

PHILOPATRY, DISPERSAL, AND SOCIAL ORGANIZATION OF GUNNISON'S PRAIRIE DOGS

JOHN L. HOOGLAND

Appalachian Laboratory, University of Maryland, Frostburg, MD 21532-1094

I examined dispersal and social organization of Gunnison's prairie dogs (*Cynomys gunnisoni*) for 7 years at Petrified Forest National Park, Arizona. Within colonies, individuals lived in harem-polygynous family groups called clans. The number of clans at the study site each year ranged from 21 to 23, with a mean of 22.3. Clan size (the number of adults living in the same territory) ranged from 1 to 19, with a mean of 5.30. Clans contained 1.06 ± 0.39 (*SD*) breeding males, 3.01 ± 2.08 breeding females, and 1.23 ± 1.65 non-breeding yearling males. Some clans contained two breeding males, and others contained no resident breeding male. The area of clan territories ranged from 0.16 ha to 1.82 ha, with a mean of 0.67 ha. Females were more likely than males to copulate as yearlings (100% versus 24%). Ninety-five percent of females (340/358) remained in the natal clan territory for life, but only 5% of males (3/66) remained in the natal clan territory for >1 year after weaning. Dispersal of both sexes was most commonly to an adjacent clan territory. Infanticide at the study colony was rare or absent.

Key words: *Cynomys gunnisoni*, Gunnison's prairie dog, clan, territory, philopatry, dispersal

Gunnison's prairie dogs (*Cynomys gunnisoni*) are hibernating, colonial, burrowing rodents of the squirrel family (Sciuridae) and inhabit parts of Arizona, Colorado, New Mexico, and Utah in the southwestern United States (Fitzgerald et al., 1994; Longhurst, 1944; Pizzimenti and Hoffmann, 1973; Waring, 1970). Marked individuals have been the focus of six other independent field studies, but five of those (Cully, 1997; Fitzgerald and Lechleitner, 1974; Lechleitner et al., 1962; Lechleitner et al., 1968; Rayor, 1988) were terminated prematurely by bubonic plague (*Pasteurella [Yersinia] pestis*), an introduced bacterial disease to which Gunnison's prairie dogs are highly susceptible (Barnes, 1982, 1993; Cully, 1989, 1991, 1993; Fitzgerald, 1993; Rayor, 1985a). The sixth study has concentrated on experimental manipulations of availability and distribution of food (Slobodchikoff, 1984; Slobodchikoff and Schulz, 1988; Travis and Slobodchikoff, 1993; Travis et al., 1995). Social organiza-

tion of Gunnison's prairie dogs living under natural conditions thus remains poorly understood. To address this shortcoming, I studied the same large undisturbed colony of *C. gunnisoni* for 7 consecutive years.

MATERIALS AND METHODS

For 7 years (March–June, 1989–1995) that involved 15,000 person-hours of research, field assistants and I studied the ecology and social behavior of Gunnison's prairie dogs at Petrified Forest National Park in northeastern Arizona (1,700 m above mean sea level). The study site occupied ca. 14 ha, contained ca. 120 breeding adults each year, and was part of a large colony that contained ca. 300 adults (≥ 1 -year-old). Using binoculars and a 60-power telescope, we watched marked individuals from 4-m high observation towers. Emergence from hibernation occurred in late February through early April at the study site, copulations occurred in mid-March through early April, and the first emergences of nearly-weaned juveniles from their natal burrows occurred in late May and June. Length of gestation was 29.3 ± 0.53 days ($n =$

124), and the length of lactation was 38.6 ± 2.08 days ($n = 112$ —Hoogland, 1997).

Methods for capturing, handling, ear-tagging, and marking Gunnison's prairie dogs were the same as those used in my long-term study of black-tailed prairie dogs (*C. ludovicianus*—Hoogland, 1983, 1986, 1992, 1995, 1996a). Each year I captured and marked all the adult and juvenile residents at the study site. My original plan was to complete detailed research at the study site through 1995 and continue less rigorous, follow-up research in later years. Bubonic plague ravaged the study site in May–June 1995, however, and by July 1995 all residents were dead.

Like females of other ground-dwelling squirrels such as black-tailed prairie dogs (King, 1955) and Belding's (*Spermophilus beldingi*—Sherman, 1980), Columbian (*S. columbianus*—Festa-Bianchet and Boag, 1982), round-tailed (*S. tereticaudus*—Dunford, 1977), and Uinta (*S. armatus*—Balph, 1984) ground squirrels, female Gunnison's prairie dogs usually reared their offspring in separate nursery burrows. Except when mothers shared the same nursery burrow (Rayor, 1988), maternity was thus easy to establish. By surrounding nursery burrows with traps shortly after juveniles first appeared aboveground (Hoogland, 1995), I captured, ear-tagged, and marked all littermate siblings before they mixed with juveniles from other litters.

