

Variance in Male and Female Reproductive Success in a Harem-Polygynous Mammal, the Black-Tailed Prairie Dog (Sciuridae: *Cynomys ludovicianus*)

John L. Hoogland¹ and David W. Foltz²*

¹ Department of Biology, Princeton University, Princeton, New Jersey, 08544, USA

² Department of Biology, University of Rochester, Rochester, New York 14627, USA

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Summary. Black-tailed prairie dogs are colonial rodents that live in contiguous social groups called coteries. A typical coterie contains one adult (≥ 2 years old) male, three or four adult females, and several yearlings and juveniles of both sexes. A large coterie sometimes contains two or more adult males. Using detailed behavioral observations on 164 females (of which 160 copulated) and data from four polymorphic loci from parents and offspring of 121 litters, we examined the black-tail mating system.

Most females (101/164 = 62%) copulated with a single adult male, and only 3 of the 102 litters with ≥ 2 offspring (3%) showed unequivocal evidence of multiple paternity. Adult males usually copulated with several different adult females.

In one-male coteries, females usually copulated exclusively with the resident adult male (RAM) (82/112 = 73%); this trend was confirmed by electrophoresis of blood samples. In multimale coteries, each female frequently copulated with at least two different RAMs (28/52 = 54%); in 4 of 5 multimale coteries (80%) which produced two or more litters whose paternities could be unequivocally resolved by electrophoresis, two different RAMs each sired at least one litter.

Of the 164 females, 30 (18%) copulated with both the RAM (or one of the RAMs, in multimale coteries) and an extracoterie adult male, but only 3 (2%) copulated exclusively with an extracoterie adult male. Electrophoresis showed that 9 of 121 litters (7%) were sired by an extracoterie adult male.

Intersexual comparisons of annual reproductive success and lifetime reproductive success both indicate that black-tails are polygynous (i.e., that

variance in reproductive success is greater for males than for females).

Introduction

The mating system of a species is commonly inferred from its social organization (e.g., Jarman 1974; Clutton-Brock and Harvey 1977a, 1977b; Alexander et al. 1979). However, the presumed correlation between mating system and social organization has rarely been verified in natural populations. The purpose of our study was to combine (a) detailed observations of behavior and social organization during the breeding season with (b) an electrophoretic analysis of blood samples in an attempt to define the mating system of the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). More specifically, our main objectives were to determine if black-tail females copulate exclusively with the adult male(s) in the home harem and to examine intersexual variance in annual and lifetime reproductive success.

Black-tails are large (700–1,500 g), diurnal, colonial rodents. In South Dakota they breed in February and March, and weaned juveniles first emerge from their natal burrows in May and June (Hoogland 1979a); the mean \pm SD litter size is 2.9 ± 1.1 ($N = 175$ l). Individuals live in social groups called coteries (King 1955), and a typical coterie contains one resident adult male (RAM), three or four adult females, and several yearlings and juveniles of both sexes. A large coterie sometimes contains two or more RAMs (King 1955; Hoogland 1981b). Females usually remain in the natal coterie for life, but males usually depart permanently 12–14 months after weaning (Hoogland 1982); consequently, the females and yearling

* Present address: Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

males within a coterie are almost invariably close genetic relatives. Males and females usually first breed as 2-year olds, and avoid mating with close genetic relatives (Hoogland 1982; Foltz and Hoogland in press). Adults and yearlings of both sexes remain within well-defined coterie territories, and interact more amicably with members of their own coterie than with members of other coterie (King 1955; Hoogland 1981a, b, in press).

The combination of electrophoresis with observations of behavior and social organization is available for only a handful of species, including greater spear-nose bats (*Phyllostomus hastatus*) (McCracken and Bradbury 1977, 1981), yellow-bellied marmots (*Marmota flaviventris*) (Schwartz and Armitage 1980, 1981), and Belding's ground squirrels (*Spermophilus beldingi*) (Hanken and Sherman 1981). For greater spear-nose bats and yellow-bellied marmots, whose social organizations suggest harem-polygyny similar to that suggested by the black-tail social organization, electrophoresis confirmed that the resident adult male sires most of the offspring produced by females in his harem. Females of Belding's ground squirrels (whose social organization does not suggest harem-polygyny) frequently copulate with two or more males, and electrophoresis showed that multiple paternity occurs at a frequency of 55%–78%.

Materials and Methods

All data in this report were obtained from a single colony located in Wind Cave National Park, Hot Springs, South Dakota. This study colony occupies approximately 500 m × 130 m (6.6 hectares), and in late spring of each year contains a mean ± SD of 142.9 ± 33.6 adults (≥2-year olds) and yearlings and 72.4 ± 36.9 juveniles (Hoogland 1979b, 1981b, in press). The mean ± SD number of coterie present each year is 24.5 ± 1.0. Since 1975, all residents at the study colony have been marked with eartags and Nyanzol fur dye; young of each litter are marked before any mixing with young from other litters, so that exact mother-offspring and sibling-sibling genetic relationships can be determined (Hoogland 1981b, 1982). Coterie compositions are determined from behavioral observations (King 1955; Hoogland 1981b) from 5-m high observation towers. The study colony is approximately 0.5 km away from all other colonies. Because all the residents at the study colony are color-marked each year, it would be almost impossible for an individual to leave or enter the study colony temporarily during the breeding season without detection.

