

# ESTRUS AND COPULATION OF GUNNISON'S PRAIRIE DOGS

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Because most animals copulate surreptitiously, estimates of male and female copulatory success are elusive. Here I describe six distinctive behaviors that coincide with underground copulations of Gunnison's prairie dogs (*Cynomys gunnisoni*): the underground consortship itself, inordinate male attention toward the estrous female, self-licking of genitals, dust-bathing, the mating call, and late final submergence of the estrous female. These diagnostic behaviors allowed me to identify sexual partners for 308 females that came into estrus during a 7-year study.

**Key words:** *Cynomys gunnisoni*, Gunnison's prairie dog, estrus, copulation

Except for certain primates, female mammals usually are sexually receptive and copulate only during a brief estrus. Usually commencing just before fertilization is possible, estrus typically starts shortly before, and ends shortly after, ovulation (Beach, 1976; Hrdy, 1977). Identification of estrus is crucial for a thorough understanding of mammalian mating systems.

For some large mammals, researchers can identify estrus easily. For example, pronounced vulvar swelling indicates estrus for hamadryas baboons (*Papio hamadryas*) and gelada baboons (*Theropithecus gelada*) (Stammbach, 1987). Unusual female behaviors denote estrus for other mammals such as wild horses (*Equus caballus*—Berger, 1986) and African lions (*Panthera leo*—Schaller, 1972). For other mammals such as mountain sheep (*Ovis canadensis*—Geist, 1971) and spotted hyenas (*Crocuta crocuta*—Kruuk, 1972), sudden inordinate male attentiveness to a single female pinpoints estrus. Researchers also can document copulations easily when they occur during daylight in open habitats, as they usually do for mammals such as patas monkeys (*Erythrocebus patas*—Cords, 1987) and northern elephant seals (*Mirounga angustirostris*—Le Boeuf and Reiter, 1988).

In contrast, researchers usually find it difficult to identify estrus and copulation among smaller mammals. Such identifica-

tion is especially formidable when individuals are nocturnal and live in closed habitats (Ebensperger and Tamarin, 1997; Kaufman, 1989). Even when individuals are diurnal and live in more open habitats, however, identification can be difficult if pairs retreat to burrows for copulation, as do black-tailed prairie dogs (*Cynomys ludovicianus*—Hoogland, 1982, 1995), black-capped marmots (*Marmota camtschatica*—Kapitonov, 1960) and Alaskan marmots (*M. broweri*—Rausch and Rausch, 1971), and most ground squirrels (*Spermophilus*—Boellstorff et al., 1994; Lacey et al., 1997; Michener and McLean, 1996; Murie, 1995; Ortega, 1990; Sherman, 1989; Slade and Balph, 1974).

Gunnison's prairie dogs (*Cynomys gunnisoni*) are diurnal, colonial, burrowing rodents of the squirrel family (Sciuridae). Individuals weigh 250–1,100 g as adults ( $\geq 1$  year old) and inhabit parts of Arizona, Colorado, New Mexico, and Utah (Pizzimenti and Hoffmann, 1973). Within colonies, they live in harem-polygynous family groups called clans (Fitzgerald and Lechleitner, 1974; Rayor, 1985, 1988). Clans typically contain 3–4 breeding females, 1 breeding male, and 1–2 nonbreeding yearling males (Slobodchikoff, 1984; Travis et al., 1995, 1996, 1997). Clan members defend a home territory of ca. 1 ha, but commonly forage

in areas >100 m from boundaries of their home territory.

Mortality in the first year is ca. 50% for both sexes. Females live  $\leq 6$  years, but no male at the study colony has lived >4 years. Females first copulate when they are ca. 11 months old, but males commonly defer sexual maturity until their second year (Hoogland, 1997a, 1998a; Rayor, 1985, 1988).

At Petrified Forest National Park, Arizona, Gunnison's prairie dogs hibernate for ca. 4 months of each year. They emerge from hibernation in late February and March, and the breeding season (i.e., the interval when copulations occur) starts in mid-March and continues into early April. Pregnancy lasts for  $29.3 \pm 0.53$  days (Hoogland, 1997a). After remaining underground for  $38.6 \pm 2.08$  days after birth, juveniles first appear aboveground in late May or early June (Hoogland, 1997a).

Gunnison's prairie dogs copulate underground. Below I describe six diagnostic aboveground behaviors that make it possible to specify the identity of sexual partners for each estrous female.

#### MATERIALS AND METHODS

For 7 consecutive 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 sea level). The study site contained ca. 120 adults each year and was part of a large colony of ca. 300 adults. Using binoculars and a 60-power telescope, we watched marked individuals from 4-m high observation towers. My methods for marking and studying Gunnison's prairie dogs were identical to those used in my long-term study of black-tailed prairie dogs (Hoogland, 1985, 1986, 1992, 1995, 1997b).

In 1989, Gunnison's prairie dogs emerged from hibernation in late February and March. Throughout March and into April, I watched marked individuals every day from dawn until dusk. I especially watched for aboveground copulations, but saw none. Although I saw no mat-

ings, I determined from vulvar examinations that females were nonetheless copulating. I thus concluded that Gunnison's prairie dogs usually must copulate underground.