I scored a male as breeding if I observed him copulate or if he had a black scrotum and descended (scrotal) testes upon his emergence from hibernation. Nonbreeding males had gray or whitish scrotums with no descended testes. I scored a female as breeding if I observed her copulate in March or April, or if she was lactating (i.e., with long, turgid nipples) in May or June.

I categorized behavioral interactions as either amicable or hostile. Without any subsequent aggression, amicable interactions involved a kiss (mouth-to-mouth contact), sniffing of the perianal region, or play. Hostile interactions usually began with a kiss or sniffing of the perianal region, then escalated into a fight or chase. I scored combinations of amicable or hostile interactions (e.g., kiss + kiss or fight + chase) as single interactions.

Colonies of Gunnison's prairie dogs consist of territorial family groups called clans (Fitzgerald and Lechleitner, 1974). I assigned individuals to

the same clan if they participated in defense of the same territory and if they spent the night in the same or different burrows located in the same territory. Behavioral interactions also helped me to identify members of the same clan, because intraclan interactions were more amicable than interclan interactions.

I determined territorial boundaries from territorial disputes between individuals of different clans, and from interactions and feeding sites of individuals of the same clan. I tracked territories and recorded the number of years that boundaries remained the same. If a large territory had the same boundaries for 3 consecutive years, for example, and then subdivided into two smaller territories whose boundaries remained the same for 2 years, I scored three longevities (1 of 3 years and 2 of 2 years). Following fission or fusion of territories, I considered longevities of the new resulting territories to be independent.

Natal dispersal is the permanent emigration of individuals from the area of parturition before first reproduction (Greenwood, 1980; Holekamp, 1984). For Gunnison's prairie dogs, the area of parturition is the territory of the natal clan. Breeding dispersal is the emigration of a sexually mature individual from the area where it copulated (Greenwood, 1980; Holekamp, 1984). No individual at the study colony dispersed more than once before its first successful reproduction. I obtained information on natal dispersal for 95 different males and 21 different females. I obtained information on 39 breeding dispersals by males (involving 25 different individuals) and 4 breeding dispersals by females (involving 4 different individuals). I assumed that multiple breeding dispersals by the same individual in consecutive years were independent.

To define the distance moved in natal dispersal, I measured the distance between the natal burrow entrance and the burrow entrance within another clan territory used for final submergence at the end of each day in May. If I could not determine the burrow entrance used for final submergence in May, I used the burrow entrance closest to the site of capture. To define the distance moved in breeding dispersal, I measured the distance between burrow entrances of different clan territories used for final submergence at the end of each day in May of consecutive years.

I investigated the possibility of infanticide at the study colony in two ways. First, I determined

which females reared juveniles that appeared aboveground at the natal burrow. When one or more juveniles emerged, whole-litter infanticide (i.e., elimination of the entire litter via killing) could not have occurred. Second, I watched entrances of natal burrows for invaders (adult conspecifics other than the mother). If a trespasser entered a burrow containing juveniles, I recorded the duration of time spent underground and watched for evidence of possible marauding (e.g., a bloody face, or body parts of a victimized juvenile) when the trespasser reappeared aboveground.

I considered data from one clan and its descendants in different years to be statistically independent. For most analyses, data were available from 159 clans. For various reasons, sample sizes for seemingly related analyses were not always identical. I show results in the text as means \pm 1 standard deviation (*SD*). All significance levels (*P*-values) result from two-tailed nonparametric statistical tests (Siegel, 1956).

RESULTS

The number of clans at the study site each year was 22.3 ± 0.96 (range = 21–23). Clan size, the number of adults living in the same territory, was 5.30 ± 3.38 in May (range = 1–19, Fig. 1a). Clans contained 1.06 ± 0.39 breeding males, 3.01 ± 2.08 breeding females, and 1.23 ± 1.65 nonbreeding yearling males (Fig. 1b). The number of breeding males ($r_s = 0.296$), breeding females ($r_s = 0.907$), and nonbreeding yearling males ($r_s = 0.789$) all increased directly with clan size ($P < 0.001$ for all three, $n = 159$ clans).

