SOCIAL GROUP FISSION AND GENE DYNAMICS AMONG BLACK-TAILED PRAIRIE DOGS (Cynomys ludovicianus)

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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 coteries, 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 coteries; and gene dynamics during and after fissions. Most new coteries occupied a subsection of the original territory. New coteries that contained a single female became extinct after about 1 year and their territories were usurped by adjacent coteries. Large coteries were more likely than smaller coteries to fission, but female coancestry within coteries usually did not influence the likelihood of fission, or the individuals that banded together in new groups. Members of new coteries interacted hostitley in the year after fission, but 1 or 2 generations elapsed before the new coteries became genetically distinct. We conclude that fission is probably driven by intraspecific competition within coteries rather than coancestry, and that coancestry does not explain the abrupt cessation of cooperation between individuals of the new coteries 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 coteries (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

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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 coteries 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 coteries 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 coteries; large coteries are more likely than smaller coteries to show fission; and close kin may or may not band together within the new coteries 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 coteries. 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 coteries that result from fission. Although coteries 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 coteries might form without high degrees of coancestry among same-coterie females, and that individuals of high coancestry that live in adjacent new coteries 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 coteries 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 fingering 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 coteries 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 coteries, 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 coteries 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 coteries” (e.g., A-1 and A-2). We designated coteries that showed no fission as “stable coteries.”
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 colony. To determine a number of dyads (a conservative procedure). Most matrilineal matrilines 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 coteries = 0), and between individuals from different coteries (a—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 coteries, n = 8 fissions).

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

$$\theta_{ij} = 1/4(\theta_{Sij} + \theta_{Sdj} + \theta_{Dij} + \theta_{DDj}),$$  

where S and D denote the sire and dam, respectively, of the ith and jth 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:

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

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

$$F_i = \theta_{SDi}.$$

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

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

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 coteries:

$$\bar{\alpha} = \frac{\sum_{i=1}^{s} \sum_{j=1}^{N_i} \sum_{k=i+1}^{N_i} \sum_{m=1}^{N_i} \theta_{ij,m}}{\sum_{i=1}^{s} \sum_{k=i+1}^{N_i} N_i N_k}.$$  

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

Statistical analysis.—We calculated all F, θij, α, and their weighted averages and confidence intervals. Most matrilines 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 coteries in different years to be statistically independent (n = 142 coteries). 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 coteries resulting from fission contained individuals that had greater coancestry than expected from chance, we calculated the average θij for individuals in the new coteries for the year after the fission. We then compared these values to the average θij for their respective original groups with Mann–Whitney U-tests. We also used 2-sample t-tests (assuming equal variances) to compare the average θij for coteries that fissioned against the average θij for all coteries 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 coteries that resulted from fission, we calculated α for the individuals in the new coteries 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 coteries. We determined the year in which the new coteries from the same fission were significantly different (i.e., had approximately the same α as we observed among stable coteries) using linear regression. If necessary, we extrapolated the regression line for the new coteries through the regression line for stable coteries 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 coteries or for new coteries 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 coteries rather than the number of dyads (a conservative procedure). P values result from 2-tailed tests.

RESULTS

Dispersal and persistence of new coteries.—For the 142 coteries 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 coteries split into 2 smaller coteries in the following year, and 1 other split into 3 smaller coteries (Table 1). In 5 cases the larger of the new coteries 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...
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 coteries varied in their persistence over time. Of the 17 new coteries that were formed, 11 were still present at the end of the study in 1989. Four of these new coteries (A-1, B-1, C-1, and E-1) split a 2nd time. Six coteries (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 coteries that contained only 1 female.

Extinction of coteries, usurpation of coterie territories, and new coteries 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 coteries 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 size and density varied among the different periods of study. For example, the average number of females per hectare prior to fission was 8.9, whereas the average number of females per hectare subsequent to fission was 6.2. The number of males per hectare also varied, with an average of 7.5 prior to fission and 14.0 subsequent to fission.

**Table 1.**—Changes in territories of new coteries 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 contingencies, we scored coterie territories, and we scored separate coterie territories.

