

Conflicting research on the demography, ecology, and social behavior of Gunnison's prairie dogs (*Cynomys gunnisoni*)

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Gunnison's prairie dogs (*Cynomys gunnisoni*) are rare, diurnal, colonial, burrowing, ground-dwelling squirrels. Studies of marked individuals living under natural conditions in the 1970s, 1980s, and 1990s showed that males are heavier than females throughout the year; that adult females living in the same territory are consistently close kin; and that females usually mate with the sexually mature male(s) living in the home territory. Research from 2007 through 2010 challenges all 3 of these findings. Here we discuss how different methods might have led to the discrepancies.

Key words: coloniality, microsatellites, multiple paternity, philopatry, sexual dimorphism

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Gunnison's prairie dogs (*Cynomys gunnisoni*) are burrowing rodents of the squirrel family (Sciuridae; Longhurst 1944; Pizzimenti 1975; Rayor 1988), and they inhabit the "Four Corners" region of Arizona, Colorado, New Mexico, and Utah (Hollister 1916; Pizzimenti and Hoffmann 1973). To investigate their demography, ecology, and social behavior, we have studied marked Gunnison's prairie dogs living under natural conditions at 8 colonies in 3 states (Arizona, Colorado, and New Mexico; Cully 1997; Fitzgerald and Lechleitner 1974; Hoogland 1996, 1997, 1998a, 1998b, 1999, 2001, 2003b, 2007; Rayor 1985, 1988). Our research shows that individuals live in discrete colonies, and forage aboveground from dawn to dusk in warm weather. Many females first mate when they are 1 year old, but males usually defer 1st mating until they are 2 years old. Within colonies, adult (≥ 1 year old) Gunnison's prairie dogs live in territorial groups called clans, which typically contain 1 sexually mature male, several sexually mature females, and 1–2 sexually immature 1-year-old males. Individuals hibernate for 4–5 months of each year. The single mating season each year occurs in late March through mid-April, and almost-weaned juveniles first emerge from their nursery burrows in late May and June. Because of a precipitous decline in overall population size over the last 150 years (Martone 2010; Seglund et al. 2005), Gunnison's prairie dogs currently are under consideration for addition as a threatened

species to the Federal List of Endangered and Threatened Wildlife and Plants.

In our research with Gunnison's prairie dogs, we have studied 3 issues that have important implications for the mating and social systems of mammalian species: sexual dimorphism, kinship among adult females living in the same territory, and mating with males from the home and outside territories. Our results indicate that males are heavier than females throughout the year; that adult females living in the same territory are almost always maternal close kin; and that, with or without mating with males from other territories, females usually mate with the male(s) of the home territory. Verdolin (2007, 2008, 2009), Verdolin and Slobodchikoff (2009, 2010), and Slobodchikoff et al. (2009) have published 5 articles and 1 book that challenge our findings for these 3 issues. Below we investigate why their results differ from ours.

METHODS AND STUDY COLONIES

Fitzgerald and Lechleitner (1974) studied a colony of Gunnison's prairie dogs near Fairplay, Colorado, from 1965



through 1966. Rayor (1985, 1988; see also Rayor and Armitage 1991) studied 1 colony at the Curecanti National Recreation Area, Colorado, and another colony near Gunnison, Colorado, from 1979 through 1981. Cully (1997) studied 4 colonies in the Moreno Valley, New Mexico, from 1984 through 1988. Hoogland (1996, 1997, 1998a, 1998b, 1999, 2001, 2003b, 2007) and 3–4 students per year studied part (21–23 clans per year) of a large colony at Petrified Forest National Park, Arizona, from 1989 through 1995.

For permanent identification of Gunnison's prairie dogs, Fitzgerald and Lechleitner (1974) toe-clipped individuals. Rayor (1988), Cully (1997), and Hoogland (1999) inserted 1 numbered National Fingerling Eartag (National Band and Tag Company, Newport, Kentucky) into each ear for permanent identification. To identify individuals from a distance (≤ 150 m), we used Nyanzol fur dye (Greenville Colorants, Clifton, New Jersey) or Lady Clairol hair dye (Proctor and Gamble, Cincinnati, Ohio) to apply unique markers on the pelage. We categorized individuals as members of the same clan if they defended the same territory; individually or in small groups, they spent the night in burrows within the defended territory; and they interacted more amicably among themselves (i.e., more mouth-to-mouth contacts and more sniffings of the anal area, without subsequent fights and chases) than with members of other clans.

To quantify matings and other aspects of behavioral ecology, Hoogland and his students observed marked individuals from 4-m-high towers every day from dawn to dusk from early March through June of 1989 through 1995; over the 7 years, they logged $>15,000$ person-hours of research (Hoogland 1999). They scored a male as sexually mature if he had a pigmented (black, versus gray or pink) scrotum with descended testes. They scored an individual as a "survivor" if it was still living within the study area, or within 1 of the 15 territories adjacent to the study area where they also livetrapped each year in search of dispersers, until emergence from hibernation in March or April of the following year; long-distance dispersers that moved outside the study area and beyond the adjacent territories would not have been scored as survivors.