From the number of resident breeding males in the territory, I recognized four different types of clans. One-male clans contained a single breeding male, and two-male clans contained two breeding males. Each breeding male of a two-male clan defended a section of the clan territory from the other male; females of two-male clans used the entire area of the clan territory. Some clans contained no resident breeding male, so I called them no-male clans. Finally, a single aggressive breeding male sometimes dominated two adjacent groups of females. I

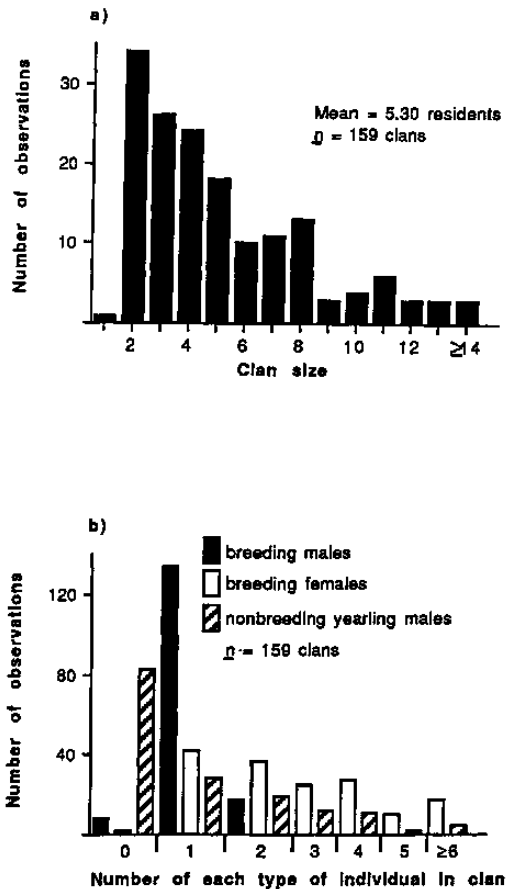


FIG. 1.—a) Variation in clan size of Gunnison's prairie dogs at Petrified Forest National Park, 1989–1995. Clan size is the number of adults living in the same territory. b) Composition of clans at Petrified Forest National Park, 1989–1995.

called each of the latter a half-male clan, because the single breeding male divided his time between the two groups of females. Frequencies of the different types of clans varied over time (Fig. 2), with one-male clans usually being the most common ($79/159 = 50\%$) and no-male clans usually being the rarest ($8/159 = 5\%$). Breeding males were more likely to reside in larger clans (Fig. 3). The larger size of two-male clans was especially pronounced.

Clans had a territory that ranged in area from 0.16 to 1.82 ha (Fig. 4). Boundaries

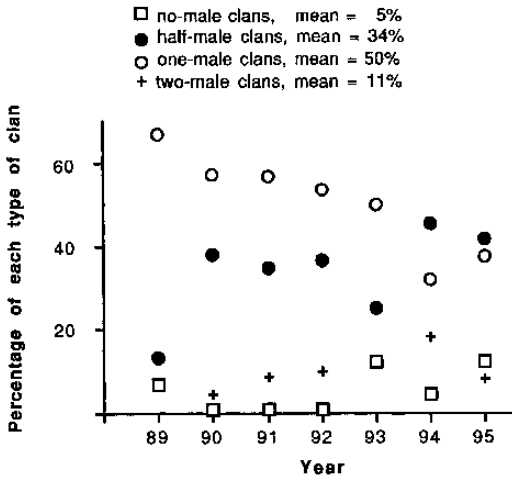


FIG. 2.—Annual variation in the percentage of no-male, half-male, one-male, and two-male clans of Gunnison's prairie dogs at Petrified Forest National Park, 1989–1995.

of clan territories were usually undetectable to human observers from physical features alone. Primarily via chasing, clan members consistently and vigorously defended central parts of the territory from individuals from other clans. In peripheral areas of the territory, however, individuals sometimes tolerated (i.e., did not chase away) individuals from other clans.

The area and boundaries of 15% of clan territories at the study colony (8/53) remained constant for 4 consecutive years, and one of these territories remained the same for 5 consecutive years. More commonly, however, territorial boundaries did not persist so long (2.06 ± 1.13 years, $n = 53$ territories that I tracked for ≥ 2 consecutive years), and most of them (42%) endured for only a single year. Larger territories generally supported larger clans, but the correlation was not significant ($r_s = 0.119$, $P = 0.195$, $n = 121$ clans for which I knew territory size).

