her 2 daughters could have moved together to increase the average $\theta_{i,j}$ for the new coterie (B-1) to 0.19 ± 0.02 after fission; instead, the mother and 2 daughters persisted in separate new groups, leaving the average $\theta_{i,j}$ at only 0.13 ± 0.03 . In contrast, the individuals in fissions E, F, and G, as well as the 1st cousins that pioneered a new group in fission H, had no close kin ($\theta_{i,j} \geq 0.25$) in the original coterie, so the postfission average $\theta_{i,j}$ listed in Table 2 was the highest possible for the individuals involved.

Coterie territories that fissioned exhibited less variation in coancestry than coterie territories that were stable (fissioned: $SD = 0.96$; stable: $SD = 4.5$; $F_{max} = 4.7$, $d.f. = 140$, $P < 0.001$), but there was no minimum coancestry at which all coterie territories split (Fig. 2). Considering the 142 coterie territories that existed during 1980–1989, adult and yearling females in 11 coterie territories were less related than females in the least-related coterie that fissioned. Further, 2 coterie territories that split had high coancestry relative to other coterie territories in our sample ($0.15 < \theta_{i,j} < 0.20$).

Multivariate comparison.—A binary logistic regression showed that the number of adult and yearling females in a coterie affected whether a coterie would split (Wald's $\chi^2 = 5.9$, $n = 142$, $P < 0.02$). The effects of coterie density measured as adult and yearling females per hectare (Wald's $\chi^2 = 0.33$, $n = 142$, $P = 0.58$) and coancestry within a coterie (Wald's $\chi^2 = 0.21$, $N = 142$, $P = 0.65$) were not statistically

TABLE 2.—Mean correlations of genes ($\theta_{i,j}$) among individuals in original and new coteries resulting from fissions at Wind Cave National Park, South Dakota, from 1980 through 1989 (all values are $\pm SE$).

Fission	Average $\theta_{i,j}$ for original coterie	Average $\theta_{i,j}$ for smallest new coterie	Average $\theta_{i,j}$ for other new coteries	Significance of difference between $\theta_{i,j}$ in original and new coteries
A	0.10 \pm 0.02	0.25	0.15 \pm 0.02	$P < 0.05$
B	0.13 \pm 0.02	0.50	0.13 \pm 0.03	$P = 0.74$
C	0.11 \pm 0.01	0.25	0.13 \pm 0.02	$P = 0.80$
D	0.07 \pm 0.01	0.50	0.084 \pm 0.021 and 0.086 \pm 0.014	$P = 0.12$
E	0.088 \pm 0.009	0.50	0.092 \pm 0.017	$P = 0.74$
F	0.17 \pm 0.01	0.50	0.12 \pm 0.07	$P = 0.64$
G	0.15 \pm 0.03	0.50	0.15 \pm 0.02	$P = 0.86$
H	0.11 \pm 0.02	0.125	0.13 \pm 0.02	$P = 0.51$

significant in this multiple regression. When we conducted the logistic procedure using calculations of coterie size and coterie density that included adults and yearlings of both sexes, results were virtually identical. This was no surprise, because the number of adult and yearling females in a coterie was significantly associated with the number of adult and yearlings of both sexes ($R^2 = 0.92, n = 142, P < 0.01$), and the density of adult and yearling females in a coterie was significantly associated with the density of adults and yearlings of both sexes ($R^2 = 0.94, n = 142, P < 0.01$).

Genetic differentiation of new coteries.—Genetic differences among the new coteries that resulted from a fission were not significant in the year immediately after fission, and were equivalent to genetic differences among other coteries after 3–4 years. Consider fission C, for example. Fig. 3 shows that when compared to stable coteries, new coteries from the same orig-

inal (i.e., C-1 and C-2) had higher between-group coancestry (α) immediately after fission. Considering α of new coteries (e.g., C-1 and C-2) as they persisted, the slope of the regression lines of α over time decreased. In 7 of 8 sets of new coteries that could be traced for 2 years or more, time accounted for more than 90% of the variation in α (Table 3). The best-fit trendlines for all α of new and stable coteries were linear. When the regression lines were extrapolated, α for new coteries approximated α of stable coteries after 3–4 years in all cases. ANCOVA revealed that the negative regression lines showing α for new coteries from the same original were different from the regression line slope showing other (stable) coteries over time.

