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Why do female prairie dogs copulate with more than one male?—Insights from long-term research

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A female usually obtains sufficient sperm to fertilize all her eggs from a single insemination, and mating can be costly. Yet, paradoxically, polyandry (i.e., copulation with 2 or more males) is common among organisms of all types, from amoebae through humans. Research that spanned 35 years shows that females of 3 species of prairie dogs benefited from polyandry by rearing more yearlings (a component of fitness that is my best estimate of female reproductive success); females of a 4th species (the black-tailed prairie dog [*Cynomys ludovicianus*]) evidently did not benefit from polyandry. Reasons for the higher production of yearlings by polyandrous females differed among species. For Gunnison's prairie dogs (*C. gunnisoni*), 3 other components of fitness contributed to the higher production of yearlings: a higher probability of conception and parturition, larger litter size at weaning, and a higher survivorship of offspring during the first 9 months after weaning. The 2nd and 3rd components applied to Utah prairie dogs (*C. parvidens*), but only the 1st component applied to white-tailed prairie dogs (*C. leucurus*). Female Gunnison's and white-tailed prairie dogs paid a cost from copulating with more than 1 male, because they were less likely to survive until the next mating season.

Key words: *Cynomys*, genetic diversity, polyandry, prairie dog, reproductive success, survivorship

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Males usually increase annual reproductive success (ARS) by copulating with multiple females (Darwin 1871; Trivers 1972). The scenario is different for females, however, because a female almost always can obtain enough sperm to fertilize all her eggs from a single insemination (Birkhead 2000; Jennions and Petrie 2000; Simmons 2005; Parker and Birkhead 2013). Moreover, copulation involves significant costs such as increased susceptibility to predation and increased exposure to diseases and parasites (Daly 1978; Johnson and Brockmann 2010; Madsen 2011; Ashby and Gupta 2013). Why, then, do females of almost every organism that has been carefully studied—from plants and amoebae through humans and other primates (Smuts et al. 1987; Kappeler and van Schaik 2004; Ishida et al. 2005; Pannell and Labouche 2013)—commonly copulate with ≥ 2 males? The numerous hypotheses to explain polyandry (i.e., copulation with ≥ 2 males) can be subdivided into 2 groups (Ivy and Sakaluk 2005; Solomon and Keane 2007; Johnson and Brockmann 2010; Pizzari and Wedell 2013; Table 1): females acquiesce to polyandry, but do not gain any clear benefits, and females benefit from polyandry. Regarding the 1st of these, males of many species attempt to copulate with unwilling females that have already copulated (Thornhill and Alcock 1983; Byrne and Roberts 2004; Arnqvist and Rowe

2005). In addition to the costs mentioned above, other possible costs to the female from these attempts include lower fecundity and physical injury that can be fatal (McKinney et al. 1983; Reale et al. 1996; den Hollander and Gwynne 2009). Because the costs of trying to avoid 2nd and 3rd suitors can be higher than the costs of additional copulations, females sometimes yield to polyandry. Behavioral ecologists sometimes call this pattern “convenience polyandry” (Thornhill and Alcock 1983; Thiel and Hinojosa 2003; Johnson and Brockmann 2010).

If polyandry delivers clear payoffs to females, then a female can profit in 2 ways (Table 1). First, benefits can be direct payoffs to the female herself, such as increased probability of obtaining fresher, younger sperm; increased sustenance from courtship feeding; higher probability of conception; lower probability of losing offspring to infanticide; or more paternal care for offspring (Thornhill and Alcock 1983; Ridley 1988; Davies et al. 1992; Jennions and Petrie 2000; Table 1). Second, benefits can be indirect and lead to offspring of higher genetic quality, via mechanisms such as promotion of sperm



TABLE 1.—Mechanisms by which polyandry might enhance female annual reproductive success (ARS).

