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

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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.

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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 none the less common for myriad species: insects (Cole 1983; Thornhill & Alcock 1983), fish (Dominey 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 costs include increased susceptibility to predation, reduced paternal care if males do not help to rear offspring of a mate that also copulates with other males, increased probability of physical harm, and increased exposure to diseases and parasites.

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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, medium-sized (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 harem-polygynous family groups called clans, and in

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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 ($\bar{X}+$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, eartagging, and marking Gunnison's prairie dogs were almost identical to those used in my longterm 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 copu-
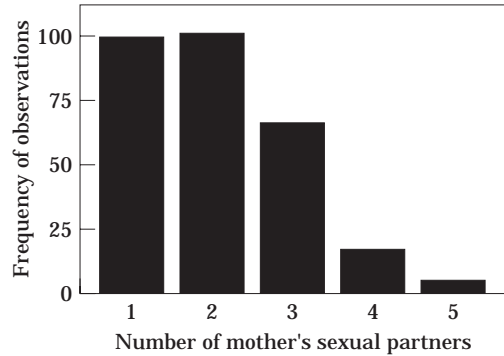

Figure 1. Number of sexual partners for female Gunnison's prairie dogs (mean ± SD = 2.05 ± 0.98; $N = 286$ oestrous periods, involving 239 different females).
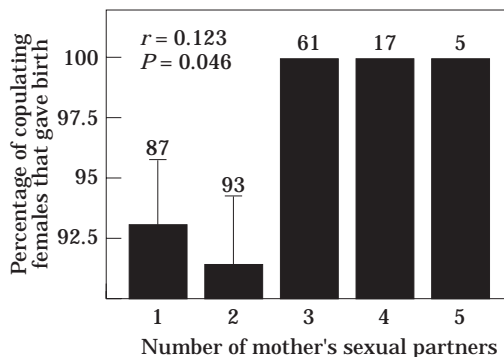

Figure 2. Probability of pregnancy and parturition for Gunnison's prairie dogs versus number of mother's sexual partners (Pearson correlation). For each female, I entered the number of sexual partners and either 0 (if she did not give birth) or 1 (if she did give birth). The number above each SE line indicates the number of oestrous females observed.

lated 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
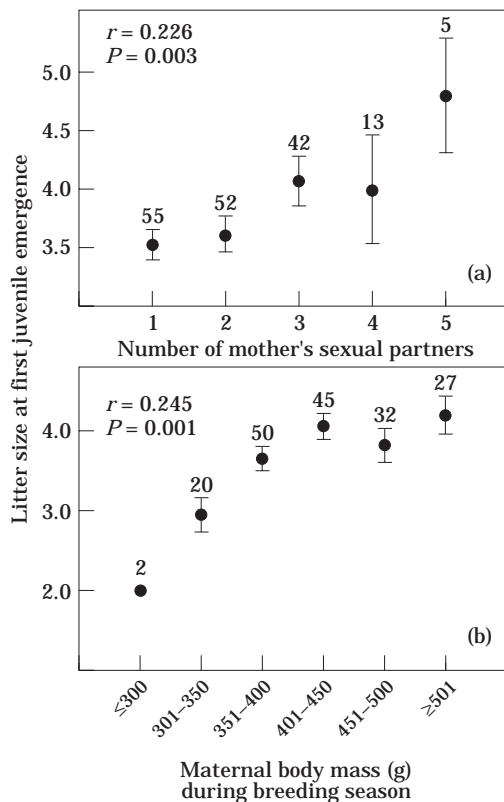
Figure 3. (a) Litter size of Gunnison's prairie dogs versus number of mother's sexual partners; (b) litter size of Gunnison's prairie dogs versus mother's body mass during the breeding season (Pearson correlation). The number above each SE line indicates the number of oestrous females observed. Both graphs include data from only those females that reared a litter to first emergence. When I included data from females that copulated but did not produce emergent offspring (i.e. litter size=0), both correlations were still significant (for both, $r \geq 0.211$, $P \leq 0.002$, and $N \geq 204$).
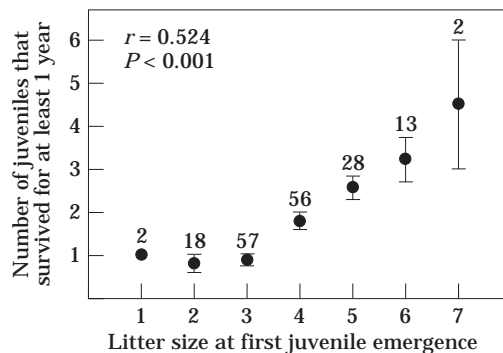
Figure 4. Number of juveniles that survived for at least one year versus litter size at first juvenile emergence for Gunnison's prairie dogs (Pearson correlation). The number above each SE line indicates the number of litters of each size. This graph includes data from only those females that reared a litter to first emergence. When I included data from females that copulated but did not produce emergent offspring (i.e. litter size=0), the positive relationship was still significant ($r=0.621$, $P<0.001$, $N=214$).

