**Why do female Gunnison’s prairie dogs copulate with more than one male?**

JOHN L. HOOGLAND
Appalachian Laboratory, University of Maryland

(Received 9 September 1996; initial acceptance 19 November 1996; final acceptance 22 February 1997; M.S. number: A7699)

**Abstract.** A female can usually obtain enough sperm to fertilize all her eggs from a single insemination, and copulation involves certain costs such as increased exposure to diseases and parasites. Why, then, do females of so many species routinely copulate with more than one male? A 7-year study of marked individuals provides an answer for 239 female Gunnison’s prairie dogs (Sciuridae: Cynomys gunnisoni) living under natural conditions. The probability of pregnancy and parturition was 92% for females that copulated with only one or two males, but was 100% for females that copulated with at least three males. Further, litter size at weaning varied directly with the mother’s number of sexual partners.

Male reproductive success in most species increases directly with the number of inseminations (Darwin 1871; Trivers 1972; Emlen & Oring 1977). Natural selection for multiple mating by males is thus widespread and easily explicable. Sperm numbers from a single insemination are usually sufficient to fertilize an entire collection of eggs (Bateman 1948; Birkhead 1988; Petrie et al. 1992), however, so the observation that females sometimes mate with several males is harder to understand. Mating with more than one male in the same breeding season is not the less common for myriad species: insects (Cole 1983; Thornhill & Alcock 1983), fish (Domrey 1984; van den Berghe 1988), reptiles (Madsen et al. 1992; Olsson et al. 1994), birds (Gladstone 1979; Westneat et al. 1990; Birkhead & Moller 1992) and mammals (Schaller 1972; Hanken & Sherman 1981; Foltz & Schwagmeyer 1989), including humans (Hrdy 1981; Smith 1984) and other primates (Hausfater 1975; Goodall 1986; Kano 1992).

Females incur both costs and benefits by mating with more than one male (e.g. Daly 1978; Schwagmeyer 1984; Eberhard 1996). Possible benefits to the female from multiple mating include increased sustenance resulting from courtship feeding, increased paternal care if males help to rear the offspring of all females with whom they copulate, assurance of conception, reduced harassment from courting males, fresh sperm for fertilization, promotion of sperm competition, opportunity to have better sire for offspring, and increased survivorship among offspring resulting from increased genetic diversity within litters via multiple paternity. Evaluating the costs and benefits of multiple matings is difficult because it requires information on both the copulatory and rearing success for the same females. Here I document two advantages of copulating with more than one male for female Gunnison’s prairie dogs, Cynomys gunnisoni, living under natural conditions.

**THE STUDY ANIMAL**

Gunnison’s prairie dogs are hibernating, mediumsized (250–1100 g for adults), colonial rodents of the squirrel family (Sciuridae) that live in Arizona, Colorado, New Mexico and Utah, U.S.A. (Pizzimenti & Hoffmann 1973). As for white-tailed and black-tailed prairie dogs, C. leucurus and C. ludovicianus (Hoogland 1979a, b, 1981), coloniality of Gunnison’s prairie dogs involves both advantages and disadvantages (Hoogland 1996b). Within colonies, individuals live in harempolygynous family groups called clans, and in
warm weather they forage above-ground from dawn until dusk (Fitzgerald & Lechleitner 1974; Rayor 1985, 1988). Clans typically contain three to four breeding females and one breeding male, but some clans contain two or three breeding males (Travis & Slobodchikoff 1993; Travis et al. 1995, 1996). Clan members defend a home territory of about 1 ha, but commonly forage in areas as far as 100 m from the home territory.

Mortality in the first year is approximately 50% for both male and female Gunnison's prairie dogs (J. L. Hoogland, unpublished data). Females that survive the first year sometimes live as long as 6 years, but no males at the study colony have lived longer than 4 years. Females copulate in the first year when they are about 11 months old, but males commonly defer sexual maturity until the second year (Rayor 1985, 1988; Hoogland 1997).