Mechanism by which polyandry enhances female ARS	Relevance of this mechanism to prairie dogs
I. Females acquiesce to polyandry, but do not gain any clear benefits (“convenience polyandry”—Thornhill and Alcock 1983; Byrne and Roberts 2004; Arnqvist and Rowe 2005)	Little relevance: Without acquiescing to matings with 2nd and 3rd males, an estrous female easily can avoid harassment from courting males by simply remaining underground after copulation with the 1st male. Or, after appearing aboveground after the 1st copulation, the estrous female can submerge alone into 1 of the 20+ burrow systems within her home territory and stay there for the remainder of the day. Some females of all 4 species did use one or the other of these strategies, and thereby remained monandrous.
II. Females obtain direct benefits	
Higher probability of fertilization/conception (Sakaluk and Cade 1980; Torok et al. 2003; Uller and Olsson 2005)	Strong relevance: Polyandrous females were significantly more likely than monandrous females to conceive for Gunnison’s and white-tailed prairie dogs.
Younger, fresher sperm for fertilization (Oring et al. 1992; Siva-Jothy 2000; Reinhardt 2007)	Little relevance: Fertilization of ova occurs within hours after mating for all 4 species, and females cannot store sperm from the current or past years (Stockard 1929; Anthony and Foreman 1951).
Increased sustenance from spermatophores or courtship feeding (Thornhill and Alcock 1983; Jennions and Petrie 2000)	Little relevance: Males neither produce spermatophores nor provide food or other resources during courtship for any of the 4 species (Stockard 1929; Bakko and Brown 1967; Hoogland 1995, 1998a).
Reduced probability of losing offspring to infanticide by sexually mature males (Hrdy 1977; Perrigo et al. 1990; Wolff and Macdonald 2004)	Little relevance: Infanticide by sexually mature males is absent or rare in 2 of the 4 prairie dog species. In the other 2 species (black-tailed and Utah), infanticide by males usually involves a male with which the mother had no good opportunity to copulate. Specifically, the infanticidal male is usually either an immigrant male from another colony or a male from a distant territory within the home colony (Hoogland 1995, 2007).
Increased paternal care, if male helps to rear offspring of all females with which he copulated (Davies et al. 1992; Hartley et al. 1995; Soltis and McElreath 2001)	Little relevance: Paternal care is minimal, and potential fathers only rarely interact with juveniles in the home or adjacent territories. Further, an invading male that copulates with a female almost never enters her territory again after the mating season.
III. Females obtain indirect benefits	
Better opportunity to obtain sperm of high genetic quality (“trading up”—Kraaijeveld-Smit et al. 2002; Pitcher et al. 2003; Klemme et al. 2006)	No information, because investigation requires assignment of paternity.
Increased survivorship of offspring with higher genetic diversity within litters via multiple paternity (“bet-hedging”—Watson 1991; Brown 1997; Yasui 2001; Fox and Rauter 2003)	No information, because investigation requires assignment of paternity.
Lower probability of producing inbred offspring (Stockley et al. 1993; Tregenza and Wedell 2002; Firman and Simmons 2008a)	No information, because investigation requires assignment of paternity.
Better opportunity to obtain sperm of high genetic compatibility (Zeh and Zeh 1997; Kraaijeveld-Smit et al. 2002; Mays and Hill 2004; Pryke et al. 2010)	No information, because investigation requires assignment of paternity.
Promotion of sperm competition (Parker 1970; Birkhead and Møller 1998; Simmons 2005; Firman and Simmons 2008b)	No information, because investigation requires assignment of paternity.

competition (Parker 1970; Kempenaers et al. 1992; Wedell and Tregenza 1999; Byrne and Rice 2005; Firman and Simmons 2008a, 2008b, 2012); higher genetic compatibility with the male that sires offspring (Brown 1997; Zeh and Zeh 1997; Newcomer et al. 1999); more genetic diversity among offspring (Yasui 2001; Foerster et al. 2003; Hopper and Rosenheim 2003); or lower probability of producing inbred offspring (Brooker et al. 1990; Stockley et al. 1993; Tregenza and Wedell 2002; Firman and Simmons 2008a; Table 1). Many of these indirect benefits involve cryptic female choice of certain types of sperm over other types (Eberhard 1996; Solomon and Keane 2007; Pryke et al. 2010; Firman and Simmons 2012).

Multiple paternity occurs when ≥ 2 males sire offspring within the same litter (Hanken and Sherman 1981; Foltz and Schwagmeyer 1989; Neff and Pitcher 2002; Van Horn et al. 2008). Many studies have compared ARS of females that

produce singly-sired litters with ARS of females that produce multiply-sired litters for animals living under either natural conditions or a combination of natural and laboratory conditions (e.g., Kawata 1988; Birkhead and Møller 1992; Bartmann and Gerlach 2001; Arnqvist and Rowe 2005; Wright et al. 2013). A smaller number of studies, most of them under laboratory conditions, have compared female ARS versus the female’s number of sexual partners (Evans and Magurran 2000; Hohoff et al. 2003; Gowaty et al. 2010; Firman and Simmons 2012). Both types of studies are important, but differ for the following key reason: multiple paternity requires polyandry, but single paternity can result from either monandry or polyandry; further, many cases of polyandry lead to multiple paternity that involves siring by only some of the males that actually copulated with the mother (Hanken and Sherman 1981; Bretman and Tregenza 2005; Gowaty 2012). Few studies combine information from the same females on both the

number of sexual partners per female under natural conditions, and the female ARS under natural conditions (Kempnaers et al. 1992; Madsen et al. 1992; Olsson and Madsen 2001; Johnson and Brockmann 2010; see also Fisher et al. [2006], who combined laboratory research on controlled matings with juvenile survivorship under natural conditions). Over the last 35 years I have collected information for both the number of sexual partners per female and the female ARS for the following 4 species of prairie dogs that inhabit grassland ecosystems of western United States: black-tailed prairie dogs (*Cynomys ludovicianus*, 11 years), Gunnison's prairie dogs (*C. gunnisoni*, 7 years), Utah prairie dogs (*C. parvidens*, 10 years), and white-tailed prairie dogs (*C. leucurus*, 7 years [Hoogland 1981, 1985, 1995, 2001, 2007]). All my results come from wild prairie dogs living under natural conditions within national parks or national wildlife refuges.

Prairie dogs of all 4 species are diurnal, colonial, herbivorous rodents of the squirrel family (Sciuridae), and individuals forage aboveground from dawn until dusk (King 1955; Clark 1977; Rayor 1988; Hoogland 1995, 2003a). Prairie dogs are excellent animals for a study of the costs and benefits of polyandry for 3 reasons (Hoogland 1995, 1998a, 2007). First, each female is sexually receptive for only 5–6 h on a single day each year. By contrast, females of many species are sexually receptive for an extended period of time over several days or weeks, so that careful documentation of all copulations is difficult (Dewsbury 1975; Beach 1976; Smuts et al. 1987; Westneat et al. 1990; Birkhead and Møller 1992, 1998). Second, both males and females remain in small territories (< 1 ha) where they are consistently visible throughout the day during the mating season. By contrast, females of many species roam over long distances during the mating season, so that nonstop watching of receptive females for possible copulations is challenging (Berger and Cunningham 1991; Birkhead and Møller 1992, 1998; Byers 1997; Westneat et al. 1990). Third, females rear their offspring in isolated burrows, so that researchers therefore can obtain accurate estimates of a female's number of weaned offspring by livetrapping entire litters at nursery burrows when offspring 1st appear aboveground.