After deducing that Gunnison's prairie dogs copulate underground, I began tracking the co-submergences of females and breeding males during March and April. I usually saw a pair submerge and thus knew exactly where they were. The search for missing males every 20 min helped me detect underground consortships whose submergences I did not see. If all males were foraging aboveground, I assumed that an underground copulation was not occurring. If a breeding male was missing, I searched for all females in his territory. If a female was also missing, I suspected an underground copulation. I watched burrow entrances carefully when a male and a female were missing during the same 20-min period to see if they emerged together, or sequentially, from the same entrance.

I scored a male as breeding in a particular year if he copulated at least once in that year, or if he had a pigmented scrotum with descended testes. When a female and breeding male entered the same burrow together (but with no other individuals) at the same time ( $\leq 15$  s apart) during daylight, I scored the co-submergence as an underground consortship. I scored the final submergence of an estrous female at the end of the day as "late" if it occurred  $\geq 15$  min after the final submergence of other nonestrous females of the home clan.

Using daily observations and daily live-trappings, I used three methods to determine the date of parturition for each female (Hoogland, 1997a): 1) fresh blood on the fur surrounding the vulva; 2) a precipitous decline in maternal body mass ( $75.9 \pm 19.1$  g; range = 37–110 g,  $n = 43$  declines), or 3) a sudden increase in the amount of time that the mother spent in the nursery burrow during daylight.

Data were available for 308 periods of estrus. I watched certain long-lived females in consecutive years, and the number of different females for which I observed estrus and copulation was 241. Data on certain behaviors were incomplete for some of these females, however, so that sample sizes for various analyses usually differed. As for black-tailed prairie dogs (Hoogland, 1995), I assumed that data from the same female in different years were independent. I show results in the text as means  $\pm 1$  SD. All signifi-

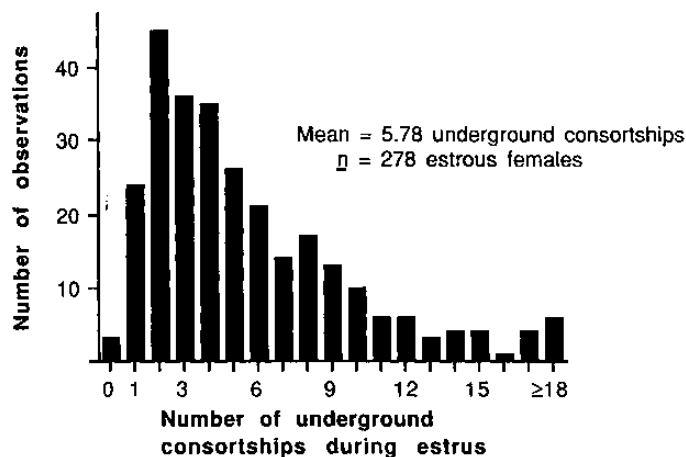


FIG. 1.—Number of underground consortships per estrus for Gunnison's prairie dogs at Petrified Forest National Park in 1989–1995. I scored an underground consortship whenever a female submerged with a breeding male for  $\geq 15$  s. The females with no underground consortships ( $n = 3$ ) copulated exclusively aboveground.

cance levels ( $P$ -values) result from two-tailed nonparametric statistical tests (Siegel, 1956).

#### RESULTS

**Underground consortships.**—Most females had numerous underground consortships on the day of estrus (Fig. 1), with a range from 0 (for females that copulated exclusively aboveground) to 34. Length of an underground consortship was  $28.8 \pm 30.2$  min ( $n = 282$  estrous females), with a range from 15 s (the shortest interval that I recorded) to 338 min. The date on which a female came into estrus and copulated was 28 March  $\pm 5$  days (range = 12 March–13 April,  $n = 308$  periods of estrus).

Each female engaged in underground consortships (i.e., was sexually receptive) on only a single day each year. The first underground consortship sometimes occurred within 15 min after a female first appeared aboveground in the morning, but it occurred more commonly in late morning or early afternoon. The starting time for the first underground consortship was  $1150 \pm 2.54$  h (range = 0639–1807 h,  $n = 276$ ). The starting time for the last underground consortship was  $1624 \pm 1.75$  h (range = 0737–1901 h,  $n = 266$ ).

The first few underground consortships for the same pair usually lasted only for several minutes. Later the pair had a longer underground consortship that lasted for  $\geq 5$  min, usually lasted for  $\geq 30$  min, and sometimes persisted for hours. Dramatic changes in aboveground behaviors immediately followed the longer underground consortship. The female no longer tolerated sniffing of her vulva, for example, and usually initiated a fight if the male came too near. Behavior of the copulating male also changed from sexual interest (sniffing and short underground consortships) to guarding. Guarding males remained close to the estrous female and quickly chased away any other breeding male that approached. From these changes in behavior, I deduced that the longer underground consortship, which I have termed the critical underground consortship (CUC), probably involved insemination. The duration for each CUC was  $54.8 \pm 47.9$  min (Fig. 2), and the starting time was  $1423 \pm 2.55$  h (range = 0700–1836 h,  $n = 492$  CUCs).