When a female showed any sign of estrus (see below), that female was watched closely until she submerged into a burrow for the night. A copulation was assumed to have occurred if an adult male and a female were in a burrow together for at least 2 min during daylight hours and if we detected at least one of those behaviours associated with underground consortships (see below). Cases in which all consorting males could not be accurately identified by observers were excluded from analysis. During the breeding seasons of 1978 through 1981, 3–6 field assistants and Hoogland recorded data for over 99%

of the time that the prairie dogs were aboveground. We observed 160 periods of estrus (17 in 1978, 32 in 1979, 45 in 1980, and 66 in 1981), involving 107 different females and 64 different males. Only 4 adult females and 1 adult male evidently did not copulate at least once each year (Table 1, Figs. 1 and 2). However, because it is easier to demonstrate that a prairie dog *has* rather than *has not* copulated, the frequency of individuals with 0 couplings in Table 1 and Figs. 1 and 2 is probably low.

From 1978 through 1981, blood samples were collected from 500 different prairie dogs at the study colony (Foltz and Hoogland 1981, in press). Blood obtained by cutting one or more foot pads with a sterilized lancet was collected in heparinized capillary tubes and was kept on ice for 2–6 h until centrifuged for 10 min. Plasma and erythrocyte fractions from each animal were stored in separate vials at –70° C or colder until electrophoresis. Blood proteins were examined by standard methods of horizontal starch-gel electrophoresis and histochemical staining (Selander et al. 1971). Four polymorphic loci were detected: 6-phosphogluconate dehydrogenase (6-Pgd, with two alleles), esterase-1 (Est-1, with two alleles), transferrin (Trf, with three alleles), and nucleoside phosphorylase (Np, with three alleles). Twenty-one other loci were monomorphic (based on samples from ≥50 individuals). All electrophoresis was performed in 1980 and 1981; because of denaturation, 6-Pgd could not be accurately scored for the samples collected in 1978 and 1979. Blood samples were obtained from the mother, all the young weaned, and all adult males at the study colony for all the litters in 1979 ($N=22$) and 1980 ($N=30$) and for most of the litters in 1978 (32 out of 34) and 1981 (37 out of 38). Although we had blood samples from all the parents and offspring each year, we did not have behavioral observations each year for all of the estrous females.

Each offspring had at least one electromorph in common with its mother at each locus, as expected for loci with codominant alleles. Multiple paternity for a single litter was inferred when either (a) the genotype of no single adult male in the study colony was consistent with all the offspring genotypes in a litter and/or the offspring in a litter showed three different paternal alleles at the Trf or Np locus ($N=2$) or (b) the only adult male in the study colony whose genotype was consistent with all the offspring genotypes in a litter lived in a coterie that was >50 m distant from the mother's home coterie, such that insemination by this single male was extremely unlikely (see below) ($N=1$). In two of the cases of multiple paternity, the offspring genotypes were consistent with multiple paternity involving two RAMs from the multimale home coterie; in the third case, the offspring genotypes were consistent with multiple paternity involving the one RAM from the home coterie and one adult male from an adjacent coterie. There is no general agreement regarding the best method for estimating the frequency of multiple paternity in natural populations (Birdsall and Nash 1973; Merritt and Wu 1975; Johnson 1977; Wilson 1981). We estimate that the probability of detecting multiple paternity in black-tails by either of our two methods was at least 25%.

For harem-polygynous species in general, we use the term "cuckoldry" in this report for cases involving the siring of offspring by males from outside the home harem. Methods for detecting cuckoldry and nonpaternity in natural populations are less complicated than are methods for detecting multiple paternity (Wiener 1968; McCracken and Bradbury 1977, 1981). For black-tails, we estimate that the probability of detecting a cuckoldry by electrophoresis (assuming single paternity per litter) was approximately 80%.

For each litter each year, the likelihood of paternity (LOP) for each adult male at the study colony was calculated from

the distribution of genotypes within the litter and the Mendelian probabilities (conditioned on the male's genotype) of obtaining those genotypes (Foltz and Hoogland 1981). The LOP method assumes that each litter was inseminated by a single adult male; as noted above, this assumption of single paternity was sometimes violated. An adult male was excluded from paternity of a litter when his genotype was inconsistent with the offspring genotypes at one or more loci; for example, an adult male whose genotype is BB at the Np locus could be excluded from paternity of a litter consisting of four offspring whose genotypes at the Np locus are all CC. The number of adult males at the study colony whose LOP values were calculated was 29 in 1978, 31 in 1979, 29 in 1980, and 25 in 1981. Eight yearling males (2 in 1978, 1 in 1980, and 5 in 1981) showed evidence of sexual maturity (dispersal from the natal coterie before the first breeding season and/or copulatory behavior), and these yearling males and all sexually mature yearling females (those observed to copulate and/or to wean a litter) were included in LOP and other paternity analyses. We use the term "adult" in the remainder of this report for ≥ 2 -year olds and for sexually mature yearlings.

