# Social assemblages and mating relationships in prairie dogs: a DNA fingerprint analysis

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Mating system characterizations have been hindered by difficulties in accurately assigning parentage to offspring. We investigated the relationship between social assemblages and mating relationships in a territorial harem polygynous mammal, the Gunnison's prairie dog, using a combination of behavioral and molecular analyses. We demonstrate multiple paternity and an extraordinarily high incidence of extraterritorial fertilizations (i.e., 61% of all progeny), in combination with the existence of female kin groups. On this basis, we conclude that social assemblages alone provide a poor description of the Gunnison's prairie dog mating system, and suggest several potential reasons for the maintenance of territoriality in this species. *Key words:* Cynomys gunnisoni, DNA fingerprinting, kin group, mating system, paternity. *[Behav Ecol 7:95–100 (1996)]*

The classification of animal mating systems has long occupied the attention of behavioral ecologists, relying traditionally on observations of social organization (Clutton-Brock, 1989). However, observation is limited by its subjectivity and in some species by environmental barriers that prevent viewing of courtship and mating behavior (Burke, 1989). With the integration of genetics into behavioral research, allozyme electrophoresis provided an objective way of sorting out genetic relationships as a means of identifying maternity and paternity within and among social groups (Arnold, 1990; Hanken and Sherman, 1981; Hoogland and Foltz, 1982; Schwartz and Armitage, 1980, 1981); however, allozymes usually have low resolving power (Lynch, 1988). Recently developed molecular techniques, such as DNA fingerprinting (Jeffreys et al., 1985a), now make it possible to establish genetic relationships among individuals (e.g., paternity) with a high degree of confidence.

Here we investigate the mating system of Gunnison's prairie dog (*Cynomys gunnisoni*) using a combination of behavioral and molecular techniques. Gunnison's prairie dogs are colonial ground squirrels occupying grasslands of the Colorado plateau in western North America (Hall and Kelson, 1959). Colonies are partitioned into territories that are stable in both space and time (Rayor, 1988; Travis and Slobodchikoff, 1993). Dispersal occurs primarily near the end of each active season, or prior to the onset of the subsequent mating season (Robinson, 1989). The mating system has been described previously as harem polygynous on the basis of above-ground associations of animals, although territories may contain either monogamous adult pairs (Travis and Slobodchikoff, 1993) or polygynous groups, together with juveniles and yearlings (Rayor, 1988; Travis and Slobodchikoff, 1993). Amicable interactions predominate within territories; aggressive interactions, particularly among adult males, occur in defense of territorial boundaries (Rayor, 1988). In spite of frequent interterritorial disputes, however, territory boundaries may become relatively porous when food rewards are high enough (Rayor, 1988); potentially, boundaries might be equally porous when copulations are at stake.

In order to accurately characterize the mating system of Gunnison's prairie dog, we used above-ground observations of social assemblages to establish territorial associations, and DNA fingerprinting to establish mating relationships. We then used this information to answer the question of whether mating relationships are restricted to members of shared territories. On the basis of Hoogland and Foltz's (1982) study of paternity in black-tailed prairie dogs (*C. ludovicianus*), we hypothesized that the majority, if not all, successful matings would take place entirely within a given social group. In addition, we used DNA fingerprinting to assess average genetic relatedness among same-sex members of shared territories in order to answer the question of whether social groups include male or female kin. This information is commonly used as an additional means of characterizing mating systems, because intraterritorial mating associations may be highly dependent on the cooperative behaviors of closely related members of the social group. For example, copulations occurring within lion (*Panthera leo*) prides are often facilitated by the formation of same-sex coalitions consisting of highly related individuals, particularly among males (Packer et al., 1988, 1991).

## METHODS

We studied two colonies of Gunnison's prairie dogs near Flagstaff, Arizona: Antelope Hill (elevation 2348 m) and Potato Lake (elevation 2579 m) (Travis and Slobodchikoff, 1993). The study colonies were separated by 13 km and were isolated from neighboring colonies by surrounding Ponderosa pine (*Pinus ponderosa*) forest. Nearest distances between neighboring colonies exceeded 2 km.