Because my research with prairie dog mating systems has spanned many years, I have evaluated possible benefits of polyandry in previous publications (Hoogland 1995, 1998a, 1998b, 2007). Novel analyses and discussions for the present report include new data from white-tailed prairie dogs, and more than 50% new data from Utah prairie dogs; documentation of enhancement of a new, 4th component of fitness via polyandry (higher survivorship of juveniles in the first 9 months after weaning); documentation of a cost of polyandry (lower female survivorship); and consideration of the relevance of the operational sex ratio (OSR) and genetic diversity to explain interspecific differences in the frequency of polyandry.

MATERIALS AND METHODS

Study animals and methods.—For all 4 species that I studied, adult (≥ 1 year old) prairie dogs are about 30 cm long

(excluding the tail), and weigh about 600 g just before the mating season in late winter or early spring (Hoogland 2003b). Colonies contain territorial, contiguous family groups, which typically include 1 or 2 sexually mature adult males, 3 or 4 sexually mature adult females, and 1 or 2 sexually immature yearling adult males (King 1955; Rayor 1988; Hoogland 1995, 2001, 2003a, 2007). Female Gunnison's, Utah, and white-tailed prairie dogs usually copulate for the 1st time as 1-year-olds in the spring of their 1st year, but males frequently do not copulate for the 1st time until they are 2 years old; both male and female black-tailed prairie dogs usually do not copulate for the 1st time until they are 2 years old. Weaned juveniles 1st appear aboveground from their nursery burrows in late May or early June. Terrestrial predators include American badgers (*Taxidea taxus*), black-footed ferrets (*Mustela nigripes*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*). Avian predators include golden eagles (*Aquila chrysaetos*), northern goshawks (*Accipiter gentilis*), and prairie falcons (*Falco mexicanus*).

To capture prairie dogs, I used Tomahawk live traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin); for permanent identification, I used numbered National fingerling ear tags (National Band and Tag Company, Newport, Kentucky). Every year I marked all residents of my study colony with unique patterns of black Nyanzol dye (Greenville Colorants, Clifton, New Jersey), and observed them with binoculars from 2-m towers (Hoogland 1995). I recorded copulations and 4 components of fitness (Shaw et al. 2008) for female black-tailed prairie dogs at Wind Cave National Park, South Dakota, from February through June of 1978 through 1988; for Gunnison's prairie dogs at Petrified Forest National Park, Arizona, from March through June of 1989 through 1995; for Utah prairie dogs at Bryce Canyon National Park, Utah, from March through June of 1996 through 2005; and for white-tailed prairie dogs at the Arapaho National Wildlife Refuge, Colorado, from March through June of 2006 through 2012. Each year, 2–5 students assisted with all aspects of my research.

Copulations for all 4 species of prairie dogs usually occurred underground, and therefore were not directly observable (Hoogland 1995, 1998a, 2007). I inferred a copulation when ≥ 3 of the following 5 criteria were satisfied. 1) A sexually mature male sniffed or licked a sexually mature female's vulva, and then 2) followed her into a burrow for ≥ 5 min, and usually for ≥ 30 min; 3) with the estrous female nearby (≤ 2 m away) the male gave a unique vocalization within 2 min before or after the underground consortship; 4) the male or the female licked its genitals within 5 min after emerging from the underground consortship; and 5) the female remained aboveground much later than usual, typically 60–90 min after nonestrous females living in her territory had submerged into burrows for the night. Females that copulated aboveground consistently satisfied ≥ 3 of these same criteria (except criterion 2). Evidence that inferred underground copulations involved insemination was 3-fold (Hoogland 1995, 1998a). First, the date of putative copulation(s) varied directly and

strongly with the date of parturition ($P < 0.001$ for all 4 species, Spearman correlation test). For black-tailed prairie dogs, $> 95\%$ of parturitions occurred 34, 35, or 36 days after the putative date of copulation(s); for the other 3 species, $> 95\%$ of parturitions occurred 28, 29, or 30 days after the putative date of copulation(s). Second, most females had a sealed vulva 1 day before the date of putative copulation(s), but the vulva was invariably open on the 1st day after copulation(s) ($P < 0.001$ for all 4 species, 2×2 chi-square test). For reasons that remain unclear, a few females ($< 5\%$ for each species) had an open vulva before copulation (Hoogland 1995, 1998a). Third, genetic studies for all 4 species have shown that multiple paternity was limited almost exclusively to cases when behavioral observations indicated that the female had copulated with ≥ 2 males (Hoogland 1995, 2007, this study; Haynie et al. 2003). Further, other behavioral ecologists have used these same criteria to document underground copulations of 3 species of ground squirrels (Sherman 1989; Lacey et al. 1997; Raveh et al. 2010).

By observing from dawn to dusk for the entire reproductive season of each year (i.e., ≥ 1 week before the 1st copulation in February or March through capture of the last weaned juvenile in June or July for 1978 through 2012, involving $> 150,000$ person-hours of watching), research assistants and I documented 2,504 copulations by 1,426 females.