not differ between females that copulated with only one male and females that copulated with exactly two males (93 versus 91%, respectively, $X_1=0.182$, $P=0.669$).

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; $F_{6,300} \geq 8.00$ 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.
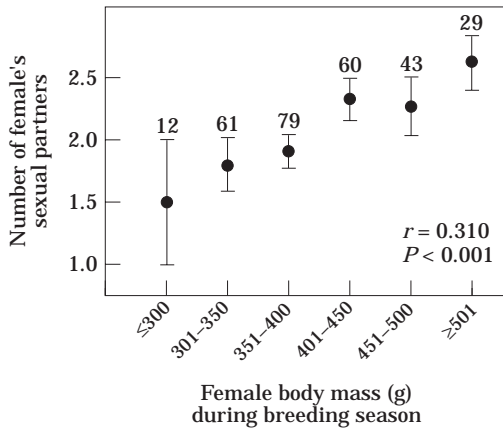
Figure 5. Number of sexual partners for females versus female body mass during the breeding season for Gunnison's prairie dogs (Pearson correlation). The number above each SE line indicates the number of oestrous females observed.

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 &
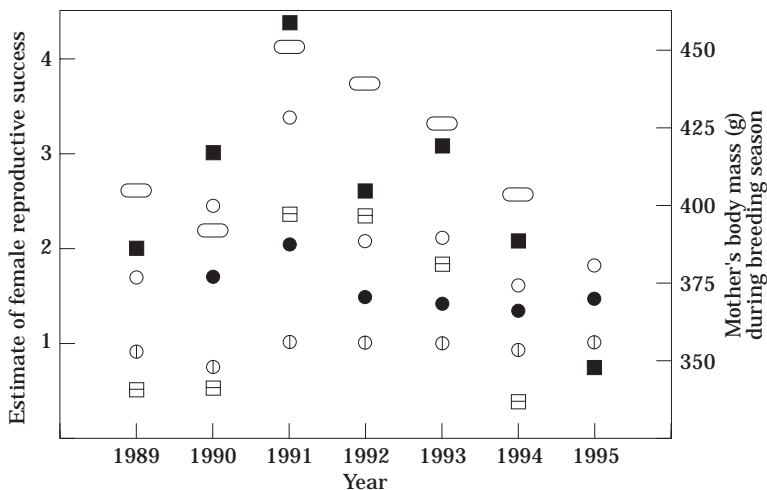

Figure 6. Annual variation of different estimates of female reproductive success (ANOVA; $P<0.001$ for all except age of copulating female, for which $P=0.014$). ■, Maternal body mass during breeding season; ⊟, number of juveniles in litter that survived for at least 1 year; ●, mean age of females that 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.

Sherman 1981; Foltz & Schwagmeyer 1989; Sherman 1989; Boellstorff 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; Keller & 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 higher probability of parturition for multiply mating females. 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.

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

'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

Alexander, R. D. & Tinkle, D. W. (Eds) 1981. *Natural Selection and Social Behavior*. New York: Chiron Press.

Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity*, **2,** 349–368.

van den Berghe, E. 1988. Piracy as an alternative reproductive tactic for males. *Nature, Lond.*, **334,** 697–698.

Birkhead, T. R. 1988. Behavioural aspects of sperm competition in birds. *Adv. Study Behav.*, **18,** 35–72.

Birkhead, T. R. 1991. Sperm depletion in the Bengalese finch *Lonchura striata*. *Behav. Ecol.*, **2,** 267–275.

Birkhead, T. R. & Fletcher, F. 1995. Male phenotype and ejaculate quality in the zebra finch *Taeniophygia guttata*. *Proc. R. Soc. Lond. Ser. B*, **262,** 329–334.

Birkhead, T. R. & Moller, A. P. 1992. *Sperm Competition in Birds*. London: Academic Press.

Birkhead, T. R., Moller, A. P. & Sutherland, W. J. 1993. Why do females make it so difficult for males to fertilize their eggs? *J. theor. Biol.*, **161,** 51–60.

Boellstorff, D. E., Owings, D. H., Penedo, M. C. T. & Hersek, M. J. 1994. Reproductive behaviour and multiple paternity of California ground squirrels. *Anim. Behav.*, **47,** 1057–1064.

Chepko-Sade, B. D. & Halpin, Z. T. (Eds) 1987. *Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics*. Chicago: The University of Chicago Press.

Clayton, D. H. 1991. The influence of parasites on host sexual selection. *Parasitol. Today*, **7,** 329–334.

Clutton-Brock, T. H. (Ed.) 1988. *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*. Chicago: The University of Chicago Press.

Cole, B. J. 1983. Multiple mating and the evolution of social behavior in the Hymenoptera. *Behav. Ecol. Sociobiol.*, **12,** 191–201.

Daly, M. 1978. The cost of mating. *Am. Nat.*, **112,** 771–774.

Darwin, C. R. 1871. *The Descent of Man and Selection in Relation to Sex*. London: John Murray.

Dewsbury, D. A. 1982. Ejaculate cost and male choice. *Am. Nat.*, **119,** 601–610.

Dewsbury, D. A. 1984. Sperm competition in muroid rodents. In: *Sperm Competition and the Evolution of Mating Systems* (Ed. by R. L. Smith), pp. 547–571. Orlando, Florida: Academic Press.

Dominey, W. J. 1984. Alternative mating tactics and evolutionarily stable strategies. *Am. Zool.*, **24,** 385–396.

Eberhard, W. G. 1996. *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton, New Jersey: Princeton University Press.

Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197,** 215–223.

Evarts, S. & Williams, C. J. 1987. Multiple paternity in a wild population of mallards. *Auk*, **104,** 597–602.

Fitzgerald, J. P. & Lechleitner, R. R. 1974. Observations on the biology of Gunnison's prairie dog in central Colorado. *Am. Midl. Nat.*, **92,** 146–163.

Foltz, D. W. & Schwagmeyer, P. L. 1989. Sperm competition in the thirteen-lined ground squirrel: differential fertilization success under field conditions. *Am. Nat.*, **133,** 257–265.

Gladstone, D. E. 1979. Promiscuity in monogamous colonial birds. *Am. Nat.*, **114,** 545–557.

Goodall, J. 1986. *The Chimpanzees of Gombe*. Cambridge, Massachusetts: Belknap Press.

Gromko, M. H., Newport, M. E. A. & Kortier, M. G. 1984. Sperm dependence of female receptivity to remating in *Drosophila melanogaster*. *Evolution*, **38,** 1273–1282.

Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: A role for parasites. *Science*, **218**, 384–387.

Hanken, J. & Sherman, P. W. 1981. Multiple paternity in Belding's ground squirrel litters. *Science*, **212**, 351–353.

Hausfater, G. 1975. Dominance and reproduction in baboons (*Papio cynocephalus*): a quantitative analysis. *Contrib. Primatol.*, **7**, 1–150.