**Inordinate attention toward an estrous female by the breeding male.**—Frequent sniffing of the vulva by a breeding male indicated that the recipient female would

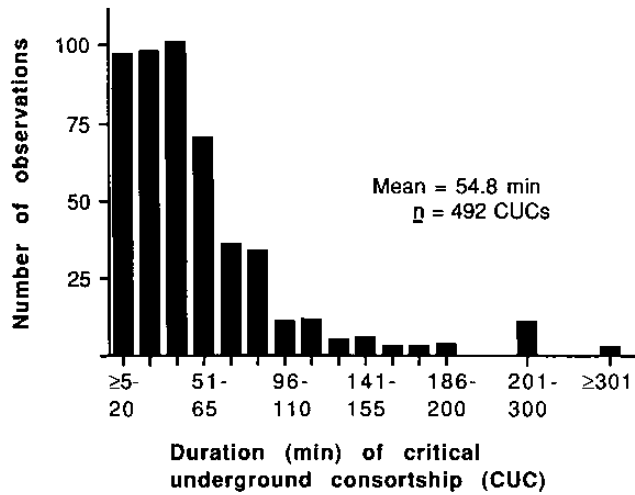


FIG. 2.—Duration of critical underground consortship (CUC), when insemination presumably occurred. When a female copulated with two or more different males, I used times for the CUC with each male.

come into estrus later in the same day. After inseminating a female, on the other hand, a breeding male frequently chased and fought with her as he tried to prevent copulations with other males via guarding. Consequently, females in heat were targets of copious attention by males that facilitated my detection of estrus and copulation (Fig. 3).

*Self-licking of genitals.*—Within 5 min after emerging from an underground consortship, and especially after the CUC, individuals of both sexes commonly licked their genitals. Specifically, 20% of estrous females (59/291) licked their genitals aboveground following copulation, and 30% of estrous females (88/291) elicited aboveground self-licking of genitals by copulating males. In contrast, only 10 individuals engaged in self-licking of genitals that was unrelated to copulation ( $\chi^2 > 15$ ,  $d.f. = 1$ ,  $P < 0.001$ —comparison of frequency of self-licking of genitals by individuals on days when they consorted underground versus the frequency on those days when they did not).

*Dustbathing.*—Individuals commonly rolled themselves in the dirt within 5 min after emerging from an underground consortship. Specifically, dustbathing by at

least one copulating male occurred for 25 of 291 estrous females (9%), and dustbathing by estrous females occurred at a frequency of 27% (78/291). In contrast, only 20 individuals engaged in dustbathing that was unrelated to copulation ( $\chi^2 > 15$ ,  $d.f. = 1$ ,  $P < 0.001$ —comparison of frequency of dustbathing by individuals on days when they consorted underground versus the frequency on those days when they did not).

*Mating call.*—Shortly before or after an underground consortship, males sometimes gave a unique vocalization that I named the mating call. The mating call(s) occurred most commonly just before the CUC, immediately after the breeding male sniffed the vulva of the estrous female. The typical mating call consisted of sets of 2–25 individual barks, with a pause of 3–15 s between each set. The mating call superficially resembled the anti-predator call (Hoogland, 1996; Slobodchikoff et al., 1991; Waring, 1970), but field assistants and I quickly learned to discriminate between the two. More important, noncalling Gunnison's prairie dogs distinguished between the two calls. They always ran to burrow mounds and scanned for predators in response to the anti-predator call, but often did not even

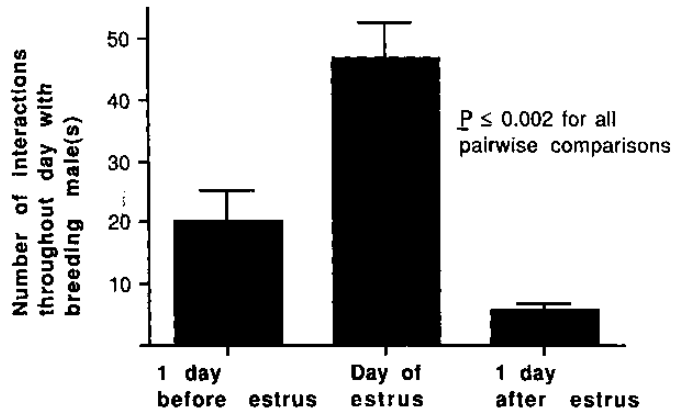


FIG. 3.—Behavioral interactions in 1995 between breeding males and the same 39 females before, during, and after estrus. Bars indicate the mean number  $\pm$  1 SE of behavioral interactions during the entire day. *P*-values are from the Wilcoxon matched-pairs signed-ranks test.

look up or respond in any other predictable way to the mating call.

Fifty-four percent of estrous females (161/297) elicited at least one mating call (Fig. 4). Mating calls unrelated to estrus were rare, and usually were elicited by females ( $n = 20$ ) on the day before estrus. Thus, except when copulations occurred aboveground, the mating call was perhaps the single best confirmation that a female was in estrus ( $\chi^2 > 15$ , *d.f.* = 1,  $P <$

0.001—comparison of elicitation or non-elicitation of mating call versus presence or absence of estrus).