Of 358 females first marked as juveniles that survived for ≥ 1 year, all reached sexual maturity and copulated in the first breeding season, when they were ca. 11 months old. Of 271 males first marked as

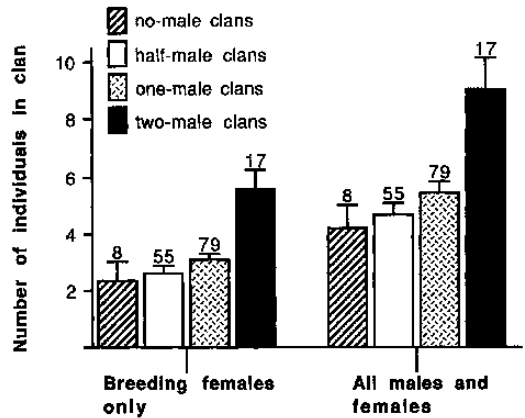


FIG. 3.—Number of individuals in no-male, half-male, one-male, and two-male clans of Gunnison's prairie dogs at Petrified Forest National Park, 1989–1995. Shown here are means ± 1 SE; the number above each SE line indicates the number of clans. The number of breeding females ($r_s = 0.353$, $P < 0.001$) and the number of males and females ($r_s = 0.328$, $P < 0.001$) varied directly with the type of clan.

juveniles that survived for ≥ 1 year, only 64 (24%) attained sexual maturity and copulated when they were ca. 11 months old. Females were thus more likely than males to copulate as yearlings ($\chi^2 = 408$, $d.f. = 1$, $P < 0.001$). Of the 207 males that did not attain sexual maturity as yearlings, I re-

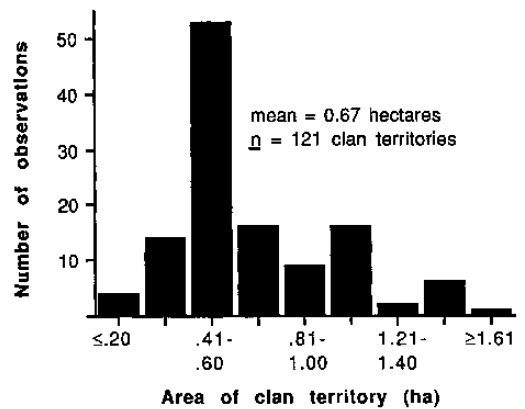


FIG. 4.—Variation in the size of clan territories of Gunnison's prairie dogs at Petrified Forest National Park, 1989–1995. These data include both central and peripheral areas of clan territories.

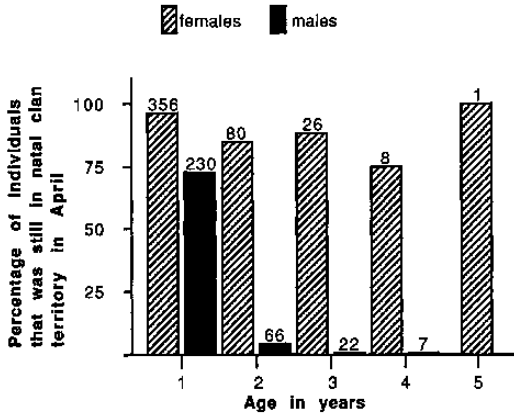


FIG. 5.—Percentages of male and female Gunnison's prairie dogs that were still in the natal clan territory at different ages at Petrified Forest National Park, 1989–1995. The number above each bar indicates the number of individuals for each age that were still alive at the study colony. Females were more likely than males to remain in the natal clan territory for ages 1–3 ($\chi^2 \geq 37.4$, $d.f. = 1$, and $P < 0.001$ for all three ages), and also for age 4 ($P = 0.007$, Fisher exact test); no male at the study colony survived ≥ 5 years.

captured 36 (17%) as 2-year-olds during the breeding season of the following year. Thirty-four of those 36 surviving males (94%) were sexually mature and copulated as 2-year olds.

Ninety-five percent of females (340/358) remained in the territory of the natal clan for life and thus were markedly philopatric (Fig. 5). Consequently, females of the same clan were almost always close kin (mothers and daughters, sisters, aunts and nieces, and so on). By contrast, 73% of males (167/230) were still in the territory of the natal clan at the end of 1 year, 5% (3/66) were there at the end of 2 years, and 0% (0/22) were there at the end of 3 years.

Of the few females that showed natal dispersal, 86% moved to the territory of an adjacent clan. The number of clan territories moved was 1.14 ± 0.36 , and the distance moved was 126 ± 49.8 m ($n = 21$ natal dispersals; ranges = 1–2 territories moved and 38–221 m for distance moved). For males, 56% of natal dispersals were to

an adjacent territory. The number of clan territories moved was 1.70 ± 0.89 , and the distance moved was 198 ± 118 m ($n = 95$ natal dispersals; ranges = 1–4 territories moved and 34–575 m for distance moved). Both measures of natal dispersal indicate that males moved farther than females (Mann-Whitney $U \geq 1,328$ and $P = 0.007$ for both).