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

6.0 ± 0.3, \(t = 4.7, df = 140, P < 0.001\) than did coterie that were stable. New coteries were not significantly smaller than stable coteries \((3.3 ± 0.6 versus 4.8 ± 1.2, t = 0.42, df = 149, P = 0.24)\). Most fissions resulted in unequal divisions of the original coterie (Table 1). New coteries 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, \(t = 6.9, df = 15, P < 0.001\)).

Coteries had slightly (but not significantly) lower densities in the year preceding fission than coteries 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 coteries were significantly less dense than original coteries 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 coteries split. In the year before fission, coteries varied widely in the number of females (range = 5–22). Coteries with numbers of females within this range encompassed 65 of...
the 142 coteries we analyzed, 57 (87.7%) of which did not fission. Coteries 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). Coteries with adult and yearling female densities in this range encompassed 126 of the 142 coteries we analyzed, 118 (93.7%) of which did not fission. Coteries with densities of adults and yearlings of both sexes in this range encompassed 132 of the 142 coteries 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 coteries 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 coteries 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 coteries that split exhibited slightly but not significantly lower coancestry than in coteries that were stable (fissioned: average \( \theta_{ij} = 0.12 \pm 0.03, n = 8 \) coteries; stable: average \( \theta_{ij} = 0.15 \pm 0.04, n = 134 \) coteries; \( t = 1.7, df = 140, P = 0.097 \)). Only 2 of the 8 fissions split such that coancestry among females in new coteries 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 \( \theta_{ij} \), than others. Even though average coancestry among adult and yearling females was low in some coteries, particular dyads were sometimes highly related (i.e., \( \theta_{ij} \geq 0.25 \)). 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 \( \theta_{ij} \) of individuals formerly in coterie A (in the new coterie A-1) increased to 0.16 ± 0.02 after the split; the average \( \theta_{ij} \) 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 \( \theta_{ij} \) 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 \( \theta_{ij} \) 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 (\( \theta_{ij} \geq 0.25 \)) in the original coterie, so the postfission average \( \theta_{ij} \) listed in Table 2 was the highest possible for the individuals involved.

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

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

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**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 coteries 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.
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 yearling females 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 original (i.e., C-1 and C-2) had higher between-group coancestry ($\alpha$) immediately after fission. Considering $\alpha$ of new coteries (e.g., C-1 and C-2) as they persisted, the slope of the regression lines of $\alpha$ 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 $\alpha$ (Table 3). The best-fit trendlines for all $\alpha$ of new and stable coteries were linear. When the regression lines were extrapolated, $\alpha$ for new coteries approximated $\alpha$ of stable coteries after 3–4 years in all cases. ANCOVA revealed that the negative regression lines showing $\alpha$ 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.

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

<table>
<thead>
<tr>
<th>Fission</th>
<th>Average $\theta_{ij}$ for original coterie</th>
<th>Average $\theta_{ij}$ for smallest new coterie</th>
<th>Average $\theta_{ij}$ for other new coteries</th>
<th>Significance of difference between $\theta_{ij}$ in original and new coteries</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0.10 ± 0.02</td>
<td>0.25</td>
<td>0.15 ± 0.02</td>
<td>$P &lt; 0.05$</td>
</tr>
<tr>
<td>B</td>
<td>0.13 ± 0.02</td>
<td>0.50</td>
<td>0.13 ± 0.03</td>
<td>$P = 0.74$</td>
</tr>
<tr>
<td>C</td>
<td>0.11 ± 0.01</td>
<td>0.25</td>
<td>0.13 ± 0.02</td>
<td>$P = 0.80$</td>
</tr>
<tr>
<td>D</td>
<td>0.07 ± 0.01</td>
<td>0.50</td>
<td>0.08 ± 0.021 and</td>
<td>$P = 0.12$</td>
</tr>
<tr>
<td>E</td>
<td>0.088 ± 0.009</td>
<td>0.50</td>
<td>0.092 ± 0.017</td>
<td>$P = 0.74$</td>
</tr>
<tr>
<td>F</td>
<td>0.17 ± 0.01</td>
<td>0.50</td>
<td>0.12 ± 0.07</td>
<td>$P = 0.64$</td>
</tr>
<tr>
<td>G</td>
<td>0.15 ± 0.03</td>
<td>0.50</td>
<td>0.15 ± 0.02</td>
<td>$P = 0.86$</td>
</tr>
<tr>
<td>H</td>
<td>0.11 ± 0.02</td>
<td>0.125</td>
<td>0.13 ± 0.02</td>
<td>$P = 0.51$</td>
</tr>
</tbody>
</table>