DISCUSSION

We studied fissions of coteries within a colony of prairie dogs to examine the gene dynamics of new coteries. As in previous research (Halpin 1987; King 1955), coteries with many members were more likely to fission. However, coterie density and coancestry did not seem to influence fission. In general, the formation of new coteries did not appear to be driven by the banding together of individuals of high coancestry into the same new coteries. Coancestry thus could not explain patterns of hostile interactions between members of the new coteries that resulted from fissions.

Natural selection might favor discrete groups within colonies, because groups are commonly better able than individuals to defend areas for reproduction. If these groups contain close kin (i.e., high coancestry among group members), natural selection might then favor the evolution of cooperative behaviors such as alarm calling and communal nursing (Chesser 1998; Hamilton 1964; Wilson 1975). Coancestry among females in the matrilineal coteries of prairie dogs should vary about an equilibrium value of 0.17, regardless of the size of the group (Dobson et al. 2000a). We detected substantial levels of coancestry within new coteries that resulted from fission, and these levels were slightly less than the theoretical value of 0.17.

If coteries fissioned along lines of relatedness, then coancestry usually should have increased. Increased coancestry, in turn, might have promoted the formation of, and cooperation within, coteries. However, coancestries increased only slightly

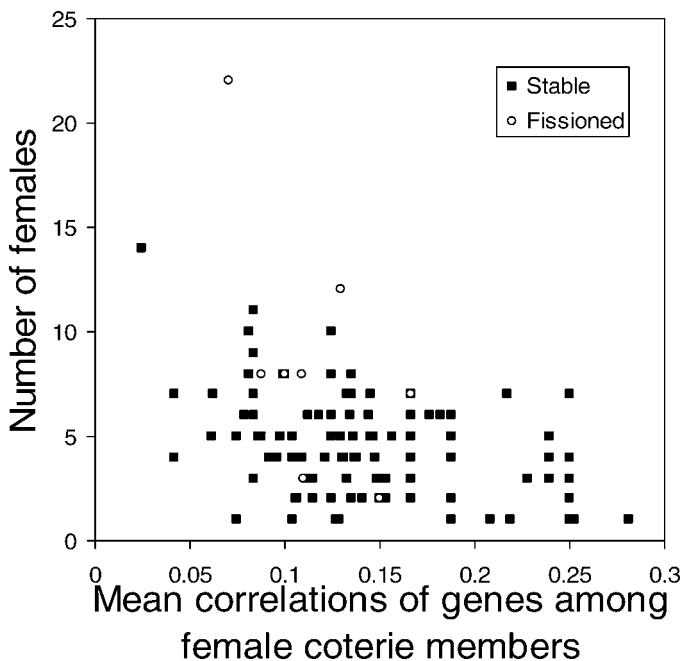


FIG. 2.—Mean correlations of genes ($\theta_{i,j}$) and group size among female members in the 1st year after fission of coteries from 1980 to 1988.

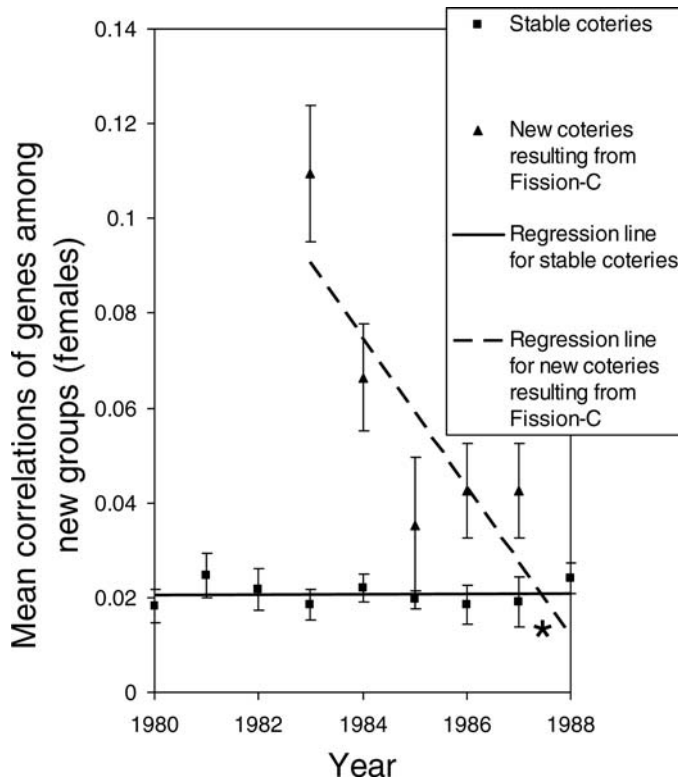


FIG. 3.—A sample of regression lines comparing α for females of stable coterie and new coterie that resulted from fission. The asterisk denotes the theoretical point at which α for the new coterie resulting from fission C (C-1 and C-2) was not significantly different than that of stable coterie, which occurred after 4 years (less than 2 generations). C-1 fissioned in 1987.

in some fissions and could have been higher. Although coancestry might have influenced the formation of new coterie that contained a single female who lacked close kin ($\theta_{i,j} \geq 0.25$) in the original territory, our results support Chesser's (1998) hypothesis that high coancestry alone is an insufficient condition for the formation of social groups.