We conducted live trapping within a single 1.44 ha study plot delineated at each colony, one to two times per week throughout the active seasons (early April through late October) of 1988 through 1992. We set 40 to 50 traps directly in front of the entrances to burrows that we determined to be active on the basis of behavioral observations. We moved traps frequently in order to ensure the capture of all adults and most juveniles from the study plots, as confirmed via observation of marked versus unmarked animals (Travis and Slobodchikoff, 1993). We marked animals with metal eartags and black hair dye for visual identification so that locations of individuals could be recorded. We collected blood samples from all captured animals by toenail clipping during the active season of 1991 only. We rinsed 0.5–2.0 ml of blood from each prairie dog into 15 ml plastic tubes using an isotonic saline buffer (1× SSC: 0.15 M NaCl, 15 mM sodium citrate, 1 mM

EDTA). We stored blood samples on ice prior to freezing at −70°C.

We determined territorial locations and membership from trapping and observational data compiled throughout each active season for all prairie dogs residing within the study plots. We recorded trap locations of captured animals in reference to a grid system demarcated by surveyor's stakes. We conducted observations during 2 h sessions one to two times per week throughout each active season from two elevated viewing blinds erected at each colony. Observations consisted of scan sampling repeated every 5 min. During this time, we located and identified all animals sighted. We used animal locations to determine spatial locations of group territories according to the methods of Travis and Slobodchikoff (1993). We determined territorial memberships on the basis of shared spatial locations and amicable interactions. We described social systems within territories during 1991 on the basis of the sex ratio of adult residents.

We used DNA fingerprints to assess levels of genetic relatedness among adults in order to better characterize the social system, and between adults and juveniles in order to assess parentage. DNA fingerprints appear as ladderlike series of bands on an autoradiograph. Each band in a fingerprint represents a single DNA fragment containing a region of homology with the probe sequence. When bands of like size appear in the fingerprints of two individuals, each band is assumed to represent an identical allele from a single genetic locus. The matching of bands over many loci helps to establish the overall level of genetic relatedness among such individuals.

We constructed DNA fingerprints from prairie dog DNA extracted from blood. DNA extraction proceeded according to Müllenbach et al. (1989). We dissolved DNA in 100 µl Tris-EDTA (pH 8.0) at a concentration of 150 µg/ml. We digested 4 µg DNA per sample with 16 units of HaeIII, in the presence of 1 mM spermidine, for 5 h at 37°C. We separated DNA fragments in 0.7% agarose gels for 24 h at 2.2 V/cm and transferred them to Amersham Hybond N+ membranes by Southern blotting in 0.40 N NaOH. We hybridized membranes with three minisatellite probes: pV47-2 (Longmire et al., 1990), 33.15 and 33.6 (Jeffreys et al., 1985a). We labeled probe DNA (10–25 ng) with $^{32}$P-dCTP by the random primer method (Feinberg and Vogelstein, 1983). We conducted our prehybridization, hybridization, and washes according to the methods of Gilbert et al. (1990). We autoradiographed membranes at −70°C for 1 to 14 days using Konica Medical X-Ray Film and intensifying screens. Prior to reprobing, we stripped DNA probes from membranes by washing in 0.5 N NaOH, 0.1% SDS, and 0.25 M Tris-HCl (pH 7.0) for 10 min each.

We loaded samples on gels in groups, determined on the basis of membership in common territories. We loaded adult males to the left and adult females to the right of all juveniles from a given territory. In addition, we loaded up to six standards, representing animals sacrificed from outside of the study plots, to the right of each territorial group. Because randomly shared fingerprinting bands occur with a very high frequency in Gunnison's prairie dogs (Travis SE, Slobodchikoff CN, Keim P, in review), these standards represented virtually all of the fragments that proved detectable by the DNA fingerprinting methods that we employed. Thus, these standards allowed us to compare fragments across gels with a high level of confidence.