One mating call on 31 March 1990 consisted of a single chirp. At the other extreme, a mating call on 24 March 1995 contained thousands of chirps and persisted for 71 consecutive min. The length of each mating call was  $3.78 \pm 6.02$  min ( $n = 663$ , in response to 161 different estrous females).

*Late final submergence of the estrous female.*—One hundred eighty-six of 264 estrous females (70%) remained aboveground later than usual (i.e., after most other non-estrous adult females in the colony had submerged for the night). This trend was especially evident when I considered only females of the same clan. Specifically, all females in a clan usually submerged for the night within 5–10 min of each other in March when no female was in estrus. An estrous female, however, typically remained aboveground for 60–90 min after the other nonestrous females of her home clan had disappeared for the night. Late estrous females did not forage seriously after sunset. Rather, they roamed around their home and adjacent territories, as though looking for males with whom they had not yet copulated.

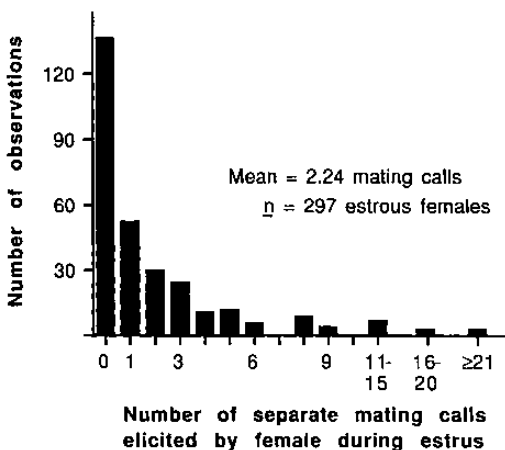


FIG. 4.—Number of mating calls per estrus at Petrified Forest National Park in 1989–1995. I scored a mating call by the same male as discrete when  $\geq 60$  s separated it from his other mating calls.

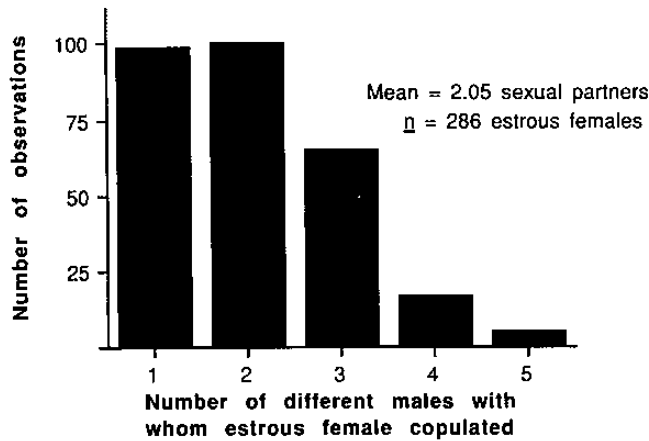


FIG. 5.—Number of different sexual partners for female Gunnison's prairie dog at Petrified Forest National Park in 1989–1995. Litters of females that copulate with more than one male commonly show multiple paternity (J. L. Hoogland et al., in litt.; Travis et al. 1996).

*Number of sexual partners per estrous female.*—By watching for the six diagnostic behaviors described above, I documented copulations for  $82.4\% \pm 9.6\%$  of the females that came into estrus at my study site each year (range = 66.7% [in 1989, year 1 of observations]–94.4%). At least one of the diagnostic behaviors occurred for each of the 286 estrous females for which I was able to record all copulations. The number of different diagnostic behaviors that I observed per estrous female was  $2.82 \pm 1.20$ .

Thirty-five percent of females copulated with only one male, 35% copulated with two different males, and 30% copulated with three or more different males (Fig. 5). When a female copulated with more than one male, the additional male was usually from either the territory of the home clan (when the home clan had  $>1$  breeding male) or an adjacent territory. In ca. 3% of copulations, however, females mated with invading males from more distant clans.

*Date of underground consortiums versus date of first juvenile emergence.*—If underground consortiums involved copulation and insemination, then females that consorted early in the breeding season should have reared their young to first emergence sooner than females that consorted later.

Data from 7 consecutive years supported this prediction ( $r_s \geq 0.814$  and  $P < 0.001$  for all years; Fig. 6a).

*Date of underground consortiums versus date of parturition.*—If copulation and insemination occurred during underground consortiums, then females that consorted early in the breeding season should have given birth earlier than females that consorted later. Data from the 4 years when I recorded both parturitions and copulations supported this prediction ( $r_s \geq 0.981$  and  $P < 0.001$  for all years; Fig. 6b).

*Aboveground copulations.*—For reasons that I never determined, mating pairs sometimes copulated aboveground rather than underground. Specifically, 8% of estrous females (24/286, but none in 1989, my first year of observations) copulated at least once aboveground. In all aboveground cases, the male mounted the female from the rear and immediately began pelvic thrusting.