Results

Behavioral Observations of Adult Males and Estrous Females

Black-tails usually copulate underground. All adult females usually come into estrus (sexual receptivity) each year; juvenile mortality during lactation is high, and only about one-half of those females that copulate wean a litter (Hoogland 1981b). Each female is in estrus for several hours of one day only, and she usually (124 out of 156 estrous females for which we had data = 79%) submerges for the night with an adult male with whom she copulated. Although copulations occur underground, two kinds of evidence often allow us to identify a copulating pair. First, a nonestrous female only rarely enters a burrow with an adult male during daylight hours, and if she does it is usually for less than 1 min. An estrous female, on the other hand, frequently enters a burrow with an adult male for long periods during daylight

hours (several minutes to several hours) in what we term an "underground consortship" (Hoogland 1982). Second, there are five behaviors which, with only rare exceptions, are associated exclusively with underground consortships (Hoogland 1982): (1) a unique "mating call" by the male just before or just after submerging with an estrous female; (2) postconsortship licking of the penis by the male; (3) postconsortship licking of the vulva by the female; (4) preconsortship taking of nest material into the burrow of consortship by the male; and (5) the estrous female's remaining aboveground long after (>60 min, in some cases) all other prairie dogs have submerged for the night. Of the 5 aboveground copulations that we observed, 2 showed 4 of the 5 behaviors associated with underground consortships, 1 showed 3 of the behaviors, and 2 showed 2 of the behaviors. No more than one of these behaviors per day was ever observed for nonconsorting prairie dogs.

Two independent lines of evidence support the assumption that underground consortships involve copulations. First, each year the date a female's young first emerged from the natal burrow varied directly with the date of underground consortship and presumed conception ($P \leq 0.008$ for 1978 through 1981, two-tailed Kendall rank correlation test). In 1981 we also were able to pinpoint the day when females first began to show signs of having given birth (late first emergence in the morning, frequent trips underground to the same burrow system, etc.), and the first date of these signs also varied directly with the date of underground consortship ($P < 0.001$, two-tailed Kendall rank correlation test). Second, paternities determined from electrophoretic analysis of blood samples agree closely with those inferred from behavioral observations alone (Foltz and Hoogland 1981, and below). For example, paternity determined from electrophoresis was consistent with pa-

Table 1. Summary of copulations by females of one-male coterie and females of multimale coterie

	No copulations	One copulation with one male of the home coterie	One copulation with one male outside the home coterie	Two or more copulations, all with males of the home coterie	Two or more copulations, involving males both inside and outside the home coterie	Two or more copulations, all with males outside the home coterie
Females in one-male coterie	4	82	2	—	23	1
Females in multimale coterie	0	17	0	28	7	0

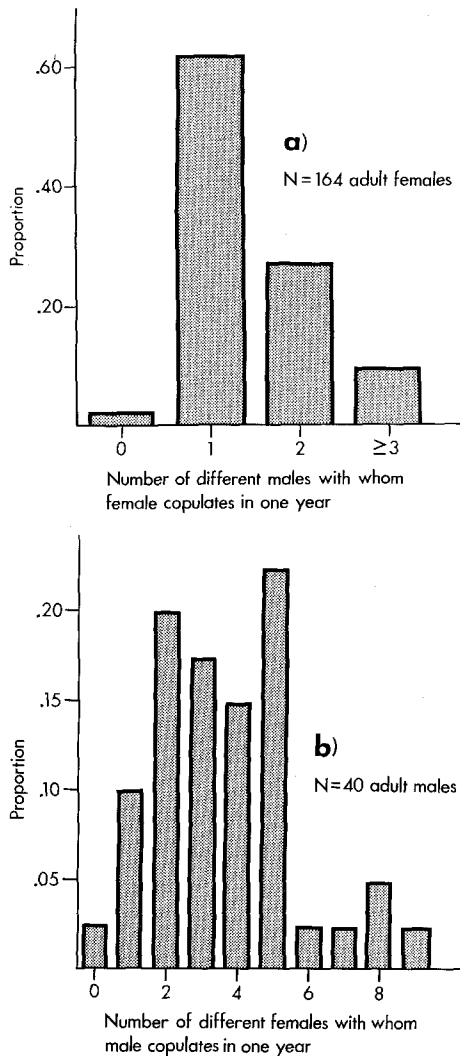


Fig. 1 a, b. Annual copulatory success of **a** adult females and **b** adult males. Only individuals that were under constant observation, so that all copulations were presumably detected, are shown here. Included here are data from 18 yearling females and 5 yearling males. Some of the data are from the same individuals in different years

ternity determined from behavioral observations alone for 53 of the 54 females (98%) that presumably copulated with a single adult male and then weaned a litter.