We combined data from the three minisatellite probes (pV47-2, 33.15, and 33.6) within each individual prairie dog to form a single composite DNA fingerprint, following a test for independence of DNA fragments across probes. We scored only those fragments falling within the range of 2.0 to 23.5 kilobases for each of the three probes. We conducted a test for independence in order to confirm that there were no DNA fragments detected simultaneously by more than one probe, thus yielding redundant information. This test consisted of a comparison, across all individuals, of each scorable fragment with each fragment of similar molecular weight from the two alternative probes. We considered fragments to be nonindependent across probes when identical patterns were revealed in over 90% of individuals scored. No cases of nonindependence were revealed.

We assessed the average relatedness of same-sex individuals sharing territories on the basis of molecular data by comparing DNA fingerprints among adults. We conducted all possible pairwise comparisons of individual DNA fingerprint patterns among adults within colonies (AH: 61 adults; PL: 49 adults), from which we determined coefficients of similarity. We then compared mean values representing intraterritorial relatedness among males and females to the overall population mean level of genetic relatedness at each colony using one-sample $t$ tests. Our calculations of population means included those males and females used to measure intraterritorial relatedness. We calculated sampling variances on the basis of formulae designed to account for covariance arising from multiple comparisons with the fingerprints of single individuals (Lynch, 1990), according to the methods of Brock and White (1992).

We were unable to assign parentage by the method traditionally employed in combination with DNA fingerprints. Briefly, this method involves the plotting of similarity coefficients (i.e., the proportion of bands shared in common between the fingerprints of two individuals) for multiple individuals representing a range of known relatedness levels, leading to the construction of a calibration curve (Gilbert et al., 1991). Assuming that there is minimal overlap between the range of similarity coefficients representing parent-offspring pairs and those representing pairs of more distant relatives, parentage may then be unambiguously assigned in the absence of established pedigree information by fitting the similarity values of unknowns to this curve. Conclusions about parentage are unsafe, however, when overlap between pairs with different coefficients of relatedness is high, an outcome that has been shown to arise from inbreeding (Lynch, 1988). Because Gunnison's prairie dogs display unusually low levels of population genetic heterogeneity suggestive of inbreeding (Travis SE, Slobodchikoff CN, Keim P, in review), coefficients of similarity among unrelated individuals tended to be quite large (e.g., 0.55–0.61).

We attempted to overcome the aforementioned difficulties in positively assigning parentage by adopting a highly conservative form of paternity testing, similar to that reported by Jeffreys et al. (1985b). We conducted this procedure as follows: First, for each juvenile captured during 1991, we scored only bands of medium and high intensity from DNA fingerprints (mean = 20.60, range = 9–30); we considered low intensity bands unreliable. We then searched for a single adult male/female pair, from among a group of putative parents, whose combined DNA fingerprints could be used to account for all of the bands present in the fingerprint of the juvenile. We sought female parents from among the entire group of adult females resident within each juvenile's natal territory, while we sought male parents from among all adult males captured at the corresponding colony (parentage could not be assigned from behavioral observations for either sex because copulations and the weaning of young both took place in subterranean burrows). If multiple male/female pairs existed as possible parents, parentage remained unassigned. If no such pair existed, we concluded that the true male parent was unlikely to have been sampled due to residency outside the study plot. In such instances, we tentatively assigned par-

**Table 1**
Coefficients of similarity calculated from comparisons of shared fragments among pairs of DNA fingerprints

| Colony | Overall | Among females sharing territories | Among males sharing territories |
|---|---|---|---|
| | Mean coefficients of similarity | | |
| Antelope Hill | 0.55 | 0.59* | 0.62 |
| Potato Lake | 0.61 | 0.66* | 0.60 |

\* $p < .001$.