Like family groups of some lagomorphs and primates (Dobson et al. 2000b; Long 1986; Pope 1992), prairie dogs have significant genetic differentiation between local breeding groups (Chesser 1983; Dobson et al. 1997, 1998, 2004).

Female members of a coterie are commonly close kin, and cooperation within a coterie might evolve via kin selection. We predicted that the magnitude of genetic similarity between new coterie that resulted from the same fission would decrease over time because females in different breeding groups usually mate with different males (Chesser 1998). Examination of our data supports this prediction, because new coterie took about 1 generation (i.e., about 3 years) to achieve the same differentiation between them as occurred among other coterie. However, the steady decline in coancestry over time does not explain the abrupt change from amicable to agonistic behaviors involving individuals in different new coterie that resulted from the same fission. Rather, differences in timing of behavior and gene dynamics further support Chesser's (1998) hypothesis that benefits of coancestry per se are insufficient to promote group formation.

If new coterie did not exhibit elevated coancestry, then why did coterie fission? Larger group size sometimes encourages fission (e.g., Chagnon 1975), probably to alleviate increased competition. For example, the probability of losing a litter to infanticide varies directly with coterie size (Hoogland 1995). Perhaps survival and reproductive success are highest at some "optimal" coterie size. In any event, fission among prairie dogs is more likely in larger coterie. We detected no maximum coterie size at which all groups split, and new coterie that resulted from fission did not always have the same number of individuals.

Although coterie size usually varies positively with coterie density (Hoogland 1995), coterie size and coterie density had different effects on the likelihood that a coterie would fission—probably because, for reasons that are not clear, coterie that fissioned had lower densities than coterie that did not fission. We were able to separate the effects of coterie size and coterie density in our multivariate analysis because they were not strongly colinear.

Five of the new coterie resulting from fissions contained only 1 female. These isolated animals presumably had few opportunities to increase their indirect fitness by promoting the survivorship and reproduction of their kin. Further, these coterie probably were too small to counter competition from other coterie. On the other hand, females that split from their familiar social group and pioneer new groups can sometimes

TABLE 3.—Linear regression analysis of α for all stable coterie and for new coterie that result from the same fission. *P* values are from the test for equality of slopes.

New coterie that resulted from fission	Number of years until 1 or both new coterie became extinct	Slope (<i>m</i>) and <i>R</i> ² of regression line	Number of years until the new coterie became genetically distinct from one another	Equality of slopes (ANCOVA)
All stable coterie	Not applicable	$m = 0.00002, R^2 = 0.0004$	Not applicable	Not applicable
A-1 and A-2	4	$m = -0.024, R^2 = 0.95$	3	$P = 0.085$
B-1 and B-2	2	$m = -0.037, R^2 = 0.91$	3	$P < 0.001$
C-1 and C-2	4	$m = -0.016, R^2 = 0.68$	4	$P < 0.005$
D-1, D-2, and D-3	2	$m = -0.020, R^2 = 0.93$	3	$P < 0.001$
E-1 and E-2	1	$m = -0.015, R^2 = 0.99$	4	$P < 0.01$
F-1 and F-2	1	$m = -0.032, R^2 = 0.94$	4	$P < 0.01$
G-1 and G-2	1	$m = -0.046, R^2 = 0.92$	3	$P < 0.01$
H-1 and H-2	2	$m = -0.048, R^2 = 0.93$	4	$P < 0.001$

increase their fitness by initiating a new matriline (Armitage 1987, 1991). With 1 exception, lone females that formed new coterie had no close kin in the original territory. With no close kin with whom they could band together, perhaps these lone females were attempting to initiate a new coterie.