Only 4 of the 164 adult females under observation (2%) evidently did not copulate (Table 1): 3 of these were in poor physical condition (as determined from body weight) and never showed any sign of estrus; the other showed signs of estrus, but may have avoided copulation in order to avoid extreme inbreeding (Hoogland 1982). Most females (62%) copulated with a single adult male (Fig. 1a). Of the 59 females (36%) that copulated with two or more different adult males, 35 were

Table 2. Association between the number of copulations per estrous female and the number of resident adult males in the home coterie. Data were analyzed by the two-tailed χ^2 test

	Copulation with one male only	Copulation with two or more different males
Females in one-male coterie	84	24
Females in multimale coterie	17	35
	$P < 0.001$	

in multimale coterie (Table 2); the association between the number of copulations per estrous female and the number of adult males in the home coterie was significant. Thirty females (18%) copulated with an extracoterie adult male in addition to copulating with an adult male from the home coterie, but only 3 females (2%) copulated *exclusively* with an extracoterie adult male (Table 1).

Annual copulatory success of adult males is shown in Fig. 1b. At one extreme, one adult male did not copulate at all; this male was a yearling who had moved with his yearling brother (who did copulate) from his natal coterie to an adjacent coterie and who may not have been sexually mature. At the other extreme, one 2-year old male in 1981 copulated with 9 different females.

Electrophoresis and Multiple Paternity

If estrous females usually copulate with a single adult male as indicated from behavioral observations (Fig. 1a), then electrophoretic evidence for multiple paternity should be rare. Of the 121 weaned litters examined, 19 contained a single offspring and thus could not have been multiply sired. Of the 102 litters that contained ≥ 2 weaned offspring, only 3 (3%) showed unequivocal evidence of multiple paternity.

Electrophoresis and Cuckoldry

If estrous females usually copulate exclusively with the adult male(s) resident in the home coterie, then electrophoretic evidence for cuckoldry should be rare. We tested this prediction in three ways (a, b, and c), as described below.

a) If a female copulates exclusively with the RAM in her home coterie, then the genotypes of resulting offspring should be consistent with the RAM's genotype (i.e., no paternity exclusion). With the

assumption of single paternity per litter, the percentage of litters that could have been sired by the RAM (or one of the RAMs, in multimale coterie) was 84% in 1978, 95% in 1979, 100% in 1980, and 92% in 1981. Of the total of 121 litters for 1978–1981, 112 (93%) were consistent with the RAM's genotype; that is, the minimum estimate of cuckoldry for black-tails is 7%. The RAM was evidently the only possible sire (i.e., all other adult males at the study colony could be excluded from paternity, with the assumption of single paternity per litter) for 3% of 1978 litters, 27% of 1979 litters, 13% of 1980 litters, and 14% of 1981 litters (overall percentage = $16/121 = 13\%$).

b) For each litter each year, every adult male at the study colony was assigned a likelihood of paternity (LOP) value (see above and Foltz and Hoogland 1981). When litters are large and numerous polymorphic loci are available for analysis, then each male should have a unique LOP for each litter. Because black-tail litters are small and there were only four polymorphic loci for analysis, two or more adult males sometimes had the same or similar (nonsignificantly different; see Foltz and Hoogland 1981) LOPs for the same litter. If females usually copulate exclusively with the RAM, then RAMs should consistently have high LOP values for litters weaned in their coterie. For all the litters in each year, Table 3a shows (a) the percentage for which the RAM (or one of the RAMs, in multimale coterie) alone had the

highest LOP, (b) the percentage for which the RAM shared the highest LOP with one or more other adult males, (c) the percentage for which the RAM had a LOP that was not the highest LOP but which did not differ significantly from the highest LOP, and (d) the percentage for which the RAM was excluded from paternity.

c) For 32 of the 33 cases (97%) in which a female copulated with an adult male from outside the home coterie, the extracoterie male lived in a contiguous coterie. Thus, the LOP data in Table 3a are conservative, since they assume that a female may have copulated with *any* adult male in the study colony. For a more rigorous analysis, we compared for each litter the LOP value for the RAM with the LOP values for only those adult males that lived in contiguous coterie (Table 3b); in this analysis, the RAM had or shared the highest LOP for 102 of the 121 litters (84%) in 1978–1981. All the adult males of contiguous coterie could be excluded from paternity for 13% of the 1978 litters, 55% of the 1979 litters, 40% of the 1980 litters, and 46% of the 1981 litters (overall percentage = $45/121 = 37\%$).