From 2003 through 2005, Verdolin (2007, 2008, 2009) and Verdolin and Slobodchikoff (2009, 2010) studied marked Gunnison's prairie dogs at 2 colonies. Both colonies were located within the city limits of Flagstaff, Arizona. Consequently, disturbance from humans at these urban colonies was probably more pronounced than at other, more rural colonies. Further, extensive flooding at 1 colony led to 100% mortality of the Gunnison's prairie dogs in 2005 (Verdolin 2007; Verdolin et al. 2008), perhaps because of poor drainage or poor conditions for excavation of burrows. All body masses for their estimates of sexual dimorphism came from July 2003 (Verdolin 2007), and all information from microsatellites for estimates of both paternity of juveniles and kinship among adult females living in the same territory came from samples collected in 2004 (Verdolin and Slobodchikoff 2009, 2010).

SEXUAL DIMORPHISM

Sexual dimorphism occurs when males and females of the same species consistently differ in 1 or more features of morphology. Sexual dimorphism in body mass, with males being heavier, is common for a diverse array of polygynous mammals (Alexander et al. 1979; Clutton-Brock et al. 1977; Jarman 1974; Weckerly 1998), including the 4 species of prairie dogs other than Gunnison's prairie dog (Hoogland 2003b) and almost every other species of ground-dwelling squirrel (e.g., Armitage 1981; Barash 1989; Dobson 1992; Michener 1984; Sherman and Morton 1984). Biologists sometimes use data on sexual dimorphism to estimate the degree of polygyny and the relative intensity of sexual selection for males versus females (Alexander et al. 1979; Clutton-Brock 1989; Davies et al. 2010; Emlen and Oring 1977; Trivers 1972).

Every biologist who has studied Gunnison's prairie dogs has reported that males are heavier than females (Cully 1997; Fitzgerald and Lechleitner 1974; Hollister 1916; Longhurst 1944; Rayor 1985, 1988; Scheffer 1947). From 4,194 body masses determined during 2-week intervals from early March through late June of 1989 through 1995, Hoogland (2003b) confirmed that adult males are significantly heavier than adult females in all intervals, even during late April when most females are in late pregnancy. Sexual dimorphism is especially striking during 2 periods when behavioral ecologists are probably most likely to study Gunnison's prairie dogs: in early and late March just before and during the peak of the mating season, and in late May and early June when juveniles first emerge from their nursery burrows (Fig. 1).

From body masses of wild Gunnison's prairie dogs captured in late July 2003, Verdolin (2007:1375–1376) also reported male-biased sexual dimorphism for Gunnison's prairie dogs. Specifically, adult males had a significantly higher body mass than females that had weaned a litter in May or June.

Verdolin (2007) also investigated the possibility of sexual dimorphism among Gunnison's prairie dogs by examining the maximal length and the maximal width of skulls at the zygomatic arch. Verdolin (2007) found no significant intersexual differences for these cranial measurements, but this conclusion is equivocal for 3 reasons. First, the sample size of Verdolin (2007) was small ($n = 21$ males and $n = 22$ females, all museum specimens of unknown ages). However, because cranial morphology for Gunnison's prairie dogs varies with age and other factors (Pizzimenti 1975), large sample sizes usually will be necessary to document sexual dimorphism in any feature of cranial morphology. Indeed, we do not understand why Verdolin (2007) did not use information from Pizzimenti's (1975, tables 1 and 3) larger sample size of 107 males and 115 females to investigate possible sexual dimorphism in cranial morphology for Gunnison's prairie dogs. Second, skulls for Verdolin's (2007) measurements did not originate from the area where Verdolin studied Gunnison's prairie dogs, but rather from 3 different states. However, Pizzimenti (1975: 3, and table 3) emphasized the importance of comparing Gunnison's prairie dog skulls from the same locality for an

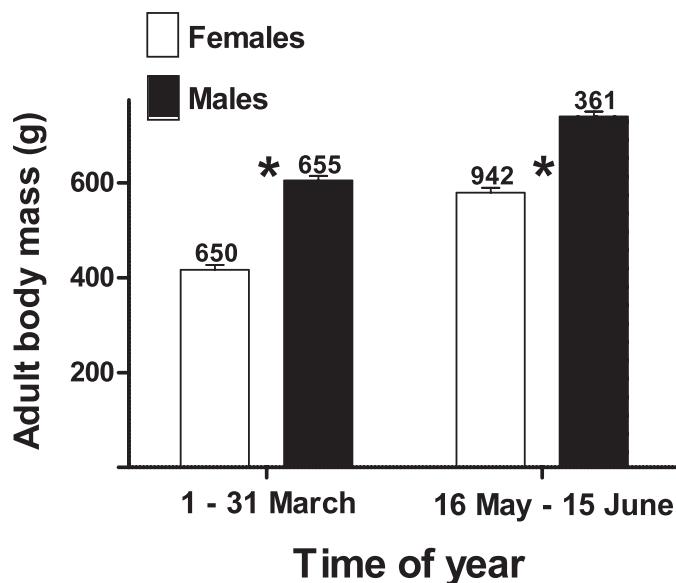


FIG. 1.—Mean (\pm SE) body mass for adult (≥ 1 -year-old) male and female Gunnison's prairie dogs just before and during the mating season (March) and when juveniles first emerge from their nursery burrows (May and June). The number above each bar indicates the number of individuals weighed; * $P < 0.001$, two-tailed Mann-Whitney U -test; $U = 356,849$ for 1–31 March, $U = 317,887$ for 16 May–15 June. For more details, see Hoogland (2003b). This figure includes 1 data point per individual for each time interval, but data from the same adult in different years were considered independent. All data come from Petrified Forest National Park, Arizona, 1989–1995.