I documented parturition from either of the following: a sudden, drastic reduction in the amount of time spent aboveground during daylight hours, or a sudden, precipitous loss of body mass (Hoogland 1995, 1998a, 2003a). Not every female that copulated gave birth. I found no reliable way to distinguish between failure to conceive versus abortion of all embryos at some point after conception (Anthony and Foreman 1951; Knowles 1987). For this reason, I frequently refer to the presence or absence of "conception and parturition" in this report.

For all 4 species, male and female juveniles usually remained in the natal territory for ≥ 9 months after weaning (approximately 10.5 months after birth), or dispersed to nearby territories where I could easily observe them (Hoogland 1995, 1999, 2013). My best estimate of female ARS, and probably the most important component of fitness as well, was therefore the number of offspring that survived until the following spring, when they were about 10.5 months old (yearlings) and before long-distance dispersal might have occurred. Three other components of fitness (Shaw et al. 2008) contributed to a female's ultimate ARS: presence or absence of conception and parturition, litter size at weaning, and survivorship or non-survivorship of juveniles for at least 9 months after weaning.

The OSR is the ratio of the number of sexually mature females ready to copulate to the number of sexually mature males ready to copulate (Emlen and Oring 1977; Clutton-Brock 2007). OSR affects both male-male competition and female choice of mates, and can influence the frequency of polyandry (Emlen and Oring 1977; Simmons 2005). Just before the mating season, I found no way to determine whether a female was sexually mature. I inferred sexual maturity for a

female if I observed her copulate, or if she showed evidence of an undetected copulation (e.g., aggressiveness associated with pregnancy, or long, turgid nipples diagnostic of lactation—see Hoogland 1995, 1998a). I scored a male as sexually mature if he had a pigmented scrotum with descended testes (Hoogland 1995, 1998a), or if I documented a copulation by him.

I used logistic regression to investigate the effect of the female's number of sexual partners on the following variables that had only 2 possible values: conception and parturition, the survivorship of a juvenile for ≥ 9 months after weaning, and the survivorship of the female until the next mating season. I used the Spearman rank correlation test to examine the effect of a female's number of sexual partners on the following variables that had several possible values that did not have a normal distribution: litter size at weaning, and the number of offspring that survived for ≥ 9 months after weaning. For all pairwise comparisons, I used either the 2×2 chi-square test ($df = 1$) or the Mann-Whitney U -test. All P -values are from 2-tailed statistical tests. I considered data on polyandry and components of fitness from the same female in different years to be independent. All figures show the mean ± 1 SE; the number above each SE line indicates the number of females for which I recorded all sexual partners.

My research was approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Maryland Center for Environmental Science, and complied with current guidelines of the American Society of Mammalogists (Sikes et al. 2011).

RESULTS

Females of all 4 species commonly copulated with ≥ 2 males (Fig. 1). The frequency of polyandry varied significantly among the 4 species ($H = 263$, $P < 0.001$, Kruskal-Wallis analysis of variance). Females of 2 species (black-tailed and white-tailed) were mostly monandrous, and females of the other 2 species (Gunnison's and Utah) were mostly polyandrous ($U = 139,588$, $P < 0.001$, Mann-Whitney U -test that compared the number of sexual partners for black-tailed and white-tailed prairie dogs considered together versus Gunnison's and Utah prairie dogs considered together). Most polyandrous females copulated with 2 or 3 males, but some copulated with as many as 6 males (Fig. 1). Consistent with these high frequencies of polyandry, multiple paternity within litters was common for all 4 species (Hoogland 1995, 2007; Haynie et al. 2003).

Polyandry occurred when the home territory contained ≥ 2 sexually mature males and the female copulated with ≥ 2 of those males, when the once-mated estrous female visited a male in an adjacent territory and copulated with him, or when a male from an adjacent territory invaded a once-mated estrous female's home territory and she copulated with him (Hoogland 1995).

The number of yearlings, the most reliable component of fitness that I could measure, was higher for polyandrous females than for monandrous females for Gunnison's, Utah,

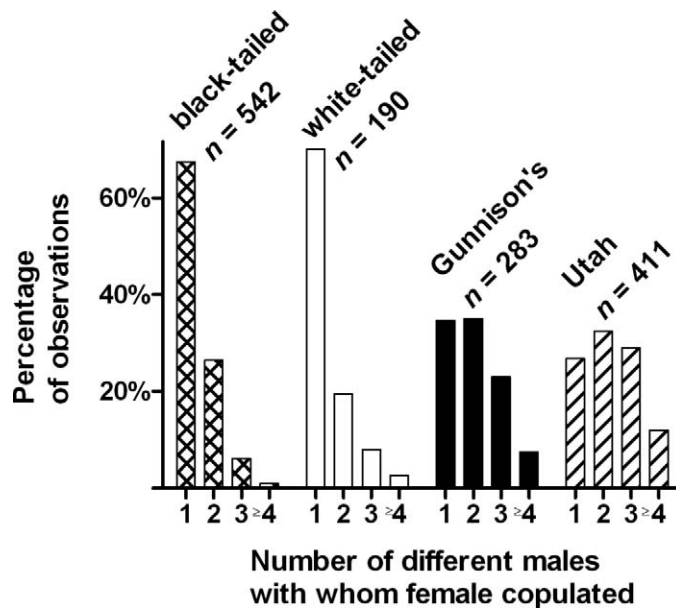


FIG. 1.—Frequency of polyandry among 4 species of prairie dogs.