Paternity in Multimale Coterie

Although most coterie contain a single RAM, 8 of the 24 coterie at the study colony in 1981 (33%, accounting for 41% of all adult and yearling colony residents) contained two or more RAMs

Table 3. Likelihood of paternity (LOP) of the resident adult male (RAM) (or one of the RAMs, in multimale coterie) when **a** all adult males in the study colony were considered as possible fathers and **b** only adult males of adjacent coterie plus the RAM were considered as possible fathers. In all three cases of multiple paternity (1 litter in 1978, 1 litter in 1979, 1 litter in 1981), there was evidence that the RAM sired at least some of the offspring, so these cases were scored under "RAM alone had highest LOP." "1" indicates the number of litters sampled

a	1978 (N=32 l)	1979 (N=22 l)	1980 (N=30 l)	1981 (N=37 l)	All years (N=121 l)
RAM alone had highest LOP	6%	41%	33%	35%	28%
RAM shared highest LOP	53%	18%	33%	30%	35%
RAM had high LOP that did not differ significantly from highest LOP	25%	36%	33%	27%	30%
RAM was excluded from paternity	16%	5%	0%	8%	7%
b	1978 (N=32 l)	1979 (N=22 l)	1980 (N=30 l)	1981 (N=37 l)	All years (N=121 l)
RAM alone had highest LOP	41%	73%	70%	62%	60%
RAM shared highest LOP	38%	14%	17%	24%	24%
RAM had high LOP that did not differ significantly from highest LOP	6%	9%	13%	5%	8%
RAM was excluded from paternity	16%	5%	0%	8%	7%

(see also King 1955; Hoogland 1981 b). The RAMs in a multimale coterie are commonly, but not always, close genetic relatives (Hoogland 1981 b). Using behavioral and electrophoretic data, we attempted to determine if copulations and the siring of litters within multimale coterie are either shared among the RAMs or monopolized by single RAMs. Regarding copulations, two lines of behavioral data both indicate that copulations are commonly shared among the RAMs of multimale coterie. First, of the 52 estrous females in multimale coterie (Table 1), 17 (33%) copulated with one RAM, 28 (54%) copulated with two different RAMs, and 7 (13%) copulated with one or more RAMs and also with one or more extracoterie adult males. Second, of the 33 RAMs in the 15 multimale coterie for which we had good behavioral data, 32 (97%) copulated with at least one of the adult females in the home coterie. Regarding the siring of litters, while the electrophoretic data showed that sharing of paternity within a litter (i.e., multiple paternity) is probably rare in multimale coterie (see above), they also showed that sharing of paternity between litters is probably common in multimale coterie. Two different RAMs each sired litters in 4 of the 5 multimale coterie in 1978–1981 (80%) that produced two or more litters for which paternity could be unequivocally resolved among the RAMs; this frequency of 80% differs from the frequency of 40% reported by Foltz and Hoogland (1981, p 709) which was determined by different criteria and from litters from 1979 and 1980 only. Sample sizes are small here since multimale coterie do not commonly produce two or more litters (Hoogland 1981 b).

Paternity in Cases Involving Copulation with an Extracoterie Adult Male

Electrophoresis alone indicates that 9 of the 121 litters (7%) were unequivocally sired by an extracoterie adult male (Table 3), but for several of these litters we had no behavioral observations of the mother's estrus. Behavioral observations alone indicate that 33 of 164 females (20%) copulated with at least one extracoterie adult male (Table 1), but many of these females never weaned a litter. For 12 cases (2 in 1978, 2 in 1979, 2 in 1980, and 6 in 1981), we had both behavioral evidence of copulation with an extracoterie adult male and electrophoretic data from the weaned litter that resulted; in all 12 cases, the estrous female also copulated with the RAM (or one of the RAMs, in multimale coterie) in her home coterie. In 4

cases (33%) the genotypes of the RAM and the extracoterie adult male were identical or very similar, so that paternity could not be unequivocally assigned to either male. In 4 cases (33%) the RAM was unequivocally the father, and in 3 cases (25%) the extracoterie adult male was unequivocally the father; in one case (8%) there was multiple paternity.

Paternity vs. Order of Copulations

Among mammalian species in which estrous females frequently copulate with more than one male, the first male to copulate sires most of the offspring in some cases, the last male to copulate sires most of the offspring in other cases, and the siring of offspring seems to be unrelated to the order of copulations in still other cases (Dewsbury and Baumgardner 1981). For the 20 black-tail females that copulated with two or more adult males in known order and then weaned a litter, we attempted to determine if the first male to copulate was more or less likely than later males to be the sire; in 18 of these 20 cases, the estrous female copulated with 2 different adult males, and in 2 cases she copulated with three different adult males. For 8 of the 20 litters (40%) the genotypes of the adult males were too similar to allow exact resolution of paternity. For 6 of the litters (30%) the first male to copulate was the sire, and for 4 of the litters (20%) the second male to copulate was the sire; for 2 litters (10%) there was multiple paternity. In this limited data base, the first male to copulate was not significantly more or less likely than the second male to sire the resulting litter ($P=0.371$, two-tailed χ^2 test, $N=10$).