investigation of possible sexual dimorphism because of substantial geographic variation. Third, Verdolin (2007:1370) did not explain the rationale for the choice of her 2 measurements of skull size to investigate possible sexual dimorphism. Other measurements might have revealed intersexual differences. Of 15 cranial measurements reported by Pizzimenti (1975, table 3), for example, 73% (11/15) showed significant sexual dimorphism in Montezuma County, Colorado. In Coconino County, Arizona, where Verdolin (2007, 2008, 2009) and Verdolin and Slobodchikoff (2009, 2010) studied Gunnison's prairie dogs, 20% (3/15) of Pizzimenti's (1975) cranial measurements were sexually dimorphic.

Because the evidence for sexual dimorphism from previous publications is abundant, and because Verdolin (2007) documented significant sexual dimorphism in body mass in her own research, we do not understand why Verdolin argued in 2 publications (2007, 2008) that Gunnison's prairie dogs are not sexually dimorphic, or why Verdolin and Slobodchikoff made the same argument in 2 other publications (2009, 2010). We also do not understand the basis for the hypotheses of Verdolin and Slobodchikoff (2009:60–61) that “A lack of sexual dimorphism... suggests that resource abundance, not mating strategies, drives social patterns observed in this species...” (and, in the next sentence) “Therefore, it remains unclear what role, if any, kinship plays in the formation and stability of Gunnison's prairie dog social groups.” On the

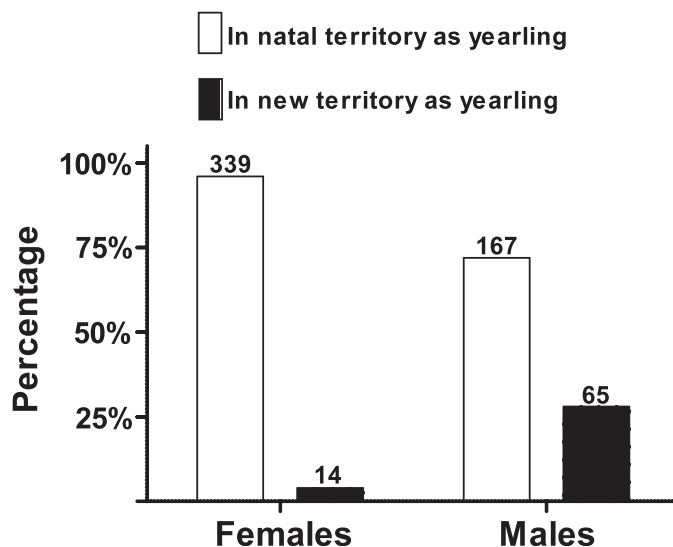


FIG. 2.—Percentages of male and female Gunnison's prairie dogs that were still living in the natal territory in the first spring after birth (i.e., when they were yearlings). The number above each bar indicates the number of juveniles that survived to be yearlings; for more details, see Hoogland (1999). All data come from Petrified Forest National Park, Arizona, 1989–1995.

contrary, we contend that sexual dimorphism is a conspicuous trait of Gunnison's prairie dogs, and that both kinship among adult females living in the same territory and mating strategies are key features of the behavioral ecology and social organization of this species.

KINSHIP AMONG ADULT FEMALES LIVING IN THE SAME TERRITORY

Natal philopatry (i.e., remaining in the natal territory) is more common for females than for males of most mammalian species (Dobson 1982; Greenwood 1980; Johnson 1986; Pusey 1987), including at least 3 species of prairie dogs other than Gunnison's prairie dogs (Hoogland 1995, 2003a, 2007; King 1955) and most other species of ground-dwelling squirrels (Armitage 1987; Barash 1989; Hare and Murie 2007; Holekamp 1984; Maher 2009; Michener 1983; Sherman 1981). When female natal philopatry consistently occurs, then adult females living in the same territory will usually be close kin (Hare and Murie 2007; Hoogland 1995; Michener 1983; Sherman 1981). Consequently, opportunities for long-term cooperation among females and their mothers, daughters, grandmothers, granddaughters, sisters, aunts, nieces, and female cousins are frequent for many mammalian species.

To determine if female Gunnison's prairie dogs tend to remain in the natal territory after birth, Hoogland (1999) and his students ear-tagged all the juvenile females in his study area ($n = 715$) as soon as they first emerged from their nursery burrows in 1989 through 1994; of these, 49% (353/715) survived for ≥ 1 year. Of the latter surviving females, 96% (339/353) remained in the natal territory as yearlings, and 93% (329/353) remained in the natal territory for their entire

lifetimes. Females thus showed striking natal philopatry (Fig. 2). Consequently, adult females living in the same territory were almost always maternal close kin—i.e., a combination of a female and ≥ 1 of the following: mother, daughter, grandmother, granddaughter, sister, aunt, niece, or female cousin. Cully (1997, in litt.), Fitzgerald and Lechleitner (1974, in litt.), and Rayer (1985, 1988) also observed that female Gunnison's prairie dogs usually remain in the natal territory as yearlings.