At Petrified Forest National Park, Arizona, Gunnison’s prairie dogs hibernate for approximately 4 months of each year (November–February). They arouse from hibernation in late February and early March, and the breeding season (i.e. the interval when copulations occur) starts in mid-March and continues into early April. Pregnancy lasts 29.3 ± 0.53 days (X ± sD; N = 124) (Hoogland 1997). After remaining underground for 38.6 ± 2.08 days after birth (N = 112), nearly weaned juveniles first emerge from their natal burrows and appear above-ground in late May or early June (Hoogland 1997).

Female Gunnison’s prairie dogs, like females of other ground-dwelling squirrels (Holekamp 1984; Holekamp & Sherman 1989), usually remain in the natal area for their entire lives. Young males, in contrast, disperse before reaching sexual maturity, and older males usually do not remain in the same breeding territory for more than 1 year (Fitzgerald & Lechleitner 1974; Rayor 1985, 1988; J. L. Hoogland, unpublished data).

**METHODS**

The study site, in Petrified Forest National Park, Arizona, occupied approximately 14 ha and contained 117 ± 42.0 adult (≥ 11 months old) residents in April of each year (range=64–174; N = 7 years). My methods for capturing, handling, ear-tagging, and marking Gunnison’s prairie dogs were almost identical to those used in my long-term study of black-tailed prairie dogs (Hoogland 1985, 1986, 1992, 1995, 1996a). Each year I captured all the adult and juvenile residents at the study site. From three 4-m high observation towers, I observed marked individuals for 4 months (March–June) of 7 consecutive years (1989–1995). Field assistants and I logged 15,000 person-hours of observations. Gunnison’s prairie dog mothers give birth underground. I inferred parturition, and simultaneously confirmed conception and pregnancy, on the first day that a mother showed a precipitous loss of body mass and a noticeable increase in the time spent in the home nursery burrow (Hoogland 1997). For copulating females that did not give birth, I did not distinguish between females that never conceived and those that conceived and then aborted.

Gunnison’s prairie dog mothers usually rear their offspring in separate nursery burrows (Fitzgerald & Lechleitner 1974; Hoogland 1996b, 1997). I therefore determined maternity and litter size by capturing juveniles as they first appeared above-ground in late May or June. Litter size at first juvenile emergence was 3.76 ± 1.17 (range=1–7; N = 178; Hoogland 1997).

A female Gunnison’s prairie dog was sexually receptive for several hours on only 1 day of the breeding season (Hoogland, in press). Most copulations occurred underground. As for black-tailed prairie dogs (Hoogland & Foltz 1982; Hoogland 1995), however, five diagnostic above-ground behaviours before or after an underground consortship allowed me to identify 587 copulations during the 286 periods of oestrus of 239 different female Gunnison’s prairie dogs: inordinately frequent sniffing and chasing of the female by breeding male(s); self-licking of the genitals by both sexual partners; dust-bathing by both partners; late final submergence by the female at the end of the day; and a unique mating call by the copulating male(s). Underground consortships that involved insemination were 53.9 ± 47.8 min long (range=5–308 min). Three independent lines of evidence indicate that my inferences of oestrus, copulation, and insemination were accurate. First, females that occasionally copulated above-ground (24/286, or 8%) showed, or elicited, the same five behaviours diagnostic of underground consortships. Second, the dates of both parturition and the first above-ground appearance of a mother’s offspring varied directly each year with the mother’s date of underground consortships (e.g.
1994; for both, Pearson’s $r \geq 0.893$, $P < 0.001$, $N \geq 48$). Third and most important, paternities determined from DNA fingerprints agree with paternities inferred from behavioural observations (J. L. Hoogland, D. A. Gilbert, A. Lowe, R. A. van den Bussche, unpublished data). Single paternity by the consorting male, for example, was the rule for litters of mothers that I observed consort underground with only one breeding male. In contrast, multiple paternity (i.e. the same mother but at least two fathers) routinely occurred within litters of mothers that consorted underground with two or more breeding males (J. L. Hoogland, D. A. Gilbert, A. Lowe, R. A. van den Bussche, unpublished data; see also Travis et al. 1996).