I documented breeding dispersal for only four females. Three of these females dispersed to the territory of an adjacent clan, and the fourth moved two territories away. The distance moved was 125 ± 65.2 m ($n = 4$, range = 59–214 m). For males, 59% of breeding dispersals were to an adjacent territory. The number of clan territories moved was 1.46 ± 0.64 , and the distance moved was 163 ± 83.8 m ($n = 39$ breeding dispersals; ranges = 1–4 territories moved and 34–529 m for distance moved). Probably because of the small sample size for females, neither of the intersexual comparisons for breeding dispersal was significant (Mann-Whitney $U \leq 103$ and $P \geq 0.306$ for both).

Behavioral interactions involving genetically related females of the same clan were more amicable than interactions involving unrelated (or distantly related) females of different clans. In 1992, for example, 37% (169/455) of intraclan interactions involving females were amicable, but only 17% (41/246) of interclan interactions showed similar amicability ($\chi^2 = 31.9$, $d.f. = 1$, $P < 0.001$).

Each year, >90% of adult females produced emergent juveniles. The frequency of whole-litter infanticide, therefore, must have been low. I also detected no evidence for partial-litter infanticide.

DISCUSSION

Coloniality involves both costs and benefits (Alexander, 1974; Bertram, 1978). As for white-tailed (*C. leucurus*) and black-tailed prairie dogs (Hoogland, 1979, 1981), the most important costs of coloniality for Gunnison's prairie dogs probably are in-

creased competition and increased ectoparasitism. The primary benefit probably is increased safety from predators (Hoogland, 1996b).

Rayor (1988) used the terms coterie and harem interchangeably to describe social groups within colonies of Gunnison's prairie dogs. Travis et al. (1995, 1996) avoided both those terms and referred to single-sex territories, single-male-single-female territories, single-male-multi-female territories, and so on. Like Fitzgerald and Lechleitner (1974), who first described the social behavior of Gunnison's prairie dogs from observations of marked individuals, I use the term clan to describe the harem-polygynous, territorial family groups within colonies of *C. gunnisoni*. Superficially, clans are similar to the harem-polygynous, territorial family groups called coterie within colonies of black-tailed prairie dogs. Clans and coterie differ markedly, however, regarding attributes such as permanence of the territory, feeding areas, cuckoldry, and infanticide (Hoogland, 1998b; Travis et al., 1995, 1996). In view of these differences, family groups within colonies of Gunnison's and black-tailed prairie dogs warrant separate terms, in my opinion.

Some clans have no resident breeding male, others have two, and still others share a breeding male with another clan. In view of this variation, should we classify Gunnison's prairie dogs as harem-polygynous? The answer here is affirmative for *C. gunnisoni* at Petrified Forest National Park for two reasons. First, the most common type of clan at the study colony (i.e., one-male clan) is a classical harem that contains one resident breeding male and several females. In the second most common type (i.e., half-male clan), females resemble females of one-male clans because they are dominated by a single breeding male that also is able to dominate females of another clan. Second, the variation in structure of clans is similar to variation in other mammals that have been designated as harem-polygynous. Harems of wild horses (*Equus caballus*—

Berger, 1986), hanuman langurs (*Presbytis entellus*—Hrdy, 1977), and African lions (*Panthera leo*—Schaller, 1972), for example, sometimes contain two breeding males and thus resemble two-male clans. Further, contiguous harems of African lions and hanuman langurs sometimes are dominated by a single breeding male and thus resemble half-male clans.

On the other hand, social organization of Gunnison's prairie dogs seems more variable near Flagstaff, Arizona (Travis and Slobodchikoff, 1993; Travis et al., 1995, 1996). One-male clans are rarer and multi-male clans are more common around Flagstaff, for example, than at Petrified Forest National Park. More research is necessary for a better understanding of intraspecific variation in social organization of Gunnison's prairie dogs.

Despite disturbances caused by either bubonic plague or experimental manipulations, previous reports of social organization and social behavior of Gunnison's prairie dogs are in general agreement (Fitzgerald and Lechleitner, 1974; Lechleitner, 1969; Rayor, 1985b, 1988; Rayor and Armitage, 1991; Travis and Slobodchikoff, 1993; Travis et al., 1995, 1996). For example, all those accounts noted that individuals live in territorial clans, that intraclan interactions are more amicable than interclan interactions, and that most adult females produce emergent juveniles each year. My long-term research at Petrified Forest National Park has confirmed all those observations, and has yielded some new insights as well. For example, females usually spend their entire lifetimes in the natal territory. Such philopatry means that females of the same clan are almost always close kin, and probably explains why females interact more amicably with females of the home clan than with females of different clans. By contrast, young males disperse from the territory of the natal clan before reaching sexual maturity, and breeding males usually do not remain in the same territory for >1 year. Dispersal of both sex-

es is most commonly to an adjacent clan territory.