Using unpublished data from Hoogland's (1999) long-term research, we investigated kinship among female Gunnison's prairie dogs in a new way. Specifically, we documented how often a mother and her daughter lived together in the daughter's natal territory when both females were still alive in the year after the daughter's weaning (i.e., when the daughter was a yearling adult), and how often a yearling female lived together with a littermate sister when ≥ 1 littermate sister was still alive in the year after birth. The results are unequivocal: 96% (103/107) of yearling females lived in the same territory with the mother when both were still alive, and 97% (210/216) of yearling females lived in the same territory with ≥ 1 littermate sister when both were still alive. Adult female kin other than mother and littermate sister that commonly lived in the same territory with a female included grandmother, granddaughter, aunt, niece, and first and second female cousins.

Examination of specific clans further illustrates the ubiquity of kinship among adult females living in the same territory. For example, in 1993 Hoogland (in litt.) documented the compositions of 22 clans: 82% (18/22) included ≥ 1 pair of mother-plus-yearling daughter or ≥ 1 pair of littermate yearling sisters; the other 18% (4/22) of clans contained only 1 adult female.

Like females, male Gunnison's prairie dogs also tend to remain in the natal territory with close kin during the 1st year after weaning (Fig. 2). Of all the juvenile males ($n = 692$) ear-tagged at the colony studied by Hoogland (1999) from 1989 through 1994, 34% (232/692) survived for ≥ 1 year. Of the latter survivors, 72% (167/232) were still living in the natal territory as yearlings. Unlike the lifelong natal philopatry for most females, however, natal philopatry of males was short-lived: only 5% (3/66) of males were still in the natal territory when they were 2 years old, and 0% (0/22) were still there when they were 3 years old. Rayer (1985, 1988) observed the same trend of natal philopatry of yearling males.

Despite the strong tendency documented from livetrapping for female Gunnison's prairie dogs to live with close kin in the same home (natal) territory (Fig. 2 and above; see also Hoogland 1999; Rayer 1985, 1988), Verdolin and Slobodchikoff (2009:59) concluded from microsatellites that "females within territorial groups were not more closely related to each other than expected at random."

How did different researchers reach such disparate conclusions for Gunnison's prairie dogs regarding kinship among adult females living in the same territory? One possible explanation concerns intraspecific variation, which is common

for many aspects of behavioral ecology (Harris and Chapman 2007; Lott 1991; Rodrigues et al. 2010; Rodriguez et al. 2010; Woolley et al. 2009). Specifically, certain factors might have favored more dispersal by female Gunnison's prairie dogs at study colonies of Verdolin and Slobodchikoff (2009) than at our study colonies. Therefore, females living in the same territories in colonies of Verdolin and Slobodchikoff (2009) might have been less likely to be close kin. For example, perhaps the proximity of both of their study colonies to humans (see above) or the poor drainage at one of these study colonies (Verdolin 2007, Verdolin et al. 2008) induced females at the study colonies of Verdolin and Slobodchikoff (2009) to disperse in ways that differ markedly from patterns in other, more natural, populations, so that typical patterns of kinship among adult females living in the same territory were disrupted.

A more likely factor to explain the between-study differences in kinship among adult Gunnison's prairie dog females living in the same territory concerns methodology. Our information for maternity and littermate sibships results from livetrapping of entire litters as soon as they first appeared aboveground, and then tracking individuals that survived for ≥ 1 year ($n = 353$ adult female survivors) over time. Other behavioral ecologists have used this same methodology over the last 40 years to document female natal philopatry and kinship among adult females within social groups for numerous species of ground-dwelling squirrels (Armitage 1987; Barash 1989; Hare and Murie 2007; Holekamp 1984; Maher 2009; Michener 1983; Sherman 1981). By contrast, Verdolin and Slobodchikoff (2009:61–64; 2010:1149, 1152) evidently did not have any independent information on maternity and littermate sibships, but instead they relied exclusively on 6 polymorphic microsatellites to estimate "mean relatedness" among 83 adult females (from 20 clans; Verdolin and Slobodchikoff 2009: table 2) from the same and different territories. However, information from microsatellites alone can sometimes lead to weak, or erroneous, conclusions about kinship between individuals, especially when the number of polymorphic microsatellites is small ($n < 10$) (Blouin 2003; Bonin et al. 2004; Coltman 2005; Csillery et al. 2006; Fernandez and Toro 2006). Verdolin and Slobodchikoff (2009: 66) are keenly aware of this problem, because they wrote, "Recently Van Horn et al. (2008) addressed the accuracy of kinship estimates when not incorporating pedigree information and suggested that relatedness estimates may be misleading." We concur with the suggestion of Van Horn et al. (2008; see also Broquet and Petit 2004; Gagneux et al. 1997; Johnson and Haydon 2007; Taberlet et al. 1996, 1999), and we propose that problems with microsatellites, without independent estimates of maternity or sibships, are primarily responsible for the differences between results of Verdolin and Slobodchikoff (2009) and our results regarding kinship among adult female Gunnison's prairie dogs living in the same territory.