To determine female body mass during the breeding season, I weighed each female a few days before she copulated, usually within 1–3 days after she aroused from hibernation.

The operational sex ratio is the number of fertilizable females divided by the number of sexually active males (Emlen & Oring 1977). Using the number of females that came into oestrus each day and the number of resident breeding males on the same day, I calculated the operational sex ratio for every day of the breeding season each year.

All levels of significance result from two-tailed statistical tests. All correlation coefficients result from the Pearson correlation test. As for black-tailed prairie dogs (Hoogland 1995), I assumed independence of data from the same female Gunnison’s prairie dog in different years. For a variety of reasons, sample sizes for seemingly related analyses were not always identical. For some females that I observed copulating, for example, I could not determine exact litter size, and for others I had no estimate of body mass.

**RESULTS**

After copulating with one male, a female Gunnison’s prairie dog can easily avoid copulating with additional males by remaining in a burrow until the following morning. Over 95% of oestrous females re-appeared above-ground, however, and solicited copulations with additional males. Despite attempts at mate guarding by the first male, most of these solicitations were successful; consequently, 65% of oestrous females copulated with more than one male (Fig. 1). The female’s number of sexual partners did not significantly correlate in any year with the daily operational sex ratio (for all years, absolute value of $r \leq 0.213$, $P \geq 0.200$).

The probability of pregnancy and parturition varied directly with the mother’s number of sexual partners (Fig. 2). The probability of parturition was 100% for females ($N = 83$) that copulated with three or more males, for example, but was only 92% for females ($N = 180$) that copulated with only one or two males ($X_1 = 6.82$, $P = 0.009$). Copulating with several males thus guaranteed pregnancy and parturition. The probability of parturition did
not differ between females that copulated with only one male and females that copulated with exactly two males (93 versus 91%, respectively, \(X^2 = 0.182, P = 0.669\)).

Litter size at first juvenile emergence from the natal burrow varied directly with the mother's number of sexual partners (\(r = 0.226, P = 0.003\); Fig. 3a). Litter size also varied directly with maternal body mass during the breeding season (\(r = 0.245, P = 0.001\); Fig. 3b) and, to a lesser extent, with maternal age (\(r = 0.125, P = 0.116, N = 160\)). A multiple regression, which separates the independent effects of different variables, showed that the mother's number of sexual partners and maternal body mass affected litter size about equally (\(t_{145} = 2.22, P = 0.028\) and \(t_{145} = 2.17, P = 0.032\) respectively); the effect of maternal age in this multiple regression was non-significant (\(t_{df} = -0.476, P = 0.635\)).

The number of emergent offspring that survived for at least 1 year (i.e. until arousal from the first hibernation, at approximately 11 months of age) varied directly with litter size at first juvenile emergence (\(r = 0.524, P < 0.001\); Fig. 4). Litter size was thus a reliable estimate of female reproductive success.

A female's number of sexual partners varied directly with her body mass during the breeding season (\(r = 0.310, P < 0.001\); Fig. 5).

All estimates of female reproductive success showed significant annual variation (ANOVA; \(F_{6,300} = 8.00\) and \(P < 0.001\) for all except age of copulating female, for which \(F_{5,277} = 2.912\) and \(P = 0.014\); Fig. 6). Most of these estimates positively correlated with each other (\(r \geq 0.123, P \leq 0.046\) for 13 of 15 possible correlations; the two exceptions involved maternal age). Large litters, high maternal body mass and several sexual partners for the mother, for example, all correlated positively.
Male Gunnison’s prairie dogs, like males of other species (e.g. Dewsbury 1982, 1984, Parker 1984; Birkhead 1991; Birkhead & Fletcher 1995), might sometimes suffer either from sterility or from temporary depletion of sperm. Temporary depletion of sperm might be especially likely on an afternoon when a male has already copulated with two or three other females earlier in the same day. If so, then females might not always obtain sufficient sperm from a single insemination to fertilize all eggs. Multiple copulations therefore might be necessary to guarantee pregnancy. Because each female Gunnison’s prairie dog comes into oestrus only once each year (Hoogland, in press), such a guarantee is important so that females do not forfeit an entire breeding season. Other animals that ensure conception by copulating with several males include black-bellied fruitflies, Drosophila melanogaster (Gromko et al. 1984), ermine moths, Atteva punctella (Taylor 1967), and house and field crickets, Acheta domesticus and Gryllus integer (Sakaluk & Cade 1980).