entage to the female sharing the largest similarity coefficient with the affected juvenile, although the precise identity of such a female was ultimately of little importance to our overall conclusions, since we were primarily interested in paternity. Only in those instances where a single pair of adults emerged, did we actually assign both a male and a female parent to the juvenile in question. By adopting such a strategy, we ruled out the possibility of any misassignments, especially resulting from physical linkage of fragments (see Brock and White, 1991), except in those situations where the true father remained un-sampled and there was, by chance, a second pair of adults that provided a match. While we concede that this may have affected our conclusions in a limited number of instances, there should have remained a much higher probability of mis-assigning the affected juvenile to the correct category (i.e., to a nonresident male) than to the incorrect category (i.e., a resident male) in such instances. Misassignments favored non-resident males simply because there were far more of them, approximately 5 to 10 times more, than there were resident males within the territory of any given juvenile. Thus, the ef-fect of these misassignments on our overall conclusions re-garding the resident status of male parents should have been negligible. The reportedly high mutation rate of minisatellite loci, on the order of 1 in 240 to 1 in 288 (Burke and Bruford, 1987; Jeffreys et al., 1985b), could also have affected our re-sults. However, all of the juveniles that we successfully assigned parentage to in this study accounted for slightly less than 1000 bands, so that on average we would have expected to misas-sign parentage to no more than four juveniles on this basis.

## RESULTS

### Social systems

We determined social systems for 174 animals residing within 15 territories at the two colonies during 1991. Nine (60%) of these territories included multimale/multifemale social groups. The remaining 40% of territories included single-male/multifemale ($n = 2$), multimale/single-female ($n = 2$), single-male/single-female ($n = 1$), and multimale/absence of female ($n = 1$) social groups. Multimale territories included two to three males (mean ± SE = 2.13 ± 0.19), and multi-female territories included 2 to 11 females (mean ± SE = 4.14 ± 0.82). The number of juveniles weaned on these ter-ritories ranged from 0 to 17 (mean ± SE = 5.60 ±1.41).

We further characterized the social system by assessing the relatedness of same-sex adults occupying common territories using DNA fingerprinting. Females were significantly more highly related to females with whom they shared territories than they were to randomly selected individuals (Table 1; AH: $t = 35.83$, df = 101, $p < .001$; PL: $t = 6.47$, df = 21, $p < .001$). Males sharing territories, however, were no more closely related to each other than were randomly selected individuals
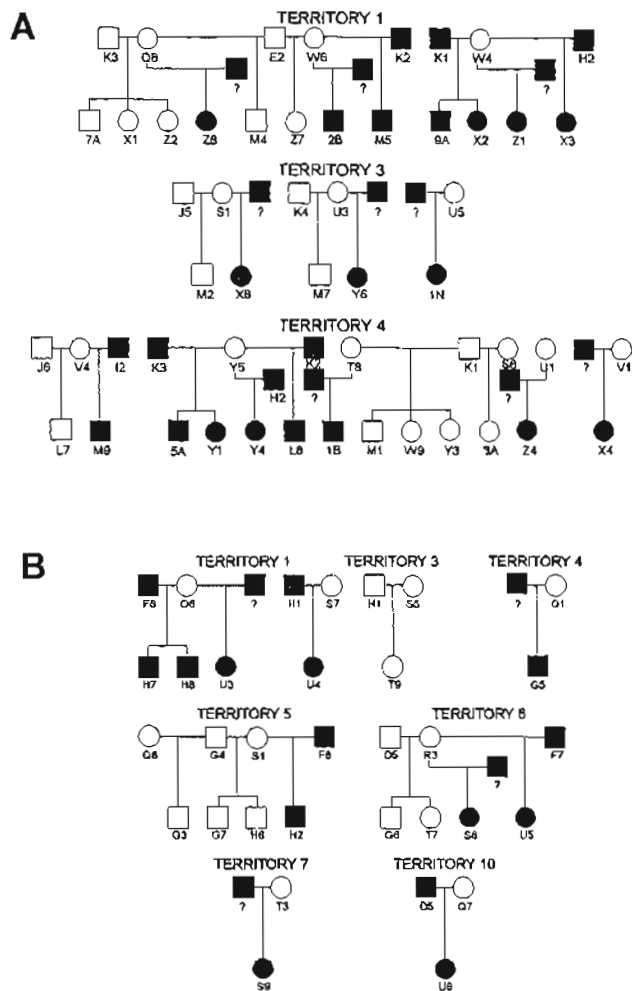