Before Verdolin and Slobodchikoff (2009), Travis et al. (1996) also studied Gunnison's prairie dogs in the vicinity of

TABLE 1.—The 6 diagnostic aboveground behaviors associated with underground matings of 285 Gunnison's prairie dogs. For more details, see Hoogland 1998a. Other behavioral ecologists have used these same diagnostic behaviors to document underground matings for 3 species of ground squirrels (Lacey et al. 1997; Manno et al. 2008; Raveh et al. 2010, 2011; Sherman 1989) and 3 other species of prairie dogs (Hoogland 1995, 2007, in litt.).

Diagnostic behavior	Description
Series of underground consortships	Estrous females cosubmerged with ≥ 1 sexually mature male repeatedly (mean \pm SD = 5.8 ± 5.0 cosubmersences, range = 0–34), for a mean \pm SD of 28.8 ± 30.2 min (range = 0.3–338 min) per cosubmergence. When a female was not sexually receptive, cosubmergence of a male and female together almost never occurred.
Frequent sniffing and chasing of estrous female	Mean \pm SD number of behavioral interactions with male(s) on the day of estrus was 46.6 ± 37.2 (range = 0–150), but the mean \pm SD number was only 5.7 ± 7.0 (range = 0–26) on the day after estrus.
Mating call	Shortly before or after ≥ 1 of her underground consortships, 54% of estrous females elicited a unique mating call from ≥ 1 sexually mature male. The mean \pm SD length of each mating call was 3.8 ± 6.0 min (range = 1 s–71 min). Mating calls unrelated to estrus almost never occurred.
Self-licking of genitals by both sexes	Within 5 min after emerging from an underground consortship, 20% of estrous females licked their genitals aboveground, and 30% of females elicited aboveground self-licking of genitals by ≥ 1 male that mated with them. Self-licking of genitals unrelated to underground consortships almost never occurred.
Dustbathing	Within 5 min after emerging from an underground consortship, 27% of estrous females rolled themselves in the dirt, and 9% of estrous females elicited dustbathing by ≥ 1 male that mated with them. Dustbathing unrelated to underground consortships almost never occurred.
Late final submergence by the estrous female at the end of the day	On the day of estrus, 70% of females remained aboveground much later than usual, typically 60–90 min after nonestrous females living in the territory had disappeared for the night.

Flagstaff, Arizona, and also attempted to use information solely from microsatellites to estimate kinships among adult females living in the same territory. The 2 research teams nonetheless reached diametrically opposed conclusions: Verdolin and Slobodchikoff (2009) concluded that adult females within territorial groups are not more closely related to each other than expected at random, but Travis et al. (1996) concluded that they are. These contradictory results involving microsatellites from colonies in the same geographic area underscore the concern of Van Horn et al. (2008) about the reliability of kinships determined from microsatellites alone.

As detailed in the next section, the sexually mature male of a Gunnison's prairie dog territory sometimes mates with females from adjacent territories. As a result, adult females of adjacent territories can be paternal half-siblings. Furthermore, a young male sometimes disperses away from his littermate sisters in his natal territory to an adjacent territory and mates there (Hoogland 1999), so that the dispersing male's daughters in his new territory can be the nieces of the dispersing male's littermate sisters in an adjacent (his natal) territory. Consequently, adult females of adjacent territories are sometimes close genetic relatives. These scenarios might have contributed to the conclusion of Verdolin and Slobodchikoff (2009:59) that adult females living in the same territory are not more genetically related to each other "than expected at random." These kinships among females of adjacent territories are not ubiquitous, however; when they occur for females of 1 territory, they typically involve females of only 1 or 2 of several adjacent territories. By contrast, close kinships among adult females living in the same territory are consistent, and, indeed, almost inevitable (Fig. 2).

In closing this section, we emphasize that we fully agree with other behavioral ecologists that evidence from microsat-

ellites can be a powerful tool for estimating kinship between individuals when combined with independent information about maternity, littermate sibships, and matings (Blouin 2003; Raveh et al. 2010, 2011; Van Horn et al. 2008). Without that combination, however, we also agree that microsatellites alone can yield misleading or incorrect conclusions regarding kinship between 2 individuals, especially when the number of polymorphic microsatellites is small (Csillery et al. 2006; Gagneux et al. 1997; Van Horn et al. 2008).

MATING WITH MALES FROM THE HOME AND OUTSIDE TERRITORIES

When groups of females defend territories, natural selection sometimes favors sexually mature males who can monopolize such groups. The result is female defense polygyny (Clutton-Brock 1989; Creel and Macdonald 1995; Emlen and Oring 1977; Heckel and Von Helversen 2002), which is evident in all 4 species of prairie dogs other than Gunnison's prairie dogs (Hoogland 1995, 2003a, 2007; King 1955; Trevino-Villarreal 1990) and several other species of ground-dwelling squirrels (Armitage 1981; Barash 1989; Michener 1983).