Variance in Male and Female Reproductive Success

Three related lines of evidence indicate that black-tails are polygynous. (a) Annual copulatory success of adults varied significantly more for males than for females in all three years (1979 through 1981) for which we had adequate sample sizes ($P \leq 0.045$ each year, two-tailed parametric F-test) (Fig. 2a). (b) Variance in the annual number of weaned offspring per adult was significantly greater for males than for females in five of the six years (1976 through 1981) for which we had data ($P \leq 0.012$). (c) Variance in the annual number of yearlings produced per adult (probably the best measure of annual reproductive success) was significantly ($P < 0.001$, $N=3$ years) or almost significantly ($P \leq 0.098$, $N=2$ years) greater for

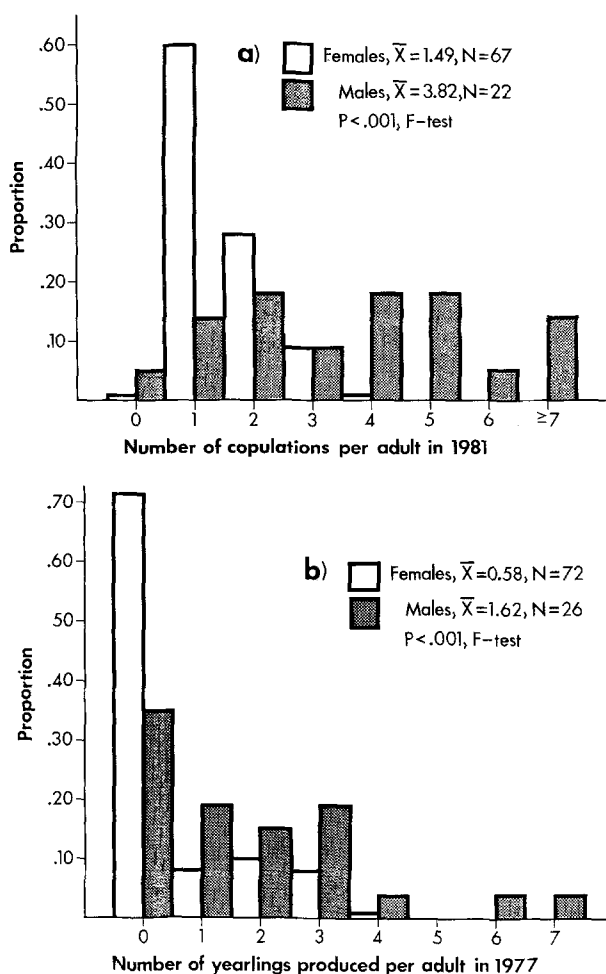


Fig. 2a, b. Intersexual comparison of variance in **a** the number of copulations per adult in 1981 and **b** the number of yearlings produced per adult in 1977. Included here are data from breeding yearlings

males than for females for all five years (1976 through 1980) for which we had data (Fig. 2b). For the intersexual comparison of variances in the number of weaned offspring and the number of yearlings produced per adult, we made two assumptions. First, we assumed that all offspring weaned in a coterie were sired by the RAM(s); as noted above, this assumption was violated at a frequency of at least 7%. Second, in multimale coterie we assumed that paternity was shared equally among all RAMs; this assumption would lead to reduced variance in annual reproductive success among adult males, and was thus conservative.

Data in Fig. 2 compare *annual* reproductive success of males and females. Polygyny, in the strict sense, occurs when variance in *lifetime* reproductive success is greater for males than for females (Clutton-Brock et al. in press). Although

sample sizes are still small because black-tails are long-lived, data to this point on variances in lifetime reproductive success also indicate polygyny. For example, the lifetime number of offspring weaned to this point by a single female at the study colony ranges from 0 to 14, but only 8 females (out of the approximately 70 females for which we have good data on lifetime reproductive success) have weaned ≥ 10 offspring. On the other hand, the lifetime number of weaned offspring sired to this point by a single male at the study colony (again assuming no cuckoldry and equal sharing of paternity among the RAMs of multimale coterie) ranges from 0 to 15, but 19 males (out of the approximately 45 males for which we have good data on lifetime reproductive success) have sired ≥ 10 weaned offspring.

Discussion

Copulations with an extracoterie adult male ($N=33$, Table 1) were easy to detect because they involved either the temporary departure of the estrous female from her home coterie ($N=9$) or the temporary invasion of the estrous female's home coterie by the extracoterie male ($N=24$). All 9 females that left the home coterie for extracoterie copulations returned home on the day of or the day after estrus. Of the 24 adult males that invaded a coterie for copulations, 9 remained there for several hours or for 1–2 days before returning home; the other 15 remained or frequently reinvaded for several days or more, usually until all the females in the invaded coterie had copulated.

Electrophoretic evidence indicates that inseminations by extracoterie adult males were most common in 1978 (16% in 1978 vs. 4% in 1979, 1980, and 1981 taken together; Table 3). Although copulations with an extracoterie adult male are usually easier to detect than are copulations with the RAM (see above), we did not observe an unusually large proportion of extracoterie copulations in 1978 (29% in 1978 vs. 19% in 1979, 1980, and 1981 taken together; $P=0.313$, two-tailed χ^2 test); however, in 1978 we detected fewer estrous cycles ($N=17$) than in any other year. Although we used several methods to reduce the possibility of mislabelling blood samples either in the field or after centrifugation in the laboratory, errors in 1978 may have been more common for two reasons: (a) we processed more samples in 1978 ($N=242$) than in any other year and (b) we regularly put samples from two different individuals in opposite sides of the same single centrifuge at the same time in 1978, whereas in later years we used

two centrifuges and put samples from only one individual in each centrifuge at a time.