and white-tailed prairie dogs (Fig. 2), but not for female black-tailed prairie dogs. The larger number of yearlings reared by polyandrous versus monandrous females (Fig. 2) was the cumulative effect of enhancements of the following 3 other components of fitness that I could measure (Table 2): presence or absence of conception and parturition, litter size at weaning, and survivorship or nonsurvivorship of offspring for ≥ 9 months after weaning. For Gunnison's prairie dogs, enhancements occurred for all 3 of these other components of fitness: polyandrous females were more likely to conceive and give birth, they weaned larger litters, and they produced offspring that were more likely to survive for ≥ 9 months after weaning (Figs. 3–5). Similar enhancements occurred for the components litter size and offspring survivorship for polyandrous Utah prairie dogs (Figs. 4 and 5), but only for the component presence or absence of conception and parturition for polyandrous white-tailed prairie dogs (Fig. 3). Enhancements did not occur for any component of fitness for polyandrous black-tailed prairie dogs.

For all 4 species, middle-aged (2–5 years old), heavy females were more productive than younger and older females of lower body mass for all 4 components of fitness, and most of these differences were significant (Hoogland 1995, 1998b, 2003b, 2007). Specifically, middle-aged, heavy females were more likely to conceive and give birth, they weaned larger litters, they produced offspring that more likely to survive for ≥ 9 months after weaning, and they produced more yearlings. Sometimes the effects of female age and female body mass overwhelmed the effects of a female's number of sexual partners, so that documenting enhancements on fitness components from polyandry per se was difficult. Multiple regression or multiple logistic regression nonetheless showed that 6 of the 9 significant effects from polyandry depicted in Figs. 2–5 were independent of effects from female age and

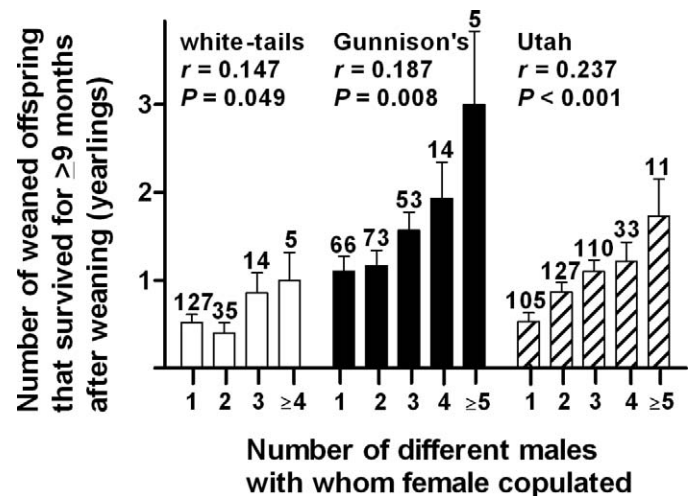


FIG. 2.—Female Gunnison's, Utah, and white-tailed prairie dogs produced more yearlings when they were polyandrous. The r -values and P -values are from the Spearman correlation test.

female body mass ($P \leq 0.045$ all 6; see also Table 2). These 6 multiple regressions were significant even though the sample sizes were smaller than for the regressions without consideration of female body mass and female age. I sometimes did not have data for 1 or both of these latter 2 variables; in the 1st and later years of research at a new study colony, for example, I did not know the exact age for any of the original adult residents.

The mean OSR for the 4 species ranged from 2.18 to 3.52 sexually mature females per sexually mature male (Table 2). The percentage of females that copulated with ≥ 2 males varied inversely and significantly with OSR for Gunnison's prairie dogs ($P = 0.037$, $r = -0.901$, Spearman correlation test, $n = 7$ years), but did not vary significantly with OSR for any of the other 3 species ($P > 0.050$, $r < |0.643|$, Spearman correlation test, $n \geq 7$ years). Across species, the frequency of polyandry did not vary predictably with OSR. Utah prairie dogs had the highest frequency of polyandry (73%), for example, but also had the lowest OSR (2.18; Table 2). By contrast, Gunnison's prairie dogs had the 2nd-highest frequency of polyandry (65%), but also had the highest OSR (3.52; Table 2).

Some females remained underground after copulating with 1 male, and thereby presumably ensured monandry. The majority of females ($>90\%$ for all 4 species), however, reappeared aboveground after the 1st copulation. Further, estrous females usually remained aboveground until most of the other prairie dogs in the study colony had submerged for the night, except for periods when they submerged for copulations with 2nd- and later-mating males. While aboveground after the 1st copulation, most females clearly searched for additional sexually mature males with which they had not yet copulated.

Polyandrous females were significantly less likely than monandrous females to survive until the next mating season for Gunnison's and white-tailed prairie dogs (Fig. 6). Part of this lower survivorship of polyandrous females might have resulted from increased susceptibility to predation while searching for

TABLE 2.—Summary of costs (Cs) of polyandry and enhancements of fitness components (FCs) from polyandry for 4 species of prairie dogs. The t -values are from logistic regression; r -values are from the Spearman rank correlation test; and chi-square (χ^2) values ($d.f. = 1$) are from the 2×2 chi-square test. A “yes” means that the species showed the predicted trend for the benefit or cost under investigation, with $P < 0.050$.