At Hoogland's (1998a, 1998b) study colony of Gunnison's prairie dogs, the mating season (i.e., the interval between 1st mating and last mating) spanned about 2 weeks each year from late March through mid-April. Each female was sexually receptive for 4–6 h on only 1 day of the mating season (Hoogland 1998a, 1998b). Most matings occurred underground, but 6 diagnostic aboveground behaviors associated with underground consortships allowed observers to specify which male(s) mated with each of 285 estrous females (Table 1). It is possible that a sexually mature male entered the same

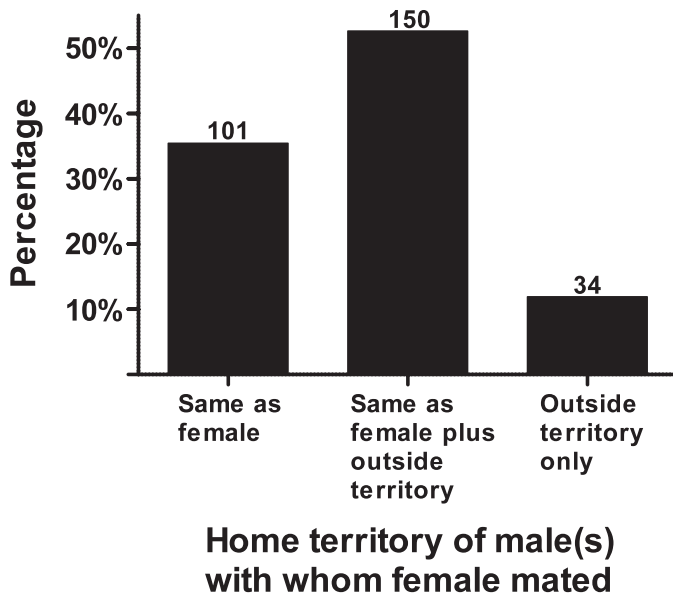


FIG. 3.—Percentages of 285 female Gunnison's prairie dogs that mated with only the male(s) of the home territory, the male(s) of the home territory and ≥ 1 male from outside territories, and only the male(s) from outside territories. The number above the bar indicates the number of females for which we recorded all sexual partners; for more details, see Hoogland (1998a, 1998b). Each female was sexually receptive only 1 time per year, but data from the same female in different years were considered independent. All data come from Petrified Forest National Park, Arizona, 1989–1995.

burrow with an estrous female for a mean of 29 min, and sometimes for as long as 338 min (Table 1), and did not mate with her, even though the pair showed the same aboveground courtship behaviors associated with aboveground matings (see below). Hoogland (1998a, 1998b) regarded this possibility as highly unlikely, however, and therefore inferred a mating when both of the following occurred: a sexually mature male entered a burrow with an estrous female and remained underground with her for ≥ 5 min, and the pair showed ≥ 2 of the 6 diagnostic aboveground courtship behaviors described in Table 1. Three independent lines of evidence indicate that these inferences of estrus and mating were accurate (Hoogland 1998a). First, the date of estrus varied directly and strongly with both the date of parturition and the date of weaning ($r \geq 0.814$ and $P < 0.001$ for both for all years, Spearman rank correlation test). Second, on the day before the series of underground consortships, 90% (108/120) of females had a swollen vulva that appeared to be sealed shut by a thin layer of skin. By contrast, on the day after the series of underground consortships, 100% (109/109) of females had an open vulva ($\chi^2_1 = 186$, $P < 0.001$, 2×2 chi-square test). Third, if underground consortships involved mating and insemination, then the 6 diagnostic aboveground behaviors associated with these consortships (Table 1) also should have been evident in aboveground matings. Data from all 24 females that mated aboveground support this hypothesis. Specifically, 100% of females that mated aboveground showed or elicited at least 2 of

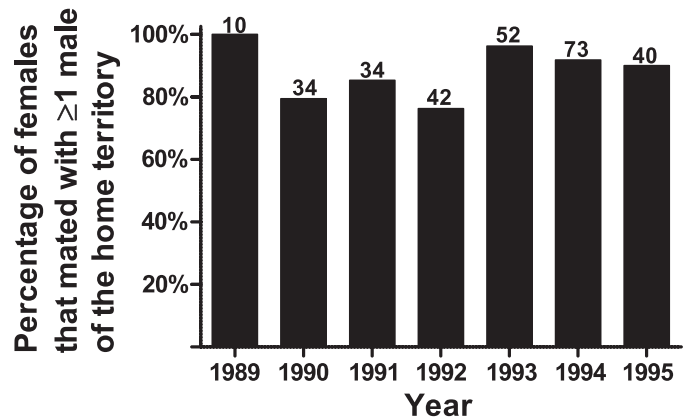


FIG. 4.—Annual variation in the percentages of 285 female Gunnison's prairie dogs that mated with the male(s) of the home territory. The mean \pm SD percentage was $88.4\% \pm 8.7\%$. The number above the bar indicates the number of females for which we recorded all sexual partners; for more details, see Hoogland (1998a, 1998b). All data come from Petrified Forest National Park, Arizona, 1989–1995.

the 6 diagnostic behaviors associated with underground consortships, and 58% (14/24) of these females showed or elicited at least 5 of the 6 diagnostic behaviors; the overall mean \pm SD of diagnostic behaviors per estrous female that mated aboveground was 4.3 ± 1.2 .

During the 4–6 h of sexual receptivity, 35% of marked females (99/285) mated with 1 male only, 35% (100/285) mated with 2 males, and the other 30% (86/285) mated with 3, 4, or 5 males (Hoogland 1998b). Some females mated exclusively with the sexually mature male(s) of the home territory, others mated with the sexually mature male(s) of the home territory and also with ≥ 1 male from a different territory, and others mated exclusively with ≥ 1 male from a different territory (Fig. 3). Matings with outside males occurred when an estrous female visited a male in an adjacent territory, or when a male from an adjacent territory temporarily invaded the female's home territory on her day of estrus.