If underground consortiums involve copulation and insemination, then the diagnostic features of these consortiums also should have been evident in aboveground copulations. Data from the 24 females that copulated aboveground supported this prediction. For example, 87% of the females

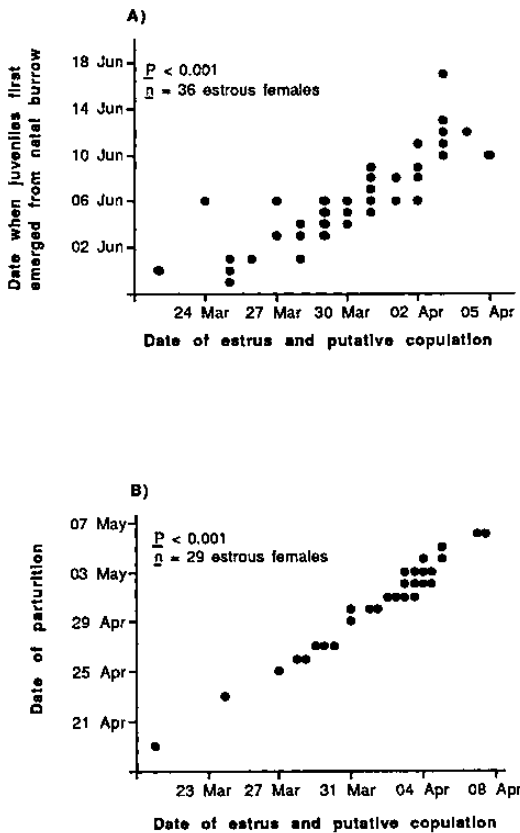


FIG. 6.—a) Date of first juvenile emergence versus date of copulation in 1992, and b) date of parturition versus date of copulation in 1991. *P*-values for both graphs are from the Spearman rank correlation test.

(20/23) had at least one underground consortship in addition to the aboveground copulation(s), 100% (24/24) were the objects of inordinate male attention, 29% (7/24) self-licked the vulva, 54% (13/24) had at least one dustbath, 54% (13/24) elicited at least one mating call, and 71% (17/24) delayed final submergence until late in the day. Further, 29% of the aboveground copulations (7/24) involved self-licking of genitals by the male, and 21% (5/24) involved dustbathing by the male. These frequencies were remarkably similar to those for females whose copulations were all underground.

*Vulvar examinations before and after underground consortships.*—When they first

emerged from hibernation, females had swollen vulvas that appeared to be sealed shut by a thin layer of skin. At the end of the breeding season in early April, however, their vulvas were always open and less swollen. If the vulva does not open until copulation, then each female should have had a closed vulva just before her underground consortships and an open vulva immediately afterwards. Before the underground consortships, I examined vulvas 2 days before estrus ( $n = 32$  females), 1 day before estrus ( $n = 44$ ), and the day of estrus ( $n = 44$ , all trapped before the CUC). After the underground consortships, I examined vulvas on the day of estrus ( $n = 1$  female, trapped after the CUC), 1 day after estrus ( $n = 82$ ), and 2 days after estrus ( $n = 26$ ). All 109 females had open vulvas after their underground consortships. Most of the 120 females had closed vulvas before their underground consortships, but 12 (10%) had open vulvas ( $\chi^2 = 186$ , *d.f.* = 1,  $P < 0.001$ —comparison of open or closed vulva versus before or after the underground consortships). A closed vulva was thus unmistakable evidence that a female had not yet copulated, but an open vulva usually meant that the female had already mated. I was unable to determine why certain females had open vulvas before copulation. On the first ( $n = 82$ ) or second ( $n = 26$ ) day after they consorted underground, 3 of 108 examined females (3%) had conspicuous, white, and rubbery copulatory plugs protruding from their vaginas.

#### DISCUSSION

Gunnison's prairie dogs are probably more vulnerable to predation while preoccupied with copulation. This increased susceptibility ultimately might explain why individuals seek refuge in burrows for underground consortships. Alternatively, like Richardson's ground squirrels (*S. richardsonii*—Davis, 1982) and black-tailed prairie dogs (Hoogland, 1995), perhaps Gunnison's prairie dogs copulate underground to avoid male-male competition for estrous females.

Several lines of evidence indicate that the six behaviors that I have labeled as “diagnostic” really do signal underground copulation and insemination for Gunnison’s prairie dogs. The first females that showed or elicited these behaviors early in the breeding season, for example, were always the first ones each year to give birth and rear their juveniles to first emergence. Further, females that copulated aboveground showed or elicited the same diagnostic behaviors at frequencies remarkably similar to those for females whose copulations were all underground.

I could only record diagnostic behaviors that occurred aboveground where I could see or hear them. However, inordinate male attention, self-licking of genitals, dustbathing, and even the mating call probably occurred underground as well. My estimates of frequencies of diagnostic behaviors associated with underground copulations are therefore minimal estimates.

One excellent way to confirm insemination would be to look for sperm taken from vaginal lavages just before and just after underground consortships (Lacey et al., 1997; Michener and McLean, 1996; Murie, 1995). Vaginal lavages require disruptive live-trapping during the breeding season (Hoogland, 1995), however, so I avoided them.