**Figure 1**
Pedigree for all juveniles successfully assigned parentage during 1991: (A) Antelope Hill, (B) Potato Lake. Animal identities are given as letter/number combinations. Shading designates extraterritorial males and their offspring.

at either colony (Table 1; AH: $t = 2.79$, df = 3, $p > .05$; PL: $t = 0.78$, df = 14, $p > .20$).

### Parentage

We successfully assigned parentage to 46 of 84 juveniles (55%) using DNA fingerprinting (Figure 1). These juveniles repre-sented an unbiased subsample, both in terms of the fertiliza-tion events and the social systems that were represented. Ju-veniles with unresolved parentage fell into one of two cate-gories. Fifty-eight percent of unresolved juveniles were mem-bers of territories that included one or more females whose DNA had degraded prior to fingerprinting. Two territories at Antelope Hill (2 and 5) were affected, accounting for 22 ju-veniles, and were therefore excluded from the analysis. The remaining 42% of unresolved juveniles were those for which no single pair of adults was identifiable as parents. This group of juveniles consisted of 16 individuals distributed randomly among all remaining territories.

Our DNA fingerprinting results suggest that females living in a social group on a territory often produced litters of mixed male parentage (7 of 21 litters, or 33%). Sixty-one percent of all progeny were sired by extraterritorial males ($n = 28$, where 15 of these males were identifiable, and 13 were unidentifia-

ble), and 39% of progeny ($n = 18$) were sired by resident males (Figure 1). The mean ($\pm$SE) number of progeny produced by extraterritorial fertilizations per female was 1.33 ($\pm$0.24), while that for intraterritorial fertilizations was 0.86 ($\pm$0.24), with a mean ($\pm$SE) overall number of progeny per female equaling 2.19 ($\pm$0.30). Because we were unable to unequivocally assign parentage to all juveniles, a small number of mating relationships may have remained unresolved among the adults; however, of those successful matings that were resolvable (i.e., those matings that resulted in the production of offspring), fully 68% involved extraterritorial males, while 32% involved resident males within the females' territories. Eighteen of 21 females (86%) produced one or more offspring by an extraterritorial male (mean number of successful matings with extraterritorial males = $1.19 \pm 0.18$): 13 females (62%) produced offspring by one extraterritorial male, while three (14%) and two (10%) females produced offspring by two and three extraterritorial males, respectively. Ten females (48%) produced offspring exclusively by extraterritorial males. Although only three females (14%) produced offspring exclusively with resident males, intraterritorial matings were not uncommon (mean number of successful matings with resident males = $0.57 \pm 0.13$). Ten females (48%) produced offspring by one resident male, while only a single female (5%) produced offspring by two resident males.

## DISCUSSION

Two straightforward conclusions can be drawn from the results of our parentage analysis: first, that Gunnison's prairie dog litters are frequently sired by multiple males, and second, that a large proportion of these males reside extraterritorially. Multiple paternity has now been documented for both invertebrates (Anderson, 1974; Burns, 1968; Gaffney and McGee, 1992; Watson, 1991) and vertebrates, including fishes (Avise and Shapiro, 1986; Borowsky and Kallman, 1976; Travis et al., 1990), reptiles (Barry et al., 1992; Schwartz et al., 1989; Stille et al., 1986), birds (Evarts and Williams, 1987; Gibbs et al., 1990; Jamieson and Craig, 1987; Price et al., 1989), and mammals (Birdsall and Nash, 1973; Boellstorff et al., 1994; Foltz and Schwagmeyer, 1989; Hanken and Sherman, 1981; Hoogland and Foltz, 1982; Searle, 1990; Sherman, 1989; Tegelström et al., 1991; Xia and Millar, 1991). Our estimate of the incidence of multiple paternity in Gunnison's prairie dog likely is conservative, perhaps explaining its relatively low position among the range of values reported for other mammals—from 3% in black-tailed prairie dogs (Hoogland and Foltz, 1982) to 89% in California ground squirrels (*Spermophilus beecheyi*; Boellstorff et al., 1994). This result may be explained in part by the conservative nature of our method of estimation.