In a polygynous mating system, the variance in reproductive success is greater for males than for females, and more females than males contribute gametes to the next generation (Trivers 1972; Alexander 1974; Borgia 1979; Howard 1981; Clutton-Brock et al. in press). Although polygyny is commonly inferred from social organization, it has rarely been verified in natural populations. Behavioral observations of estrous females and electrophoresis of blood samples both indicate that black-tails are polygynous. When compared to similar studies (e.g., McCracken and Bradbury 1977, 1981, Schwartz and Armitage 1980, 1981; Hanken and Sherman 1981), the greatest strengths of our study are the large sample sizes for both behavioral observations ($N=160$ estrous females) and electrophoresis ($N=121$ litters with mothers and all possible fathers). These strengths are offset by the small number of polymorphic loci available for analysis, small litter sizes, and the frequent electrophoretic similarity among the closely related adult males within multimale coterie.

The combination of behavior and electrophoresis is available for only three species of harem-polygynous mammals: black-tailed prairie dogs, yellow-bellied marmots, and greater spear-nose bats. The minimal estimate of cuckoldry is 7% for black-tails ($N=121$ litters; Table 3), 0% for yellow-bellied marmots ($N=26$ litters; Schwartz and Armitage 1980, p. 665), and 12% for greater spear-nose bats ($N=104$ litters, McCracken and Bradbury 1981, Table 5). Some of the difference in cuckoldry between yellow-bellied marmots and black-tails might result from the small number of marmot litters that were sampled, but most of the difference probably results because yellow-bellied marmot copulations occur when the ground is snow-covered and when male movements between harems (which are usually isolated or in small groups) are therefore rare (Schwartz and Armitage 1980). Cuckoldry is probably more common in greater spear-nose bats than in black-tails for two reasons. First, greater spear-nose bat harems are larger than are black-tail harems, and monopolization of estrous females by harem males is thus presumably more difficult for the bats than for the prairie dogs; in both cases, females breed synchronously (McCracken and Bradbury 1981; Hoogland 1981a). Second, the turnover of resident adult males between the stages of mating and weaning is evidently more common in greater spear-nose bats than in black-tails (McCracken and Bradbury 1981; Hoogland 1981b); since juveniles were sampled just before (greater spear-nose bats) or just

after (black-tails) weaning, such turnovers would lead to cases of apparent cuckoldry.

For Belding's ground squirrels, Hanken and Sherman (1981) showed by electrophoresis that between 55% and 78% of 38 litters examined were multiply sired. By contrast, we found unequivocal evidence of multiple siring in only 3 of the 102 litters with ≥ 2 offspring (3%). The obvious reason for this interspecific difference is that estrous black-tail females usually copulate with a single adult male ($101/160=63\%$, Table 1) whereas estrous Belding's ground squirrel females usually copulate with two or more adult males ($16/19=84\%$, Hanken and Sherman 1981, Fig. 1). However, if copulating with ≥ 2 adult males at a frequency of 84% in Belding's ground squirrels leads to multiple paternity at a frequency of 55%–78%, then why in black-tails does copulating with ≥ 2 adult males at a frequency of 37% lead to multiple paternity at a frequency of only 3%? At least five factors may be involved. (a) Because Belding's ground squirrel litters are larger than are black-tail litters (4.87 [Sherman 1981, p. 252] vs. 2.90), and because they had six (vs. our four) polymorphic loci for electrophoretic analysis, Hanken and Sherman (1981) were probably better able to detect cases of multiple paternity. (b) Detecting cases of multiple paternity is probably easier when multiply copulating females usually copulate with several different adult males than when multiply copulating females usually copulate with only two different adult males. Multiply copulating Belding's ground squirrel females copulated with a mean \pm SD of 3.1 ± 1.0 different males ($N=16$ females, range = 2–5, Hanken and Sherman 1981, Fig. 1), but multiply copulating black-tail females copulated with a mean of only 2.3 ± 0.5 males ($N=59$ females, range = 2–4; Fig. 1a). (c) Whereas the different adult males with which an estrous Belding's ground squirrel female copulates are almost never close genetic relatives (Sherman 1981), the different adult males in a multimale coterie with which an estrous black-tail female copulates (Table 2) are commonly close genetic relatives and thus electrophoretically similar (Hoogland 1981b). (d) Belding's ground squirrels copulate above-ground, and Hanken and Sherman (1981) could thus determine exactly how many different adult males copulated with each estrous female. Black-tails, on the other hand, copulate underground, and we could never be certain that each underground consortship involved a copulation; that is, the observed frequency of multiply copulating black-tail females (Fig. 1a) may be inflated. (e) Sperm competition is probably more intense and multiple paternity is probably more common

when different adult males copulate with the same estrous female in rapid succession than when copulations are separated by long periods of time (Parker 1970; Voss 1979; Dewsbury and Baumgardner 1981). In Belding's ground squirrels, copulations by the same estrous female with different adult males usually occur in rapid succession (Sherman, pers. comm). In black-tails, by contrast, an estrous female's underground consortships with different adult males are frequently separated by > 60 min.