	Black-tailed	White-tailed	Gunnison's	Utah
Frequency of polyandry (%)	33	30	65	73
Mean \pm SD estimate of operational sex ratio	2.38 \pm 0.56	2.92 \pm 1.22	3.52 \pm 1.28	2.18 \pm 0.40
No. years observed	11	7	7	10
Visibility within the home territory	High	Low	Low	Low
Reproductive synchrony of females of the same territory	Low	High	High	High
FC 1: Higher probability of conception and parturition for polyandrous versus monandrous females	No $t = 0.863$ $P = 0.388$ $n = 316$	Yes* $t = 2.33$ $P = 0.020$ $n = 189$	Yes $t = 2.05$ $P = 0.040$ $n = 269$	No $t = 1.17$ $P = 0.241$ $n = 409$
FC-2: Larger litter size at weaning for polyandrous versus monandrous females that gave birth	No $r = 0.069$ $P = 0.250$ $n = 247$	No $r = 0.065$ $P = 0.402$ $n = 188$	Yes $r = 0.152$ $P = 0.036$ $n = 191$	Yes* $r = 0.177$ $P < 0.001$ $n = 343$
FC-3: Higher survivorship of offspring for ≥ 9 months after weaning, for polyandrous versus monandrous females that weaned ≥ 1 offspring	No $r = -0.004$ $P = 0.832$ $n = 252$	No $r = 0.082$ $P = 0.435$ $n = 97$	Yes* $t = 0.252$ $P = 0.012$ $n = 642$	Yes* $t = 2.79$ $P = 0.005$ $n = 884$
FC-4: More offspring that survived for ≥ 9 months after weaning (yearlings), which results from cumulative effects of FC 1, FC 2, and FC 3 for polyandrous versus monandrous females	No $r = 0.019$ $P = 0.660$ $n = 498$	Yes $r = 0.147$ $P = 0.049$ $n = 181$	Yes* $r = 0.187$ $P = 0.008$ $n = 211$	Yes* $r = 0.237$ $P < 0.001$ $n = 388$
C1: Lower survivorship of polyandrous versus monandrous females	No $r = 0.006$ $P = 0.898$ $n = 542$	Yes $\chi^2 = 4.20$ $P = 0.040$ $n = 155$	Yes* $t = -2.77$ $P = 0.006$ $n = 174$	No $t = 0.957$ $P = 0.338$ $n = 381$

* For these P -values, a multiple regression or a multiple logistic regression showed that the significant effect of a female's number of sexual partners was independent of effects from female age and female body mass ($P \leq 0.045$ for all).

additional males with which to copulate (Madsen 2011) or while dealing with consequences of polyandry (e.g., higher probability of conception and parturition, or larger litter size). To investigate this possibility, I compared the number of predations on monandrous versus polyandrous females for the

3 species (black-tailed, Utah, and white-tailed prairie dogs) for which research assistants and I observed ≥ 9 predations of females whose copulations we documented. For Utah and white-tailed prairie dogs, the observed number of predations on

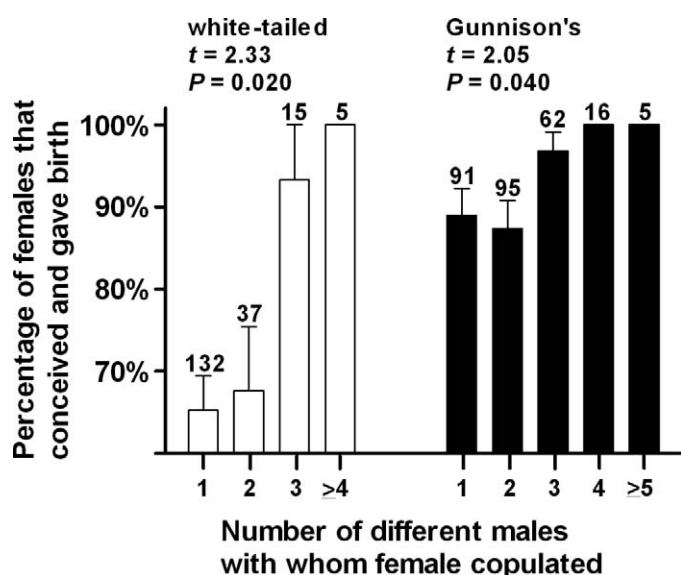


FIG. 3.—Female white-tailed and Gunnison's prairie dogs were more likely to conceive and give birth when they were polyandrous. The t -values and P -values are from logistic regression.

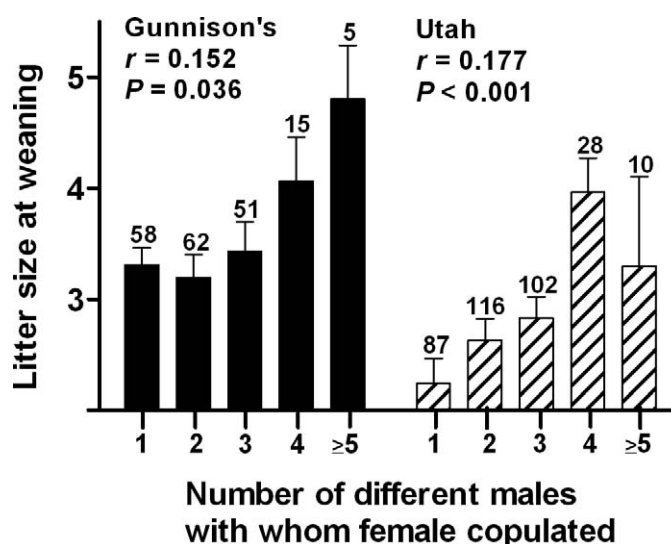


FIG. 4.—Female Gunnison's and Utah prairie dogs weaned larger litters when they were polyandrous. The r -values and P -values are from the Spearman correlation test. These data are only from females that gave birth; litter size at weaning for this analysis ranged from 0 (no weaning, even though parturition occurred) to 8.