**Fig. 2.** Mean correlations of genes ($\theta_{ij}$) and group size among female coterie members in the 1st year after fission of coteries from 1980 to 1988.
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 coteries 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 coteries took about 1 generation (i.e., about 3 years) to achieve the same differentiation between them as occurred among other coteries. However, the steady decline in coancestry over time does not explain the abrupt change from amicable to agonistic behaviors involving individuals in different new coteries 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 coteries did not exhibit elevated coancestry, then why did coteries 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 coteries. We detected no maximum coterie size at which all groups split, and new coteries 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, coteries that fissioned had lower densities than coteries 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 coteries 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 coteries probably were too small to counter competition from other coteries. On the other hand, females that split from their familiar social group and pioneer new groups can sometimes

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

<table>
<thead>
<tr>
<th>New coteries that resulted from fission</th>
<th>Number of years until 1 or both new coteries became extinct</th>
<th>Slope ($m$) and $R^2$ of regression line</th>
<th>Number of years until the new coteries became genetically distinct from one another</th>
<th>Equality of slopes (ANCOVA)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All stable coteries</td>
<td>Not applicable</td>
<td>$m = 0.00002, R^2 = 0.0004$</td>
<td>Not applicable</td>
<td>Not applicable</td>
</tr>
<tr>
<td>A-1 and A-2</td>
<td>4</td>
<td>$m = -0.024, R^2 = 0.95$</td>
<td>3</td>
<td>$P = 0.085$</td>
</tr>
<tr>
<td>B-1 and B-2</td>
<td>2</td>
<td>$m = -0.037, R^2 = 0.91$</td>
<td>3</td>
<td>$P &lt; 0.001$</td>
</tr>
<tr>
<td>C-1 and C-2</td>
<td>4</td>
<td>$m = -0.016, R^2 = 0.68$</td>
<td>4</td>
<td>$P &lt; 0.005$</td>
</tr>
<tr>
<td>D-1, D-2, and D-3</td>
<td>2</td>
<td>$m = -0.020, R^2 = 0.93$</td>
<td>3</td>
<td>$P &lt; 0.001$</td>
</tr>
<tr>
<td>E-1 and E-2</td>
<td>1</td>
<td>$m = -0.015, R^2 = 0.99$</td>
<td>4</td>
<td>$P &lt; 0.01$</td>
</tr>
<tr>
<td>F-1 and F-2</td>
<td>1</td>
<td>$m = -0.032, R^2 = 0.94$</td>
<td>4</td>
<td>$P &lt; 0.01$</td>
</tr>
<tr>
<td>G-1 and G-2</td>
<td>1</td>
<td>$m = -0.046, R^2 = 0.92$</td>
<td>3</td>
<td>$P &lt; 0.01$</td>
</tr>
<tr>
<td>H-1 and H-2</td>
<td>2</td>
<td>$m = -0.048, R^2 = 0.93$</td>
<td>4</td>
<td>$P &lt; 0.001$</td>
</tr>
</tbody>
</table>
increase their fitness by initiating a new matriline (Armitage 1987, 1991). With 1 exception, lone females that formed new coteries 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 coteries would inherit smaller areas than the larger new coteries (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 coteries. Cooperation abruptly ceases between prairie dogs of new, adjacent coteries that result from fission, even though coancestry among the individuals of the 2 coteries remains high in the 1st year or so. This trend from fission, even though coancestry among the individuals of new, adjacent coteries that result from fission, even though coancestry among the individuals of 2 coteries 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.

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