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References

- Alexander RD (1974) The evolution of social behavior. *Annu Rev Ecol Syst* 5:325-383
- Alexander RD, Hoogland JL, Howard RD, Noonan KM, Sherman PW (1979) Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. In: Chagnon NA, Irons W (eds) *Evolutionary biology and human social behavior*. Duxbury, North Scituate, Massachusetts, pp 402-435
- Birdsall DA, Nash D (1973) Occurrence of successful multiple insemination of females in natural populations of deer mice (*Peromyscus maniculatus*). *Evolution* 27:106-110
- Borgia G (1979) Sexual selection and the evolution of mating systems. In: Blum MF, Blum N (eds) *Sexual selection and reproductive competition in insects*. Academic Press, New York London, pp 19-80
- Clutton-Brock TH, Harvey PH (1977a) Primate ecology and social organization. *J Zool* 183:1-39
- Clutton-Brock TH, Harvey PH (1977b) Sexual dimorphism, socionomic sex ratio, and body weight in primates. *Nature* 269:797-800
- Clutton-Brock TH, Guinness FE, Albon SD (in press) Red deer: the ecology of the two sexes. Chicago University Press, Chicago
- Dewsbury DA, Baumgardner DJ (1981) Studies of sperm competition in two species of muroid rodents. *Behav Ecol Sociobiol* 9:121-133
- Foltz DW, Hoogland JL (1981) Analysis of the mating system in the black-tailed prairie dog (*Cynomys ludovicianus*) by likelihood of paternity. *J Mammal* 62:706-712
- Foltz DW, Hoogland JL (in press) Genetic evidence of outbreeding in the black-tailed prairie dog (*Cynomys ludovicianus*). *Evolution*
- Hanken J, Sherman PW (1981) Multiple paternity in Belding's ground squirrel litters. *Science* 212:351-353
- Hoogland JL (1979a) The effect of colony size on individual alertness of prairie dogs (Sciuridae: *Cynomys* spp.). *Anim Behav* 27:394-407
- Hoogland JL (1979b) Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae: *Cynomys* spp.) coloniality. *Behaviour* 69:1-35
- Hoogland JL (1981a) The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology* 62:252-272
- Hoogland JL (1981b) Nepotism and cooperative breeding in the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). In: Alexander RD, Tinkle DW (eds) *Natural selection and social behavior*. Chiron, New York, pp 283-310
- Hoogland JL (1982) Prairie dogs avoid extreme inbreeding. *Science* 215:1639-1641
- Hoogland JL (in press) Nepotism and alarm calling in the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). *Anim Behav*
- Howard RD (1981) Male age-size distribution and male mating success in bullfrogs. In: Alexander RD, Tinkle DW (eds) *Natural selection and social behavior*. Chiron, New York, pp 61-77
- Jarman PJ (1974) The social organization of antelope in relation to their ecology. *Behaviour* 48:215-267
- Johnson J (1977) The use of gene frequencies in estimating the mean number of mates in a multiple-mate and stored-sperm system of mating. *Theor Appl Genet* 49:181-185
- King JA (1955) Social behavior, social organization, and population dynamics in black-tailed prairie dog town in the Black Hills of South Dakota. *Contrib Lab Vertebr Biol Univ Mich* 67:1-123
- McCracken GF, Bradbury JW (1977) Paternity and genetic heterogeneity in the polygynous bat, *Phyllostomus hastatus*. *Science* 198:303-306
- McCracken GF, Bradbury JW (1981) Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. *Behav Ecol Sociobiol* 8:11-34
- Merritt RB, Wu BJ (1975) On the quantification of promiscuity (or "*Promyscus*" *maniculatus*). *Evolution* 29:575-578
- Parker GA (1970) Sperm competition and its evolutionary consequences in the insects. *Biol Rev* 45:525-567
- Schwartz OA, Armitage KB (1980) Genetic variation in social mammals: the marmot model. *Science* 207:665-667
- Schwartz OA, Armitage KB (1981) Social substructure and dispersion of genetic variation in the yellow-bellied marmot (*Marmota flaviventris*). In: Smith MH, Joule J (eds) *Mammalian population genetics*. University of Georgia Press, Athens, pp 139-159
- Selander RK, Smith MH, Yang SY, Johnson WE, Gentry JB (1971) Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). *Stud Genet Univ Texas* 6:49-90
- Sherman PW (1981) Kinship, demography, and Belding's ground squirrel nepotism. *Behav Ecol Sociobiol* 8:251-259
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell BH (ed) *Sexual selection and the descent of man*. Aldine, Chicago, pp 136-179
- Voss R (1979) Male accessory glands and the evolution of copulatory plugs in rodents. *Occas Pap Mus Zool Univ Mich* 689:1-27
- Wiener AS (1968) Chances of proving nonpaternity with a system determined by triple allelic codominant genes. *Am J Hum Genet* 20:279-282
- Wilson J (1981) Estimating the degree of polyandry in natural populations. *Evolution* 35:664-673