Holekamp, K. E. 1984. Dispersal in ground-dwelling sciurids. In: *The Biology of Ground-dwelling Squirrels* (Ed. by J. O. Murie & G. R. Michener), pp. 297–320. Lincoln, Nebraska: University of Nebraska Press.

Holekamp, K. E. & Sherman, P. W. 1989. Why male ground squirrels disperse. *Am. Scient.*, **77**, 232–239.

Hoogland, J. L. 1979a. Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae: *Cynomys* spp.) coloniality. *Behaviour*, **69**, 1–35.

Hoogland, J. L. 1979b. The effect of colony size on individual alertness of prairie dogs (Sciuridae: *Cynomys* spp.). *Anim. Behav.*, **27**, 394–407.

Hoogland, J. L. 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology*, **62**, 252–272.

Hoogland, J. L. 1985. Infanticide in prairie dogs: lactating females kill offspring of close kin. *Science*, **230**, 1037–1040.

Hoogland, J. L. 1986. Nepotism in prairie dogs varies with competition but not with kinship. *Anim. Behav.*, **34**, 263–270.

Hoogland, J. L. 1992. Levels of inbreeding among prairie dogs. *Am. Nat.*, **139**, 591–602.

Hoogland, J. L. 1995. *The Black-tailed Prairie Dog: Social Life of a Burrowing Mammal*. Chicago: The University of Chicago Press.

Hoogland, J. L. 1996a. *Cynomys ludovicianus*. *Mamm. Sp. Acct.*, **535**, 1–10.

Hoogland, J. L. 1996b. Why do Gunnison's prairie dogs give anti-predator calls? *Anim. Behav.*, **51**, 871–880.

Hoogland, J. L. 1997. Duration of gestation and lactation for Gunnison's prairie dogs. *J. Mammal.*, **78**, 173–180.

Hoogland, J. L. In press. Estrus and copulation for Gunnison's prairie dogs. *J. Mammal.*

Hoogland, J. L. & Foltz, D. W. 1982. Variance in male and female reproductive success in a harem-polygynous mammal, the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). *Behav. Ecol. Sociobiol.*, **11**, 155–163.

Hrdy, S. 1981. *The Woman That Never Evolved*. Cambridge, Massachusetts: Harvard University Press.

Kano, T. 1992. *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*. Stanford, California: Stanford University Press.

Keane, B., Waser, P. M., Creel, S. R., Creel, N. M., Elliott, L. F. & Minchella, D. J. 1994. Subordinate reproduction in dwarf mongooses. *Anim. Behav.*, **47**, 65–75.

Keller, L. & Reeve, H. K. 1995. Why do females mate with multiple males? The sexually selected sperm hypothesis. In: *Advances in the Study of Behavior. Vol. 24* (Ed. by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowden & M. Milinski), pp. 291–315. New York: Academic Press.

Madsen, T., Shine, R., Loman, J. & Hakansson, T. 1992. Why do female adders copulate so frequently? *Nature, Lond.*, **355**, 440–441.

Michener, G. R. 1989. Reproductive effort during gestation and lactation by Richardson's ground squirrels. *Oecologia (Berl.)*, **78**, 77–86.

Murie, J. O. 1996. Mating behavior of Columbian ground squirrels. I. Multiple mating by females and multiple paternity. *Can. J. Zool.*, **73**, 1819–1826.

Murie, J. O. & Dobson, F. S. 1987. The costs of reproduction in female Columbian ground squirrels. *Oecologia (Berl.)*, **73**, 1–6.

Murie, J. O. & Michener, G. R. (Eds) 1984. *The Biology of Ground-dwelling Squirrels*. Lincoln, Nebraska: University of Nebraska Press.

Olsson, M., Gullberg, A., Tegelstrom, H., Madsen, T. & Shine, R. 1994. Can female adders multiply? *Nature, Lond.*, **369**, 528.

Parker, G. A. 1984. Sperm competition and the evolution of animal mating systems. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 1–60. Orlando, Florida: Academic Press.