The incidence of extraterritorial paternity in Gunnison's prairie dogs (61%) greatly exceeds values reported for other species of mammals and birds. Among mammalian species with complete spatial overlap between male and female territories, few studies of paternity have sought for or included male parents from outside the natal territory (Arnold, 1990; Hoogland and Foltz, 1982; McCracken and Bradbury, 1981; Schwartz and Armitage, 1980). Reported estimates of extraterritorial fertilizations range from 0% in yellow-bellied marmots (*Marmota flaviventris*; Schwartz and Armitage, 1980), to 12% in greater spearnose bats (*Phyllostomus hastatus*; McCracken and Bradbury, 1981). Only among birds have the reported incidences of extrapair parentage even begun to approach that in Gunnison's prairie dog, accounting for up to 40% of all offspring in some species (Brooker et al., 1990; Lifjeld et al., 1992; Sherman and Morton, 1988; Westneat, 1987, 1990).

These unusually high rates of extraterritorial paternity suggest that social assemblages existing within group-occupied territories of Gunnison's prairie dogs are poor predictors of mating relationships. Although all members of a territory, including the young, vigorously defend its borders against intruders (Rayor, 1988; Slobodchikoff, 1984), this defense is apparently inadequate to preclude copulations between males and females occupying separate territories. Because Gunnison's prairie dogs mate underground within the burrow system, we cannot say for certain at this point whether the members of one gender are primarily responsible for traveling into neighboring territories in search of extraterritorial copulations, or whether this behavior is equally characteristic of both males and females. However, we may speculate that extraterritorial copulations are being actively solicited primarily by females traveling into nearby territories, rather than by nonresident males entering the burrows of females who then are either forced or are passively accepting copulations. This tentative conclusion may be drawn on the basis of previous reports suggesting that males are particularly vigorous in their defense against territorial intrusion by rival males. Not only are territorial confrontations most dramatic among adult males, frequently involving contests during which each of the two combatants lock incisors and attempt to force the other male's head toward the ground (Rayor, 1988), they also occur with greater frequency among adult males than among adult females (Creef, 1993). Thus, we suggest that resident males are capable of preventing other males from entering their territories, but may be incapable of preventing females from crossing boundaries to breed with extraterritorial males. Why females should choose such a mating strategy remains an unanswered question, the solution to which may be related to the possible advantages of multiple female matings as reviewed by Schwagmeyer (1984). Solicitation of multiple males by females with nonoverlapping home ranges has been reported for Belding's (*S. beldingi*; Sherman and Morton, 1984) and California ground squirrels (Boellstorff et al., 1994).

In light of the high mating permeability that exists among Gunnison's prairie dog territories, it is unclear why a territorial social system is maintained in this species. Perhaps, as suggested by Dobson (1983) and Slobodchikoff and Schulz (1988), a territorial system is maintained in order to provide access to necessary resources other than potential mates. Two major resources not directly related to mating are available on prairie dog territories. One is an extensive burrow system, which is used as shelter from inclement weather and as a refuge from predators. Such burrow systems are costly to dig de novo (King, 1984), and thus may be worth defending. Another resource is food. Gunnison's prairie dogs feed on seeds in spring, then switch to grasses and herbaceous plants in the summer during the growing season, finally switching back to seeds again in the fall as the vegetation dies (Shalaway and Slobodchikoff, 1988). Territoriality might provide a mechanism for ensuring that each territorial group would have an adequate food supply throughout the year.