After fission, we expected that smaller new coterie would inherit smaller areas than the larger new coterie (Cords and Rowell 1986). Examination of our data does not support this prediction, but we recognize that our sample sizes are small. In some cases, the smaller new coterie after fission defended the smaller territory and avoided extinction, so securing the larger territory was not a prerequisite for persistence. In other cases, the smaller new coterie became extinct and the fate of the female(s) that disappeared was unknown. Long-distance dispersal by prairie dogs sometimes occurs (Garrett and Franklin 1988), but we did not document intercolony dispersal by any of the females that disappeared after fission.

Fission is more likely in large coterie. Cooperation abruptly ceases between prairie dogs of new, adjacent coterie that result from fission, even though coancestry among the individuals of the 2 coterie remains high in the 1st year or so. This trend suggests that advantages of maintaining the new social group might be more important than cooperation among kin per se. More research will be necessary for a better understanding of the effects of fission on cooperation and competition among prairie dogs.

ACKNOWLEDGMENTS

We thank the staff at Wind Cave National Park and JLH's many volunteer research assistants. We are indebted to R. K. Chesser for his instruction on gene dynamics. This research was partially funded by a United States National Science Foundation research grant to FSD (DEB-0089473) and by Auburn University awards to TGM. Financial support was also provided by National Science Foundation, National Geographic Society, American Philosophical Society, Center for Field Research, Eppley Foundation for Research, University of Maryland, University of Michigan, University of Minnesota, Princeton University, and the Harry Frank Guggenheim Foundation. Two anonymous reviewers provided helpful comments that improved the manuscript.

LITERATURE CITED

- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- ARMITAGE, K. B. 1987. Social dynamics of mammals: reproductive success, kinship and individual fitness. *Trends in Ecology and Evolution* 2:279–284.
- ARMITAGE, K. B. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. *Annual Review of Ecology and Systematics* 22:379–407.
- AVILES, L. 2000. Nomadic behaviour and colony fission in a cooperative spider: life history evolutions at the level of the colony? *Biological Journal of the Linnean Society* 70:325–339.
- BROWN, J. L. 1987. *Helping and communal breeding in birds*. Princeton University Press, Princeton, New Jersey.
- CHAGNON, N. A. 1975. Genealogy, solidarity, and relatedness: limits to local group size and patterns of fissioning in an expanding population. *Yearbook of Physical Anthropology* 19:95–110.
- CHEPKO-SADE, B. D., K. P. REITZ, AND D. S. SADE. 1989. Sociometrics of *Macaca mulatta*. IV. Network analysis of social structure of a pre-fission group. *Social Networks* 11:293–314.
- CHEPKO-SADE, B. D., AND D. S. SADE. 1979. Patterns of group splitting within matrilineal kinship groups. *Behavioral Ecology and Sociobiology* 5:67–86.
- CHESSER, R. K. 1983. Genetic variability within and among populations of the black-tailed prairie dog. *Evolution* 37:320–331.
- CHESSER, R. K. 1991. Gene diversity and female philopatry. *Genetics* 127:437–447.
- CHESSER, R. K. 1998. Relativity of behavioral interactions in socially structured populations. *Journal of Mammalogy* 79:713–724.
- COCKERHAM, C. C. 1967. Group inbreeding and coancestry. *Genetics* 56:89–104.
- COCKERHAM, C. C. 1969. Variance of gene frequencies. *Evolution* 23:72–84.
- COCKERHAM, C. C. 1973. Analysis of gene frequencies. *Genetics* 74:679–700.
- CORDS, M., AND T. E. ROWELL. 1986. Group fission in blue monkeys of the Kakamega Forest, Kenya. *Folia Primatologia* 46:70–82.
- DAMON, R. A., AND W. R. HARVEY, JR. 1987. *Experimental design, ANOVA, and regression*. Harper & Row, New York.
- DE RUITER, J. R., AND E. GEFFEN. 1998. Relatedness of matriline, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*). *Proceedings of the Royal Society of London, B. Biological Sciences* 265:79–87.
- DOBSON, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* 30:1183–1192.
- DOBSON, F. S. In press. Gene dynamics and social behavior. In *Rodent societies: an ecological and evolutionary perspective* (J. O. Wolff and P. W. Sherman, eds.). University of Chicago Press, Chicago, Illinois.
- DOBSON, F. S., R. K. CHESSER, J. L. HOOGLAND, D. W. SUGG, AND D. W. FOLTZ. 1997. Do black-tailed prairie dogs minimize inbreeding? *Evolution* 51:970–978.
- DOBSON, F. S., R. K. CHESSER, J. L. HOOGLAND, D. W. SUGG, AND D. W. FOLTZ. 1998. Breeding groups and gene dynamics in a socially structured population of prairie dogs. *Journal of Mammalogy* 79:671–680.
- DOBSON, F. S., R. K. CHESSER, J. L. HOOGLAND, D. W. SUGG, AND D. W. FOLTZ. 2004. The influence of social breeding groups on effective population size in black-tailed prairie dogs. *Journal of Mammalogy* 85:146–154.
- DOBSON, F. S., R. K. CHESSER, AND B. ZINNER. 2000a. The evolution of infanticide: genetic benefits of extreme nepotism and spite. *Ethology Ecology and Evolution* 12:131–148.
- DOBSON, F. S., A. T. SMITH, AND W. X. GAO. 2000b. The mating system and gene dynamics of plateau pikas. *Behavioural Processes* 51:101–110.
- DOBSON, F. S., AND B. ZINNER. 2003. Social groups, genetic structure, and conservation. Pp. 211–228 in *Animal behavior and wildlife conservation* (M. Festa-Bianchet and M. Apollonia, eds.). Island Press, Washington, D.C.
- FRANKS, N. R. 1989. Army ants: a collective intelligence. *American Scientist* 77:139–145.
- GARRETT, M. G., AND W. L. FRANKLIN. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. *Journal of Mammalogy* 69:236–250.
- GREENWOOD, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- HALPIN, Z. T. 1987. Natal dispersal and the formation of new social groups in a newly established town of black-tailed prairie dogs