Petrie, M., Hall, M., Halliday, T., Budgey, H. & Pierpont, C. 1992. Multiple mating in a lekking bird: why peahens mate with more than one male and with the same male more than once? *Behav. Ecol. Sociobiol.*, **31**, 349–358.

Pizzimenti, J. J. & Hoffmann, R. S. 1973. *Cynomys gunnisoni*. *Mammal. Sp.*, **25**, 1–4.

Rayor, L. S. 1985. Effects of habitat quality on growth, age of first reproduction, and dispersal in Gunnison's prairie dogs (*Cynomys gunnisoni*). *Can. J. Zool.*, **63**, 2835–2840.

Rayor, L. S. 1988. Social organization and space-use in Gunnison's prairie dog. *Behav. Ecol. Sociobiol.*, **22**, 69–78.

Sakaluk, S. K. & Cade, W. H. 1980. Female mating frequency and progeny production in singly and doubly mated house and field crickets. *Can. J. Zool.*, **58**, 404–411.

Sauer, J. R. & Slade, N. A. 1987. Uinta ground squirrel demography: is body mass a better categorical variable than age? *Ecology*, **68**, 642–650.

Schaller, G. B. 1972. *The Serengeti Lion*. Chicago: The University of Chicago Press.

Schwagmeyer, P. L. 1984. Multiple mating and intersexual selection in thirteen-lined ground squirrels. In: *The Biology of Ground-dwelling Squirrels* (Ed. by J. O. Murie & G. R. Michener), pp. 275–293. Lincoln, Nebraska: University of Nebraska Press.

Schwagmeyer, P. L. 1986. Effects of multiple mating on reproduction in female thirteen-lined ground squirrels. *Anim. Behav.*, **34**, 297–298.

Seger, J. & Hamilton, W. D. 1988. Parasites and sex. In: *The Evolution of Sex: An Examination of Current Ideas* (Ed. by R. E. Michod & B. R. Levins), pp. 176–193. Sunderland, Massachusetts: Sinauer Associates.

Sherman, P. W. 1989. Mate guarding as paternity insurance in Idaho ground squirrels. *Nature, Lond.*, **338,** 418–420.

Smith, R. L. 1984. Human sperm competition. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 601–660. Orlando, Florida: Academic Press.

Taylor, O. R. 1967. Relationship of multiple mating to fertility in *Atteva punctella* (Lepidoptera: Yponomeutidae). *Ann. entomol. Soc. Am.*, **60,** 583–590.

Thornhill, R. & Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Cambridge, Massachusetts: Harvard University Press.

Travis, S. E. & Slobodchikoff, C. N. 1993. Effects of food resource distribution on the social system of Gunnison's prairie dogs. *Can. J. Zool.*, **71,** 1186–1192.

Travis, S. E., Slobodchikoff, C. N. & Keim, P. 1995. Ecological and demographic effects on intraspecific variation in the social system of prairie dogs. *Ecology*, **76,** 1794–1803.

Travis, S. E., Slobodchikoff, C. N. & Keim, P. 1996. Social assemblages and mating relationships in prairie dogs: a DNA fingerprint analysis. *Behav. Ecol.*, **7,** 95–100.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man (1871–1971)* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine Press.

Westneat, D. F. 1987. Extra-pair fertilizations in a predominantly monogamous bird: genetic evidence. *Anim. Behav.*, **35,** 877–886.

Westneat, D. F., Sherman, P. W. & Morton, M. L. 1990. The ecology and evolution of extra-pair copulation in birds. In: *Current Ornithology. Vol. 7* (Ed. by D. M. Power), pp. 331–369. New York: Plenum Press.

Williams, G. C. 1975. *Sex and Evolution*. Princeton, New Jersey: Princeton University Press.

Wynne-Edwards, K. E. & Lisk, R. D. 1984. Djungarian hamsters fail to conceive in the presence of multiple males. *Anim. Behav.*, **32,** 626–628.