A female Gunnison’s prairie dog presumably does not ovulate more eggs in response to copulations with more than one male. Why, then, does copulating with several males increase litter size? One possible mechanism involves multiple paternity, which occurs when two or more males sire offspring of a single clutch or litter for animals such as mallards, Anas platyrhynchos (Evarts & Williams 1987), indigo buntings, Passerina cyanea (Westneat 1987), dwarf mongooses, Helogale parvula (Keane et al. 1994), and five species of ground squirrels, Spermophilus (Hanken &

![Figure 5](image.png)

**Figure 5.** Number of sexual partners for females versus female body mass during the breeding season for Gunnison’s prairie dogs (Pearson correlation). The number above each line indicates the number of oestrous females observed.

**DISCUSSION**

Male Gunnison’s prairie dogs, like males of other species (e.g. Dewsbury 1982, 1984, Parker 1984; Birkhead 1991; Birkhead & Fletcher 1995), might sometimes suffer either from sterility or from temporary depletion of sperm. Temporary depletion of sperm might be especially likely on an afternoon when a male has already copulated with two or three other females earlier in the same day. If so, then females might not always obtain sufficient sperm from a single insemination to fertilize all eggs. Multiple copulations therefore might be necessary to guarantee pregnancy. Because each female Gunnison’s prairie dog comes into oestrus only once each year (Hoogland, in press), such a guarantee is important so that females do not forfeit an entire breeding season. Other animals that ensure conception by copulating with several males include black-bellied fruitflies, Drosophila melanogaster (Gromko et al. 1984), ermine moths, Atteva punctella (Taylor 1967), and house and field crickets, Acheta domesticus and Gryllus integer (Sakaluk & Cade 1980).

A female Gunnison’s prairie dog presumably does not ovulate more eggs in response to copulations with more than one male. Why, then, does copulating with several males increase litter size? One possible mechanism involves multiple paternity, which occurs when two or more males sire offspring of a single clutch or litter for animals such as mallards, Anas platyrhynchos (Evarts & Williams 1987), indigo buntings, Passerina cyanea (Westneat 1987), dwarf mongooses, Helogale parvula (Keane et al. 1994), and five species of ground squirrels, Spermophilus (Hanken &

![Figure 6](image.png)

**Figure 6.** Annual variation of different estimates of female reproductive success (ANOVA; \( P < 0.001 \) for all except age of copulating female, for which \( P = 0.014 \)). ■, M aternal body mass during breeding season; ◼, number of juveniles in litter that survived for at least 1 year; ●, mean age of females that copulated; ○, mean number of different sexual partners for each oestrous female; ⊙, proportion of copulating females that gave birth; □, litter size at first juvenile emergence from natal burrow.
Male and female Gunnison’s prairie dogs appear to have a conflict of interest regarding the optimal number of sexual partners for each female. Via assurance of parturition and larger litters, females maximize reproductive success by copulating with more than one male. A copulating male, in contrast, maximizes reproductive success with a particular female whenever he can monopolize her so that she cannot copulate with additional males. Figure 1 shows that 35% of females copulate with only one male, 35% copulate with exactly two males, and 30% copulate with ≥3 males. Thus, neither sex is completely