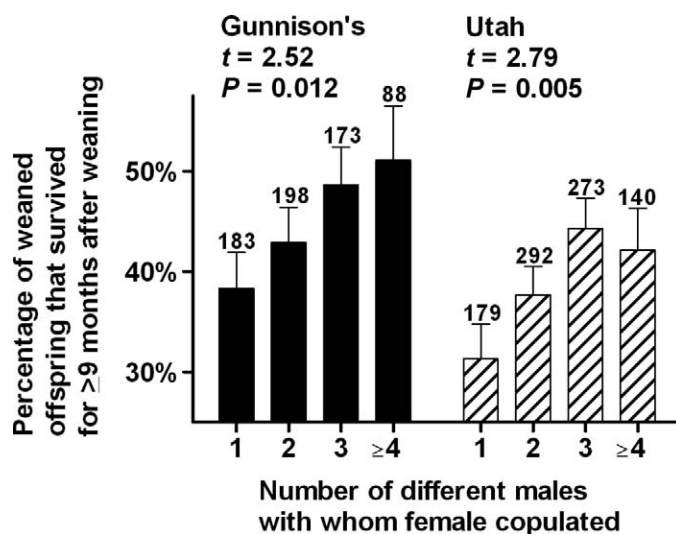


FIG. 5.—Offspring of Gunnison's and Utah prairie dogs were more likely to survive for ≥ 9 months after weaning when the mother was polyandrous. The t -values and P -values are from logistic regression. These data are only from females that weaned at least 1 offspring; litter size at weaning for this analysis ranged from 1 to 8.

polyandrous females was higher than the number expected by chance alone, and the observed number of predations on monandrous females was lower than the number expected by chance alone; black-tailed prairie dogs showed the opposite trend. None of these trends was significant ($P \geq 0.300$, chi-square goodness-of-fit test, $d.f. = 1$), however, possibly because of small sample sizes ($n = 9$ predations of female black-tailed prairie dogs, $n = 12$ predations of female Utah prairie dogs, $n = 13$ predations of female white-tailed prairie dogs).

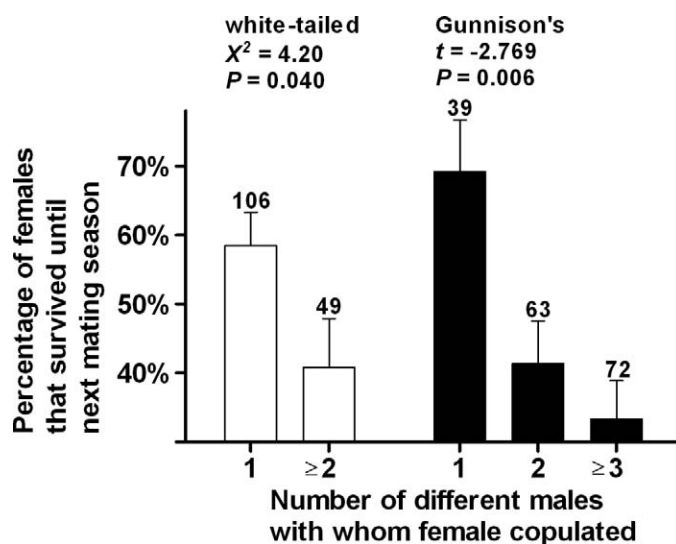


FIG. 6.—Female Gunnison's and white-tailed prairie dogs were less likely to survive until the next mating season when they were polyandrous. For white-tailed prairie dogs, the chi-square (χ^2) value ($d.f. = 1$) and the P -value are from the 2×2 chi-square test. For Gunnison's prairie dogs, the t -value and the P -value are from logistic regression.

Three other factors might have contributed to the lower survivorship until the next mating season for polyandrous versus monandrous females. First, the amount of time that a female spent underground, where she could not forage, on her day of estrus varied directly and significantly with the female's number of sexual partners for all 4 species (Fig. 7A). Highly polyandrous females, for example, remained underground for a mean of > 200 more minutes than monandrous females on the day of estrus for white-tailed and Gunnison's prairie dogs. Polyandry thus forced females to forfeit valuable foraging time on a day in late winter or early spring when vegetation for food was limited. Second, the number of hostile interactions (fights, chases, and territorial disputes) on a female's day of sexual receptivity tended to increase directly with the female's number of sexual partners for all 4 species (Fig. 7B); this trend was not significant for any species, however. Third, probably because of the trend in Fig. 7B, the number of wounds and scars on females shortly after the mating season tended to increase directly with a female's number of sexual partners for 3 of the 4 species (Fig. 7C); this trend was significant for only white-tailed prairie dogs.