Most critical underground consortships persisted for >30 min, but copulation and insemination sometimes occurred more quickly (Fig. 2). On two occasions, for example, females copulated once aboveground for 5 min, with no underground consortships. Both females later gave birth.

The copulatory plugs that I observed in the vaginas of certain female Gunnison’s prairie dogs were similar to those described for other squirrels (Koprowski, 1992; Michener, 1984; Murie and McLean, 1980). Among numerous possibilities (Hoogland, 1995), I was unable to determine the function of the copulatory plug for Gunnison’s prairie dogs. Nor could I determine why

only 3% of females had a copulatory plug on the day after copulation.

Like females of California (*S. beecheyi*—Boellstorff et al., 1994), arctic (*S. parryi*—Lacey et al., 1997), and Columbian (*S. columbianus*—Murie, 1995) ground squirrels and females of white-tailed (*C. leucurus*) and Utah (*C. parvidens*) prairie dogs (J. L. Hoogland, in litt.), female Gunnison’s prairie dogs were sexually receptive on only a single day of the breeding season each year (Hoogland 1998a, 1998b). A lone female came into estrus a second time in the same breeding season after she had not conceived in the first estrus. Second estrus in the same breeding season also occurs among Richardson’s ground squirrels (Michener and McLean, 1996) and black-tailed prairie dogs (Hoogland, 1995).

Not surprisingly, males showed more interest toward pre-estrous females than toward post-estrous females. Specifically, like black-tailed prairie dog males (Hoogland, 1995), Gunnison’s prairie dog males interacted least frequently with females on the day after estrus, more frequently with the same females on the day before estrus, and most frequently with the same females on the day of estrus (Fig. 3).

Functions of the aboveground diagnostic behaviors that accompany underground copulations of Gunnison’s prairie dogs remain unknown. Perhaps self-licking of genitals deters certain genital infections or sexually transmitted diseases (Hart, 1990; Hart et al., 1987; Read, 1990). Like female gray and fox squirrels (*Sciurus carolinensis* and *S. niger*—Koprowski, 1992), however, female Gunnison’s prairie dogs might lick the vulva to remove either sperm or the copulatory plug. Perhaps the function of dustbathing is to remove fleas or other ectoparasites that an individual might have acquired during sexual intercourse (Hamilton and Zuk, 1982; Hart, 1990). Perhaps the mating call announces competitive status, good health, and freedom from parasites, and thereby renders the caller more attractive to estrous females and less vulnerable



to invasions and takeovers by other males (Hoogland, 1995).

Mating pairs usually had several underground consortships before the CUC that involved insemination. If Gunnison's prairie dogs resemble black-tailed prairie dogs (Hoogland, 1995), then early underground consortships probably involve copulation and intromission without ejaculation. Perhaps early non-ejaculatory copulations open a closed vulva before actual transmission of sperm. They also might initiate neuro-endocrine reflexes in the female necessary for ovulation and pregnancy (Dewsbury and Estep, 1975; Eberhard, 1985; Ginsberg and Huck, 1989).

Like females of California, arctic, and Columbian ground squirrels (Boellstorff et al., 1994; Lacey et al., 1997; Murie, 1995) but unlike female black-tailed prairie dogs (Hoogland, 1995), female Gunnison's prairie dogs usually copulate with more than one male (Fig. 5). As a result, multiple paternity, in which two or more males sire offspring of a single litter (Hanken and Sherman, 1981; Keane et al., 1994), is common (Travis et al., 1996; J. L. Hoogland et al., in litt.).

Perhaps aboveground behaviors that are diagnostic of underground copulations of Gunnison's prairie dogs also are diagnostic for other species of ground-dwelling squirrels that mate underground. Self-licking of genitals after a presumed underground copulation, for example, occurs among California (Boellstorff et al., 1994), Columbian (Murie, 1995), and thirteen-lined ground squirrels (*S. tridecemlineatus*—Schwagmeyer and Parker, 1987), and among black-tailed, white-tailed, and Utah prairie dogs (Hoogland, 1995; J. L. Hoogland, in litt.). Further, unique vocalizations by males just before or just after a presumed underground copulation occur among Richardson's (Davis, 1982), arctic (Lacey et al., 1997), and Idaho ground squirrels (*S. brunneus*—Sherman, 1989) and among black-tailed, white-tailed, and Utah prairie dogs (Hoogland, 1995; J. L. Hoogland, in litt.).

Diagnostic aboveground behaviors associated with underground copulations might be ubiquitous among species of ground-dwelling squirrels, but detailed information on these behaviors is available only from black-tailed and Gunnison's prairie dogs (Hoogland, 1995, this study). In qualitative terms, similarities between black-tailed and Gunnison's prairie dogs regarding diagnostic behaviors are striking. Specifically, five of the six diagnostic behaviors are common to both species. Black-tailed prairie dogs have one diagnostic behavior that Gunnison's prairie dogs lack: nestbuilding by the breeding male just before copulation (Hoogland, 1995). And Gunnison's prairie dogs show one diagnostic behavior that black-tailed prairie dogs lack: dustbathing shortly after copulation.