With or without mating with additional males from outside territories, 88% (251/285) of female Gunnison's prairie dogs mated with the sexually mature male(s) of the home territory (Fig. 3). In 4 of 7 years of research, this percentage was $\geq 90\%$, and it was never lower than 76% (Fig. 4). Thirty-five percent of females (101/285) mated exclusively with the male(s) of the home territory (Fig. 3). The implication is that the sexually mature male(s) of a territory sires many of the offspring born in his home territory. By contrast, Verdolin and Slobodchikoff (2010:1145) concluded from microsatellites that "Resident males sired the majority of offspring from their respective territories only 10.5% of the time" (and, page 1157) "...males do not gain a significant advantage securing paternity of offspring produced by females living in their territories."

How did different researchers reach such dissimilar results regarding male reproductive success for Gunnison's prairie dogs? As explained below, at least 4 factors might explain the

differences: methodology, sample size and length of study, ability to specify estrus and matings, and intraspecific variation.

Methodology is the most obvious factor that might explain the different results regarding paternity. Hoogland's (1998a, 1998b; Figs. 3 and 4) conclusions result exclusively from behavioral observations of matings during the 4–6 h when each female was sexually receptive. By contrast, the conclusions of Verdolin and Slobodchikoff (2010) result entirely from assignments of paternity from microsatellites, without any independent information about maternities, sibships, and matings. Both methodologies have specific weaknesses. As noted above for Hoogland's (1998a, 1998b) research, for example, some pairs might not have mated underground despite showing the diagnostic aboveground courtship behaviors. Further, even though quantification of matings is eminently feasible, Hoogland (1998a, 1998b) and his students probably did not detect every mating of the 285 estrous females under observation. Regarding the research of Verdolin and Slobodchikoff (2010), assignments of paternity from microsatellites alone, without independent information about maternity, sibships, and matings, can sometimes lead to erroneous conclusions (Chakraborty et al. 1988; Neff and Pitcher 2002; Neff et al. 2000; Van Horn et al. 2008; see also references in previous section about kinship). Hoogland and his collaborators experienced these same problems in their attempts to use microsatellites to assign paternities for both Utah (*C. parvidens*) and Gunnison's prairie dogs (Haynie et al. 2003), even though they had good information on putative matings from behavioral observations and good information on mother–offspring and sibling–sibling kinships from livetrapping.

Sample size and length of study are additional factors that might help to explain why results from Verdolin and Slobodchikoff (2010) regarding paternity are so different from results from Hoogland (1998a, 1998b). Hoogland and his students recorded whether a female did or did not mate with a sexually mature male(s) of the home territory for 285 females observed over 7 years (Fig. 3). By contrast, the sample size of Verdolin and Slobodchikoff (2010:1154) was 35 females from a single year, for which they tried to infer matings solely from microsatellites. However, because of the significant annual variation in probability of mating with male(s) of the home territory (Fig. 4), the information of Verdolin and Slobodchikoff (2010) from a single year might be misleading. Many long-term studies have shown that a single year's information can differ dramatically from overall trends observed over many years (Clutton-Brock et al. 1982; Hoogland 1995; Moss et al. 2011; Raveh et al. 2010; Schwartz et al. 2006; Sherman and Morton 1984).

Ability to specify estrus and matings is a 3rd factor that might help to explain the different conclusions regarding paternity for Verdolin and Slobodchikoff (2010) and Hoogland (1998a, 1998b; Figs. 3 and 4). For a male Gunnison's prairie dog to be reproductively successful, the critical time for him to live in a territory is the mating season. Hoogland (1998a, 1998b) and his students were able to determine the single day when each female came into estrus, which male(s) lived in her

territory on that single day, and the male(s) with whom that female mated during her 4–6 h of sexual receptivity. Consequently, they were able to document 9 cases in which a male resided in a territory during the mating season and mated with 1–2 females in that same territory, but then died or dispersed from that territory after the mating season but before the weaning of offspring approximately 2 months after mating (Hoogland, in litt.). Furthermore, Hoogland and his students documented 2 cases in which a 2-year-old female mated with a male of her home (natal) territory, and then dispersed to a different territory before she weaned her litter (Hoogland, in litt.). For each of these 11 cases, Hoogland (1998a, 1998b; Fig. 3) recorded a mating with the resident male by the female. By contrast, Verdolin and Slobodchikoff (2010) did not identify the date of estrus for females, and they did not document any matings. Consequently, they were unable to specify which male(s) lived in a female's home territory on the single day when she came into estrus and mated. If the study colonies of Verdolin and Slobodchikoff (2010) had cases in which a sexually mature male of the female's home territory disappeared after the mating season, or cases in which a female dispersed after she mated but before she weaned her litter, then their information from microsatellites probably would have indicated that all the offspring of the females in these cases were sired by a male from outside the home territory; in reality, however, some or all the offspring in each case might have been sired by a male that resided in the same home territory with the female during all or part of the mating season.