- (*Cynomys ludovicianus*). Pp. 104–118 in Mammalian dispersal patterns: the effects of social structure on population genetics (B. D. Chepko-Sade and Z. T. Halpin, eds.). University of Chicago Press, Chicago, Illinois.
- HAMILTON, W. D. 1964. The genetical evolution of social behavior. I and II. *Journal of Theoretical Biology* 7:1–52.
- HARRIS, M. A., AND J. O. MURIE. 1984. Inheritance of nest sites in female Columbian ground squirrels. *Behavioral Ecology and Sociobiology* 15:97–102.
- HOOGLAND, J. L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois.
- HOOGLAND, J. L., AND D. W. FOLTZ. 1982. Variance in male and female reproductive success in a harem-polygynous mammal, the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). *Behavioral Ecology and Sociobiology* 11:155–163.
- KING, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. *Contributions from the Laboratory of Vertebrate Biology, University of Michigan* 67:1–123.
- LEHMER, E. M., B. VAN HORNE, B. KULBARTZ, AND G. L. FLORANT. 2001. Facultative torpor in free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*). *Journal of Mammalogy* 82: 551–557.
- LONG, J. C. 1986. The allelic correlation structure of Gainj- and Kalam-speaking people. I. The estimation and interpretation of Wright's *F*-statistics. *Genetics* 112:629–647.
- MELNICK, D. J., AND K. K. KIDD. 1983. The genetic consequences of social group fission in a wild population of rhesus monkeys (*Macaca mulatta*). *Behavioral Ecology and Sociobiology* 12: 229–236.
- NASH, L. T. 1976. Troop fission in free-ranging baboons in the Gombe Stream National Park, Tanzania. *American Journal of Physical Anthropology* 44:63–78.
- OI, T. 1988. Sociological study on the troop fission of wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island. *Primates* 29:1–29.
- PACKER, C., D. SCHEEL, AND A. E. PUSEY. 1990. Why lions form groups: food is not enough. *American Naturalist* 136:1–19.
- POPE, T. R. 1992. The influence of dispersal patterns and mating system on genetic differentiation within and between populations of the red howler monkey (*Alouatta seniculus*). *Evolution* 46: 1112–1128.
- SAS Institute Inc. 2005. SAS system for Windows. SAS Institute Inc., Cary, North Carolina.
- SUGG, D. W., R. K. CHESSER, F. S. DOBSON, AND J. L. HOOGLAND. 1996. Population genetics meets behavioral ecology. *Trends in Ecology and Evolution* 11:338–342.
- TEMPLETON, A. R. 1980. The theory of speciation via the founder principle. *Genetics* 94:1011–1038.
- WILSON, E. O. 1975. *Sociobiology: the new synthesis*. Harvard University Press, Cambridge, Massachusetts.
- WRIGHT, S. 1922. Coefficients of inbreeding and relationship. *American Naturalist* 56:330–338.

Submitted 23 March 2006. Accepted 12 September 2006.

Associate Editor was Nancy G. Solomon.