In quantitative terms as well, black-tailed and Gunnison's prairie dogs show some striking similarities regarding estrus and copulation. For example, percentages of estrous black-tailed and Gunnison's prairie dog females that elicited at least one mating call were 57% and 54%, respectively. Mean numbers of underground consortships for black-tailed and Gunnison's prairie dog estrous females were 5.90 and 5.78, respectively. And the percentages of estrous black-tailed and Gunnison's prairie dog females that stayed aboveground late into the evening were 68% and 70%, respectively.

Despite certain striking similarities regarding estrus and copulation, black-tailed and Gunnison's prairie dogs nonetheless differ in several qualitative and quantitative ways. For example, 8% of black-tailed prairie dog females remain underground for the entire day with a breeding male on the day of estrus; estrous Gunnison's prairie dog females, by contrast, never have all-day underground consortships. Further, 67% of black-tailed prairie dog females copulate with only one male, and 84% copulate exclusively with the resident breeding male(s) of the home territory (Hoogland, 1995). In contrast, only 35% of Gunnison's prairie dog females copulate with only one male

(Fig. 5), and only 35% copulate exclusively with the resident breeding male(s) of the home territory. More research is necessary for a better understanding of estrus, copulation, and male and female reproductive success for the different species of prairie dogs and other ground-dwelling squirrels.

#### ACKNOWLEDGMENTS

I thank my field assistants who have helped over the years, especially M. Bjorge, K. Brown, D. Fitzgerald, A. Hoogland, J. Hoogland, M. A. Hoogland, M. V. Hoogland, S. Hoogland, A. Hoskins, J. Jackson, S. Kain, C. May, L. Molles, M. Paulson, J. Tawil, D. Ton-That, and G. Turner. I also thank the staff at Petrified Forest National Park, especially C. Bowman, G. Cummins, E. Gastellum, M. Hellickson, K. Isensee, P. Pappas, V. Santucci, and W. Towery. For financial assistance, I thank the National Geographic Society, the National Science Foundation, Petrified Forest Museum Association, and the University of Maryland. This paper is contribution 3041-AL from the Appalachian Laboratory, the University of Maryland's Center for Environmental Studies. For help with the manuscript, I thank D. T. Blumstein, J. O. Murie, C. N. Slobodchikoff, D. Van Vuren, and P. M. Waser.

#### LITERATURE CITED

- BEACH, F. A. 1976. Sexual attractivity, proceptivity, and receptivity in female mammals. *Hormones and Behavior*, 7:105-138.
- BERGER, J. 1986. Wild horses of the Great Basin: social competition and population size. The University of Chicago Press, Chicago, Illinois, 326 pp.
- BOELLSTORFF, D. E., D. H. OWINGS, M. C. PENEDO, AND M. J. HERSEK. 1994. Reproductive behaviour and multiple paternity of California ground squirrels. *Animal Behaviour*, 47:1057-1064.
- CORDS, M. 1987. Forest guenons and patas monkeys: male-male competition in one-male groups. Pp. 98-111, in *Primate societies* (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, eds.). The University of Chicago Press, Chicago, Illinois, 578 pp.
- DAVIS, L. S. 1982. Copulatory behavior of Richardson's ground squirrels (*Spermophilus richardsonii*) in the wild. *Canadian Journal of Zoology*, 60:2953-2955.
- DEWSBURY, D. A., AND D. Q. ESTEP. 1975. Pregnancy in cactus mice: effects of prolonged copulation. *Science*, 187:552-553.
- EBENSPERGER, L. A., AND R. H. TAMARIN. 1997. Use of fluorescent powder to infer mating activity of male rodents. *Journal of Mammalogy*, 78:888-893.
- EBERHARD, W. G. 1985. Sexual selection and animal genitalia. Harvard University Press, Cambridge, Massachusetts, 244 pp.
- 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.
- GEIST, V. 1971. Mountain sheep: a study in behavior and evolution. The University of Chicago Press, Chicago, Illinois, 383 pp.
- GINSBERG, J. R., AND U. W. HUCK. 1989. Sperm competition in mammals. *Trends in Ecology and Evolution*, 4:74-79.
- HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites. *Science*, 218:384-387.
- HANKEN, J., AND P. W. SHERMAN. 1981. Multiple paternity in Belding's ground squirrel litters. *Science*, 212:351-353.
- HART, B. L. 1990. Behavioral adaptations to pathogens and parasites. *Neuroscience and Biobehavior Review*, 14:273-294.
- HART, B. L., E. KORINEK, E., AND P. BRENNAN. 1987. Postcopulatory genital grooming in male rats: prevention of sexually transmitted infections. *Physiological Behavior*, 41:321-325.
- HOOGLAND, J. L. 1982. Prairie dogs avoid extreme inbreeding. *Science*, 215:1639-1641.
- . 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, 557 pp.
- . 1996. Why do Gunnison's prairie dogs give antipredator calls? *Animal Behaviour*, 51:871-880.
- . 1997a. Duration of gestation and lactation for Gunnison's prairie dogs. *Journal of Mammalogy*, 78:173-180.
- . 1997b. *Cynomys ludovicianus*. *Mammalian Species*, 535:1-10.
- . 1998a. Philopatry, dispersal, and social organization of Gunnison's prairie dogs. *Journal of Mammalogy*.
- . 1998b. Why do Gunnison's prairie dog females copulate with more than one male? *Animal Behaviour*.
- HRDY, S. B. 1977. The langurs of Abu: female and male strategies of reproduction. Harvard University Press, Cambridge, Massachusetts, 361 pp.
- KAPITONOV, V. I. 1960. An essay on the biology of the black-capped marmot (*Marmota camtschatica* Pall.). *Zoologicheskii Zhurnal*, 39:448-457.
- KAUFMAN, G. A. 1989. Use of fluorescent pigments to study social interactions in a small nocturnal rodent, *Peromyscus maniculatus*. *Journal of Mammalogy*, 70:171-174.
- KEANE, B., P. M. WASER, S. R. CREEL, N. M. CREEL, L. F. ELLIOTT, AND D. J. MINCHELLA. 1994. Subor-