A 4th factor that might explain the different results regarding paternity is intraspecific variation. Specifically, certain ecological factors might have favored more siring of offspring by males from outside the home territory at the study colonies of Verdolin and Slobodchikoff (2010) than at the study colony of Hoogland (1998a, 1998b). For example, perhaps the human disturbance at the urban study colonies of Verdolin and Slobodchikoff (2009, 2010) disrupted typical patterns of mating.

Because 88% (251/285) of female Gunnison's prairie dogs at the study colony of Hoogland (1998a, 1998b) mated with the male(s) of the home territory, and 35% (101/285) of females mated exclusively with the male(s) of the home territory (Fig. 3), the implication is that the sexually mature male(s) of a territory sires many of the offspring born in that territory. Despite these trends, perhaps males from outside territories somehow sire more offspring than males of the home territory, as suggested by Verdolin and Slobodchikoff (2010). Perhaps, for example, 1st-mating (or last-mating) males are more likely to sire offspring (Foltz and Schwagmeyer 1989; Hanken and Sherman 1981; Hoogland 1995; Lacey et al. 1997; Raveh et al. 2010), and females consistently mate first (or last) with males from outside territories. Alternatively, perhaps cryptic female choice (Andersson and Simmons 2006; Eberhard 1996; Tregenza and Wedell 2000) allows females to bias fertilizations in favor of outside males. Despite the opposite implication from our behavioral observations of estrus and matings (Figs. 3 and 4), we cannot exclude the possibility that

1 of these latter mechanisms might allow male Gunnison's prairie dogs from outside territories to frequently sire more offspring than male(s) of the home territory. With the small sample size ($n = 35$ litters from a single year) and the problems with trying to assign paternity solely from microsatellites (Chakraborty et al. 1988; Neff and Pitcher 2002; Neff et al. 2000; Van Horn et al. 2008), however, the suggestion of Verdolin and Slobodchikoff (2010) that outside males sire more offspring than resident males is not compelling.

Hoogland's (1998a, 1998b) research on the mating system of Gunnison's prairie dogs depended almost entirely on behavioral observations of estrus and matings over 7 years, with only minimal, equivocal information from microsatellites for 1 year (Haynie et al. 2003). The research of Verdolin and Slobodchikoff (2010) on the mating system, by contrast, depended entirely on assignments of paternity from microsatellites for 1 year, with no information on estrus or actual matings. A careful long-term study that incorporates information from both observations of matings and assignments of paternity from microsatellites or some other biochemical technique (e.g., Hanken and Sherman 1981; Hoogland 1995; Lacey et al. 1997; Raveh et al. 2010, 2011) would be a valuable next step toward a better understanding of the mating system of Gunnison's prairie dogs.

In every carefully studied species with distinct groups of females living with single sexually mature males, females sometimes mate with males from outside the group (e.g., Gibbs et al. 1990; Hoogland 1995; McCracken and Bradbury 1977). We are fully aware that mating with outside males also occurs for Gunnison's prairie dogs (Fig. 3), but we propose that "female defense polygyny" (Emlen and Oring 1977) is nonetheless a useful term to approximately describe the mating system for this species.

CONCLUSIONS

Our thinking about behavioral ecology is always changing (Alcock 2009; Danchin et al. 2008; Davies et al. 2010; Westneat and Fox 2010). To make a convincing case that the current understanding of an issue for a particular species is inaccurate, a researcher should provide contrary data that are both copious and decisive. In their publications about Gunnison's prairie dogs regarding 2 issues (i.e., sexual dimorphism and kinship among adult females living in the same territory) that have significant, far-reaching implications for the mating and social systems of mammalian species, Verdolin (2007, 2008, 2009), Verdolin and Slobodchikoff (2009, 2010), and Slobodchikoff et al. (2009) have not provided the definitive data necessary to refute earlier findings. Their conclusions for these 2 issues are incompatible not only with our previous results from 8 colonies of Gunnison's prairie dogs in 3 states (Cully 1997; Fitzgerald and Lechleitner 1974; Hoogland 1998a, 1998b, 1999, 2001, 2003b, 2007; Rayor 1985, 1988), but also with results for the other 4 species of prairie dogs (Clark 1977; Hoogland 1995, 2001; 2003b, 2007; King 1955; Trevino-Villarreal 1990) and for most other species

of ground-dwelling squirrels (e.g., Armitage 1981, 1987; Barash 1989; Dobson 1992; Hare and Murie 2007; Holekamp 1984; Michener 1983, 1984; Sherman and Morton 1984). For now, we contend that the following 2 conclusions remain secure for Gunnison's prairie dogs living under natural conditions. First, adult males are consistently heavier than adult females throughout the year. Second, because they usually remain in the natal territory for life, adult females living in the same territory are almost always maternal close kin.

Hoogland's (1998a, 1998b; Fig. 3) research derived from behavioral observations of marked individuals over 7 years indicates that 88% of 285 females mated with the sexually mature male(s) of the home territory, with or without matings with additional males from outside territories. By contrast, Verdolin and Slobodchikoff's (2010) research with microsatellites from 35 litters from 1 year indicates that most offspring were sired by males from outside the home territory. Intraspecific variation might explain these different results. More likely, in our opinion, is that the discrepancies result from differences in methodology, sample size, length of study, and the ability to specify estrus and matings.

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