animal Behaviour, 55, 2

Sherman 1981; Foltz & Schwagmeyer 1989; Sherman 1989; Boelstorff et al. 1994; Murie 1996). Multiple paternity, which is common among Gunnison’s prairie dogs (Travis et al. 1996; J. L. Hoogland, D. A. Gilbert, A. Lowe, R. A. van den Bussche, unpublished data), promotes genetic diversity among litter-mates and thus maximizes the advantages of sexual reproduction (Westneat et al. 1990; Birkhead & Moller 1992). In an unpredictable environment, especially one with co-evolving diseases and parasites, genetic diversity might be especially important to fetal and infantile survivorship (Williams 1975; Hamilton & Zuk 1982; Seger & Hamilton 1988; Clayton 1991). Multiple copulations might also enhance the quality of offspring via intra-uterine sperm competition (Parker 1984; Madsen et al. 1992; Birkhead et al. 1993; Kellner & Reeve 1995), so that mortality of unweaned infants and abortions are less likely and larger litters at first emergence are more likely. Regardless of mechanism, two payoffs from multiple matings are clear for female Gunnison’s prairie dogs: assurance of bringing pregnancy to term and larger litters.

Is the positive correlation between litter size and the mother’s number of sexual partners (Fig. 3a) merely a secondary consequence of the higher rate of pregnancy and parturition for multiply mating female Gunnison’s prairie dogs? The answer here is no, because Fig. 3a excludes data from females that failed to rear a litter to first emergence; that is, I have removed the effect of the higher probability of parturition for multiply mating females. A assurance of parturition and larger litters are thus independent benefits that female Gunnison’s prairie dogs reap by copulating with more than one male.

The mother’s number of sexual partners (Fig. 3a) is not the only factor that affects litter size. As for other squirrels (Murie & Dobson 1987; Sauer & Slade 1987; Michener 1989; Hoogland 1995, 1996a), maternal body mass (Fig. 3b) and maternal age also promote larger litters for Gunnison’s prairie dogs. Do additional copulations directly promote larger litters for females? Alternatively, do larger litters result from additional copulations simply because heavier, older, more fecund females are more likely to copulate with several males (Fig. 5)? A multiple regression analysis shows that the independent effect of the mother’s number of sexual partners on litter size was equivalent to the independent effect of maternal body mass. A Pearson partial correlation analysis, which removes the effects of maternal body mass and maternal age, also indicates a significant, independent effect of the mother’s number of sexual partners on litter size (r = 0.182, P = 0.028). Female Gunnison’s prairie dogs thus seem to increase directly litter size, and hence reproductive success, by copulating with several males.

Are the two benefits of multiple mating for female Gunnison’s prairie dogs typical and representative, so that they might explain why females of so many other species commonly copulate with more than one male? Of the many social mammals that behavioural ecologists have studied under natural conditions (e.g. chapters in Alexander & Tinkle 1981; Murie & Michener 1984; Chepko-Sade & Halpin 1987; Clutton-Brock 1988), Gunnison’s prairie dogs provide the first good evidence that females enhance reproductive success by copulating with more than one male. Females of two other vertebrate species, adders, Vipera berus (Madsen et al. 1992), and sand lizards, Lacerta agilis (Olssen et al. 1994), also improve reproductive success via additional copulations. By contrast, copulation with a second male evidently does not affect female reproductive success under natural conditions for thirteen-lined ground squirrels, S. tridecemlineatus (Schwagmeyer 1986), Columbian ground squirrels, S. columbianus (Murie 1996) or black-tailed prairie dogs (Hoogland 1995). At the other extreme, copulation with a second male seems to reduce female reproductive success for deer mice, Peromyscus maniculatus (Dewsbury 1982), and Djungarian hamsters, Phodopus sungorus campbelli (Wynne-Edwards & Lisk 1984), under laboratory conditions. More research is necessary for a better understanding of multiple mating by females of so many species.
‘winning’ the conflict of interest regarding the optimal number of sexual partners for females. Heavy female Gunnison’s prairie dogs can resist monopolization by males better than lighter females. Furthermore, because they rear larger litters (Fig. 3b), heavy females are probably more attractive to, and thus generate more interest among, breeding males. Heavy females are thus more likely than lighter females to copulate with several males (Fig. 5) and thereby to ‘win’ the inter-sexual conflict of interest regarding the optimal number of sexual partners for females.

ACKNOWLEDGMENTS


REFERENCES