Our finding that females occupying shared territories are significantly more closely related than are randomly chosen members of the corresponding population suggests the potential for fitness gains through kin selection in Gunnison's prairie dog. However, because of the striking amount of genetic homogeneity apparent in our populations, specific relatedness levels among adults (e.g., full sibs, half-sibs, cousins, etc.) were impossible to determine. Therefore, it is difficult to say whether related groups of females represent close kin in the sense that genetic relatedness is relatively high within the group and relatively low without. In black-tailed prairie dogs, the existence of female kin groups has led to the evolution of several nepotistic behaviors that may result in in-

creased indirect fitness. For example, adult female black-tails have been shown to nurse the immature offspring of close genetic relatives with whom they share a territory (Hoogland, 1983a), presumably increasing the chances that these young will themselves survive to reproductive maturity. Further, female black-tails perform antipredator alarm calls as a nepotistic behavior (Hoogland, 1983b). It is possible that Gunnison's prairie dog females are behaving similarly, thereby increasing their overall level of genetic fitness beyond what would be possible in the presence of a random array of females.

Our genetic evidence does not support the existence of kin-based male coalitions within territories occupied by more than one male. However, our sample sizes may not have provided sufficient power to detect significant relatedness among males, particularly at Antelope Hill where the total sample consisted of only four male dyads. Mean levels of genetic relatedness among males occupying common territories were not significantly different from those representing nonrelatives. Tentatively, it appears that, unlike some other mammalian species whose mating systems are characterized by cooperation among related males for acquisition of mates (e.g., lions; Packer et al., 1988, 1991), Gunnison's prairie dog males form random associations with respect to genetic relatedness. These associations may exist due to the difficulty of excluding additional males from establishing residency in territories already occupied by one or more males, especially during years of high population density when the energetic demands of defense are high. Once these groups are formed, however, males may benefit from joint efforts at excluding the entry of extraterritorial males, particularly during the breeding season when females are receptive to copulations.

Our study demonstrates the danger of characterizing a mating system solely on the basis of behavioral data, because of the incomplete understanding it provides of female mating behavior. Traditionally there has been a scarcity of studies capable of identifying paternity, resulting in mating system classifications based frequently on observer expectations. For example, it has often been assumed that females occupying spatially fixed social groups should be forced to mate exclusively with males establishing residency therein (Clutton-Brock, 1989). The latter expectation has consistently been applied to a variety of social ground squirrel species, such as the yellow-bellied marmot (*Marmota flaviventris*; Downhower and Armitage, 1971) and the Columbian ground squirrel (*S. columbiana*; Murie and Harris, 1978). This has occurred in spite of the fact that copulations are frequently impossible to observe in these species because they occur below ground (Sherman and Morton, 1984). In order to overcome this problem, attempts have been made to gain information on paternity through the use of allozymes (Arnold, 1990; Hanken and Sherman, 1981; Hoogland and Foltz, 1982; Schwartz and Armitage, 1980, 1981). However, these studies have been hampered by low resolving power, as exemplified by Arnold's (1990) study using two informative allozymic loci to demonstrate that 5 of 245 offspring, affecting 4 of 76 litters, were the result of extraterritorial fertilizations by male alpine marmots (*M. marmota*).

In conclusion, we see a need for a more adequate description of mating systems traditionally classified as female defense polygyny, such as that represented by the Gunnison's prairie dog. Because of the high rate of apparent promiscuity in this species, we are in agreement with Boellstorff et al. (1994) that a better descriptor of this and other mating systems like it is "overlap promiscuity" (Wittenberger, 1979). However, even this classification scheme fails to recognize the potentially pivotal role of females in the process of forming mating associations. Therefore, we suggest that future work in this area

would benefit from a closer scrutiny of the primary gender controlling mating systems. We suspect that females will play a much more important role in this process than has been traditionally believed.

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