Distances for dispersals by males and females include only dispersals within the study colony. I made no effort to locate Gunnison's prairie dogs that might have dispersed to other colonies. If such inter-colonial dispersal occurs, I have underestimated distances for natal and breeding dispersal.

Presence of a black (versus gray or whitish) scrotum and descended testes shortly after emergence from hibernation easily distinguished breeding males from non-breeding males. That distinction was not easy for long, however, because scrotal testes quickly ascended to the abdominal cavity after the end of the breeding season, and scrotal pigmentation soon faded as well. To classify clans as no-male, half-male, one-male, or two-male (Fig. 2), I only considered presence or absence of breeding males in the clan. Earlier investigators did not attempt to use the number of resident breeding males to distinguish different types of clans (Fitzgerald and Lechleitner, 1974; Rayor, 1988; Travis et al., 1995, 1996), perhaps because they were unable to capture and examine males shortly after emergence from hibernation.

Without access to a resident breeding male, how did females of no-male clans get pregnant? One solution was for females of no-male clans to leave the clan territory on the single day of estrus in search of breeding males of other clans. More commonly, a breeding male from an adjacent clan temporarily invaded and then defended the territory of a no-male clan during the few days when females there came into estrus (Hoogland, 1998a, 1998b).

For both black-tailed (Garrett et al., 1982) and Gunnison's (Rayor, 1985b) prairie dogs, the age of first reproduction for females seems to depend on availability of forage. Specifically, females copulate as yearlings when food is abundant, but do not attain sexual maturity until the 2nd year when food is limiting. Forage must have

been plentiful at my study colony of Gunnison's prairie dogs, because all females copulated as yearlings. Only 24% of males at the study colony copulated as yearlings, however, probably because they could not easily compete with older, larger males.

Territorial boundaries between coterries of black-tailed prairie dogs are remarkably constant across generations. At Wind Cave National Park, South Dakota, for example, several coterries maintained the same territories for 14 consecutive years (Hoogland, 1995). Territorial boundaries of clans of Gunnison's prairie dogs at Petrified Forest National Park, by contrast, usually persisted for only 1–2 years.

Black-tailed prairie dogs spend >99% of their time in the home territory and obtain almost all their food there (Hoogland, 1995; King, 1955). Gunnison's prairie dogs, on the other hand, frequently feed in the weakly defended peripheral sections of territories belonging to other clans (Rayor, 1985b, 1988; Travis et al., 1995, 1996). Perhaps for this reason, Fitzgerald and Lechleitner (1974) called such peripheral sections "common feeding areas" and did not consider them as parts of clan territories.

Infanticide is the major cause of juvenile mortality among black-tailed prairie dogs, accounting for the partial or total demise of 39% of all litters (Hoogland, 1985, 1995). Infanticide among Gunnison's prairie dogs, by contrast, is rare or absent. Specifically, I watched carefully but did not observe a single unequivocal case of infanticide in 7 years of research at the study colony. The reason for this striking interspecific difference remains unknown.

Male and female black-tailed prairie dog adults commonly have as many as 30–40 behavioral interactions per day during the period of lactation as they attempt to execute and defend against killings (Hoogland, 1985, 1995). In the absence of infanticide, adult Gunnison's prairie dogs usually engage in only a handful of behavioral interactions per day during the period of lactation (this study; Rayor, 1988, table 4). The

lower density of individuals within colonies of *C. gunnisoni* (Fitzgerald and Lechleitner, 1974; Hoogland, 1995; Pizzimenti, 1975) also helps to explain why behavioral interactions are less common for them than for *C. ludovicianus*.

Despite numerous similarities, Gunnison's and black-tailed prairie dogs show many puzzling differences. More research is necessary for a better understanding of these and other species of *Cynomys*.

ACKNOWLEDGMENTS

I thank my field assistants who have helped over the years, especially M. Borge, D. Fitzgerald, A. Hoogland, J. Hoogland, M. A. Hoogland, M. V. Hoogland, S. Hoogland, A. Hoskins, S. Kain, C. May, L. Molles, M. Paulson, J. Tawil, and D. Ton-That. I also thank the staff at Petrified Forest National Park, especially C. Bowman, G. Cummins, E. Gastelum, M. Hellickson, K. Isensee, V. Santucci, and W. Towery. For valuable suggestions about live-trapping, I thank C. N. Slobodchikoff and his students. For financial assistance, I thank National Geographic Society, National Science Foundation, Petrified Forest Museum Association, and the University of Maryland. This paper is contribution number 3042-AL from the University of Maryland's Appalachian Laboratory. For help with the manuscript, I thank D. T. Blumstein, J. F. Cully, F. S. Dobson, J. P. Fitzgerald, K. R. McKaye, and L. S. Rayor.