- dinate reproduction in dwarf mongooses. *Animal Behaviour*, 47:65–75.
- KOPROWSKI, J. L. 1992. Removal of copulatory plugs by female tree squirrels. *Journal of Mammalogy*, 73: 572–576.
- KRUUK, H. 1972. The spotted hyena: a study of predation and social behavior. The University of Chicago Press, Chicago, Illinois, 335 pp.
- LACEY, E. A., J. R. WIECZOREK, AND P. K. TUCKER. 1997. Male mating behaviour and patterns of sperm precedence in arctic ground squirrels. *Animal Behaviour*, 53:767–779.
- LE BOEUF, B. J., AND J. REITER. 1988. Lifetime reproductive success in northern elephant seals. Pp. 344–362, in *Reproductive success: studies of individual variation in contrasting breeding systems* (T. H. Clutton-Brock, ed.). The University of Chicago Press, Chicago, Illinois, 538 pp.
- MICHENER, G. R. 1984. Copulatory plugs in Richardson's ground squirrels. *Canadian Journal of Zoology*, 62:267–270.
- MICHENER, G. R., AND I. G. MCLEAN. 1996. Reproductive behaviour and operational sex ratio in Richardson's ground squirrels. *Animal Behaviour*, 52: 743–758.
- MURIE, J. O. 1995. Mating behavior of Columbian ground squirrels. I. Multiple mating by females and multiple paternity. *Canadian Journal of Zoology*, 73: 1819–1826.
- MURIE, J. O., AND I. G. MCLEAN. 1980. Copulatory plugs in ground squirrels. *Journal of Mammalogy*, 61:355–356.
- ORTEGA, J. C. 1990. Reproductive biology of the rock squirrel (*Spermophilus variegatus*) in southeastern Arizona. *Journal of Mammalogy*, 71:448–457.
- PIZZIMENTI, J. J., AND R. S. HOFFMANN. 1973. *Cynomys gunnisoni*. *Mammalian Species*, 25:1–4.
- RAUSCH, R. L., AND V. R. RAUSCH. 1971. The somatic chromosomes of some North American marmots (Sciuridae), with remarks on the relationships of *Marmota broweri* Hall and Gilmore. *Mammalia*, 35: 85–101.
- RAYOR, L. S. 1985. 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.
- READ, A. F. 1990. Parasites and the evolution of host sexual behaviour. Pp. 117–157, in *Parasitism and host behaviour* (C. J. Barnard and J. M. Behnke, eds.). Taylor and Francis, London, United Kingdom, 332 pp.
- SCHALLER, G. B. 1972. *The Serengeti lion*. The University of Chicago Press, Chicago, Illinois, 480 pp.
- SCHWAGMEYER, P. L., AND G. A. PARKER. 1987. Queuing for mates in thirteen-lined ground squirrels. *Animal Behaviour*, 35:1015–1025.
- SHERMAN, P. W. 1989. Mate guarding as paternity insurance in Idaho ground squirrels. *Nature*, 338:418–420.
- SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York, 312 pp.
- SLADE, N. A., AND D. F. BALPH. 1974. Population ecology of Uinta ground squirrels. *Ecology*, 55:989–1003.
- 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, 515 pp.
- SLOBODCHIKOFF, C. N., J. KIRIAZIS, C. FISCHER, AND E. CREEF. 1991. Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. *Animal Behaviour*, 42:713–719.
- STAMMBACH, E. 1987. Desert, forest, and montane baboons: multilevel societies. Pp. 112–120, in *Primate societies* (B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, eds.). The University of Chicago Press, Chicago, Illinois, 578 pp.
- TRAVIS, S. E., C. N. SLOBODCHIKOFF, AND P. KEIM. 1995. Ecological and demographic effects on intraspecific 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.
- . 1997. DNA fingerprinting reveals low genetic diversity in Gunnison's prairie dog (*Cynomys gunnisoni*). *Journal of Mammalogy*, 78:725–732.
- WARING, G. H. 1970. Sound communications of black-tailed, white-tailed, and Gunnison's prairie dogs. *The American Midland Naturalist*, 83:167–185.

Submitted 6 September 1997. Accepted 10 December 1997.

Associate Editor was Robert K. Rose.