LITERATURE CITED

- ALEXANDER, R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics*, 5:325-383.
- BALPH, D. F. 1984. Spatial and social behavior in a population of Uinta ground squirrels: interrelations with climate and annual cycle. Pp. 336-352, in *The biology of ground-dwelling squirrels* (J. O. Murie and G. R. Michener, eds.). The University of Nebraska Press, Lincoln Nebraska.
- BARNES, A. M. 1982. Surveillance and control of bubonic plague in the United States. *Symposia of the Zoological Society of London*, 50:237-270.
- . 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. Pp. 28-37, in *Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of black-footed ferrets* (J. L. Oldemeyer, D. E. Biggins, B. J. Miller, and R. Crete, eds.). United States Fish and Wildlife Service, Biological Report, 93:1-96.
- BERGER, J. 1986. Wild horses of the Great Basin: social competition and population size. The University of Chicago Press, Chicago, Illinois.
- BERTRAM, B. C. R. 1978. Living in groups: predators and prey. Pp. 64-96, in *Behavioural ecology: an evolutionary approach* (J. R. Krebs and N. B. Davies, eds.). First ed. Blackwell Scientific Publications, Oxford, United Kingdom.
- CULLY, J. F. 1989. Plague in prairie dog ecosystems: importance for black-footed ferret management. Pp. 47-55, in *The prairie dog ecosystem: managing for biological diversity* (T. W. Clark, D. Hinkley, and T. Rich, eds.). *Wildlife Technical Bulletin* 2:1-300.
- . 1991. Response of raptors to reduction of a Gunnison's prairie dog population by plague. *The American Midland Naturalist*, 125:140-149.
- . 1993. Plague, prairie dogs, and black-footed ferrets: implications for management. Pp. 38-49, in *Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of black-footed ferrets* (J. L. Oldemeyer, D. E. Biggins, B. J. Miller, and R. Crete, eds.). United States Fish and Wildlife Service, Biological Report 93:1-96.
- . 1997. Gunnison's prairie dog growth and life-history change after a plague epizootic. *Journal of Mammalogy*, 78:146-157.
- DUNFORD, C. 1977. Social system of round-tailed ground squirrels. *Animal Behaviour*, 25:885-906.
- FESTA-BIANCHET, M. AND D. A. BOAG. 1982. Territoriality in adult female Columbian ground squirrels. *Canadian Journal of Zoology*, 60:1060-1066.
- FITZGERALD, J. P. 1993. The ecology of plague in Gunnison's prairie dogs and suggestions for the recovery of black-footed ferrets. Pp. 50-59, in *Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of black-footed ferrets* (J. L. Oldemeyer, D. E. Biggins, B. J. Miller, and R. Crete, eds.). United States Fish and Wildlife Service, Biological Report 93:1-96.
- FITZGERALD, J. P., AND R. R. LECHLEITNER. 1974. Observations on the biology of Gunnison's prairie dog in central Colorado. *The American Midland Naturalist*, 92:146-163.
- FITZGERALD, J. P., C. A. MEANEY, AND D. M. ARMSTRONG. 1994. *Mammals of Colorado*. Denver Museum of Natural History and University Press of Colorado, Niwot, Colorado.
- GARRETT, M. G., J. L. HOOGLAND, AND W. L. FRANKLIN. 1982. Demographic differences between an old and a new colony of black-tailed prairie dogs (*Cynomys ludovicianus*). *The American Midland Naturalist*, 108:51-59.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28:1140-1162.
- HOLEKAMP, K. E. 1984. Dispersal in ground-dwelling sciurids. Pp. 297-320, in *The biology of ground-dwelling squirrels* (J. O. Murie and G. R. Michener, eds.). The University of Nebraska Press, Lincoln, Nebraska.
- HOOGLAND, J. L. 1979. The effect of colony size on individual alertness of prairie dogs (Sciuridae: *Cynomys* spp.). *Animal Behaviour*, 27:394-407.
- . 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: Cy-

- nomys leucurus* and *C. ludovicianus*). *Ecology*, 62: 252–272.
- . 1983. Nepotism and alarm calling in the black-tailed prairie dog (*Cynomys ludovicianus*). *Animal Behaviour*, 31:472–479.
- . 1985. Infanticide in prairie dogs: lactating females kill offspring of close kin. *Science*, 230:1037–1040.
- . 1986. Nepotism in prairie dogs varies with competition but not with kinship. *Animal Behaviour*, 34:263–270.
- . 1992. Levels of inbreeding among prairie dogs. *The American Naturalist*, 139:591–602.
- . 1995. The black-tailed prairie dog: social life of a burrowing mammal. The University of Chicago Press, Chicago, Illinois.
- . 1996a. *Cynomys ludovicianus*. *Mammalian Species*, 535:1–10.
- . 1996b. Why do Gunnison's prairie dogs give anti-predator calls? *Animal Behaviour*, 51:871–880.
- . 1997. Duration of gestation and lactation for Gunnison's prairie dogs. *Journal of Mammalogy*, 78: 173–180.
- . 1998a. Estrus and copulation for Gunnison's prairie dogs. *Journal of Mammalogy*, 79:887–897.
- . 1998b. Why do Gunnison's prairie dog females copulate with more than one male? *Animal Behaviour*, 55:351–359.
- HRDY, S. B. 1977. The langurs of Abu: female and male strategies of reproduction. Harvard University Press, Cambridge, Massachusetts.
- 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.
- LECHLEITNER, R. R. 1969. Wild mammals of Colorado. Pruett, Boulder, Colorado.
- LECHLEITNER, R. R., J. V. TILESTON, AND L. KARTMAN. 1962. Die-off of a Gunnison's prairie dog colony in central Colorado. I. Ecological observations and description of the epizootic. *Zoonoses Research*, 1: 185–199.
- LECHLEITNER, R. R., L. KARTMAN, M. I. GOLDBERG, AND B. W. HUDSON. 1968. An epizootic of plague in Gunnison's prairie dogs (*Cynomys gunnisoni*) in south-central Colorado. *Ecology*, 49:734–743.
- LONGHURST, W. 1944. Observations on the ecology of the Gunnison prairie dog in Colorado. *Journal of Mammalogy*, 25:24–36.
- PIZZIMENTI, J. J. 1975. Evolution of the prairie dog genus *Cynomys*. *Occasional papers of the Museum of Natural History, University of Kansas*, 39:1–73.
- PIZZIMENTI, J. J., AND R. S. HOFFMANN. 1973. *Cynomys gunnisoni*. *Mammalian Species*, 25:1–4.
- RAYOR, L. S. 1985a. Dynamics of a plague outbreak in Gunnison's prairie dog. *Journal of Mammalogy*, 66:194–196.
- . 1985b. Effects of habitat quality on growth, age of first reproduction, and dispersal in Gunnison's prairie dogs (*Cynomys gunnisoni*). *Canadian Journal of Zoology*, 63:2835–2840.
- . 1988. Social organization and space-use in Gunnison's prairie dog. *Behavioral Ecology and Sociobiology*, 22:69–78.
- RAYOR, L. S., AND K. B. ARMITAGE. 1991. Social behavior and space-use of young of ground-dwelling squirrel species with different levels of sociality. *Ethology, Ecology, and Evolution*, 3:185–205.
- SCHALLER, G. B. 1972. *The Serengeti lion: a study of predator-prey relations*. The University of Chicago Press, Chicago, Illinois.
- SHERMAN, P. W. 1980. The limits of ground squirrel nepotism. Pp. 504–555, in *Sociobiology: beyond nature/nurture?* (G. W. Barlow and J. Silverberg, eds.). Westview Press, Boulder, Colorado.
- SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York.
- SLOBODCHIKOFF, C. N. 1984. Resources and the evolution of sociality. Pp. 227–251, in *A new ecology: novel approaches to interactive systems* (P. W. Price, C. N. Slobodchikoff, and W. Gaud, eds.). John Wiley & Sons, New York.
- SLOBODCHIKOFF, C. N., AND W. C. SCHULZ. 1988. Cooperation, aggression, and the evolution of social behavior. Pp. 13–32, in *The ecology of social behavior* (C. N. Slobodchikoff, ed.). Academic Press, New York.
- TRAVIS, S. E., AND C. N. SLOBODCHIKOFF. 1993. Effects of food resource distribution on the social system of Gunnison's prairie dogs. *Canadian Journal of Zoology*, 71:1186–1192.
- TRAVIS, S. E., C. N. SLOBODCHIKOFF, AND P. KEIM. 1995. Ecological and demographic effects on intra-specific variation in the social system of prairie dogs. *Ecology*, 76:1794–1803.
- . 1996. Social assemblages and mating relationships in prairie dogs: a DNA fingerprint analysis. *Behavioral Ecology*, 7:95–100.
- WARING, G. H. 1970. Sound communications of black-tailed, white-tailed, and Gunnison's prairie dogs. *The American Midland Naturalist*, 83:167–185.

Submitted 30 October 1997. Accepted 9 February 1998.

Associate Editor was Edward J. Heske.