DISCUSSION

Like many other behavioral ecologists over the last 10–15 years (Zeh and Zeh 1997; Bretman and Tregenza 2005; Firman and Simmons 2008a; Johnson and Brockmann 2010; Gowaty 2012; Pizzari and Wedell 2013), I have used the term “polyandry” in this report to indicate copulation with ≥ 2 males by a single female. I recognize, however, that other behavioral ecologists in the 1970s and 1980s used the term to describe an overall mating system in which the variance in female lifetime reproductive success is greater than the variance in male lifetime reproductive success (Trivers 1972; Emlen and Oring 1977; Alexander et al. 1979). For some species, polyandry can have significant consequences for the viability of populations, the risk of extinction, and plans for conservation (Johnson and Brockmann 2010; Holman and Kokko 2013).

For possible enhancements from polyandry, I was able to quantify 4 components of fitness for females: probability of conception and parturition, litter size at weaning, probability of survivorship of offspring for ≥ 9 months after weaning, and production of yearlings. An important discovery from my long-term comparative research is that copulation with ≥ 2 males affected these 4 components of fitness in different ways for 4 similar, closely related species. For Gunnison's prairie dogs, for example, polyandry enhanced all 4 components. For Utah prairie dogs, polyandry enhanced the 2nd, 3rd, and 4th components; for white-tailed prairie dogs, polyandry enhanced the 1st and 4th components. Black-tailed prairie dogs evidently did not experience enhancements from polyandry for any component of fitness.

Costs of polyandry also affected the 4 species of prairie dogs in different ways. For example, polyandrous females were significantly less likely than monandrous females to survive

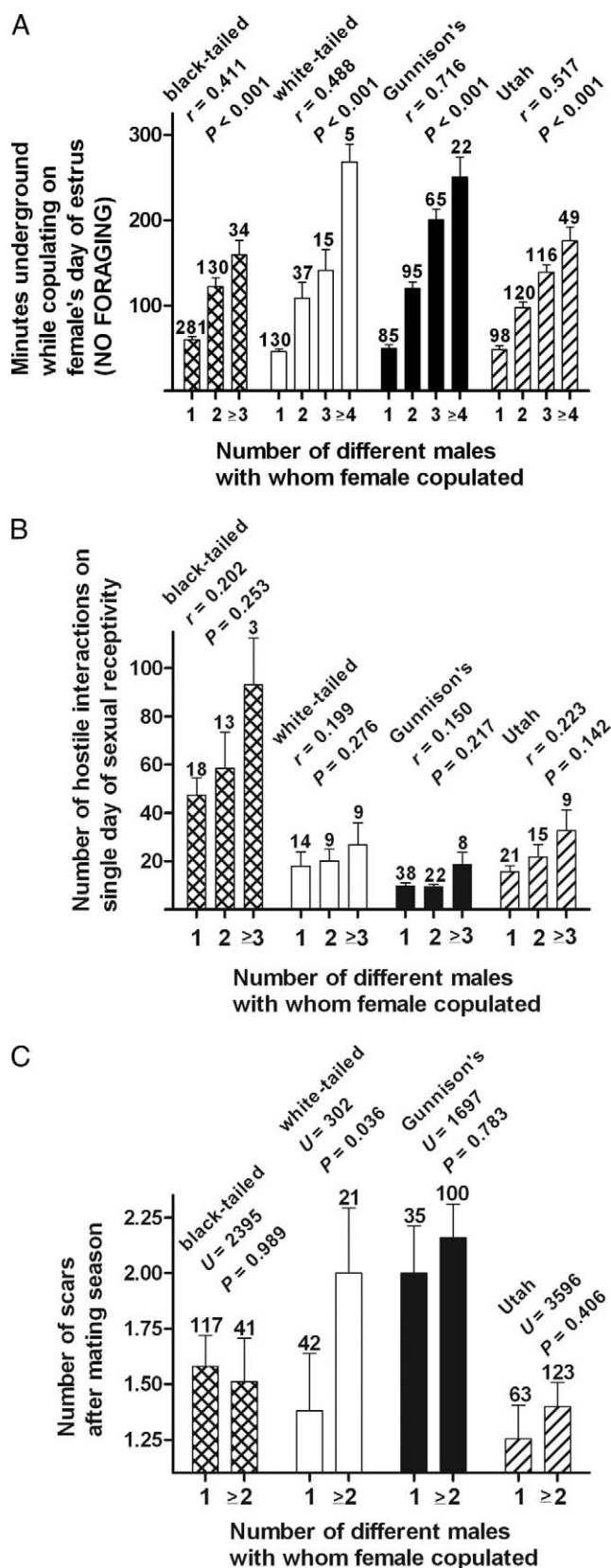


FIG. 7.—A) The cumulative time spent underground (when no foraging occurred) for copulation(s) by a female on her single day of estrus varied directly with her number of sexual partners. B) The number of hostile interactions for a female on her day of estrus tended

to vary directly with her number of sexual partners. C) The number of injuries and scars for a female shortly after the mating season tended to vary directly with her number of sexual partners. The r -values and P -values for A–C are from the Spearman correlation test.

until the next mating season for Gunnison's and white-tailed prairie dogs, but this cost was not evident for either Utah or black-tailed prairie dogs. By contrast, the amount of time that a female spent underground, where she was unable to feed, on her single day of estrus varied directly and significantly with the female's number of sexual partners for all 4 species. The number of aggressive interactions on a female's day of estrus, and the number of wounds and scars that resulted from these interactions, also tended to increase directly with the female's number of sexual partners for all 4 species, but most of these trends were not significant.

One estimate of an individual's annual fitness is the number of reproductive offspring produced by that individual within a single year. For many reasons, the most important of which concerns dispersal of juveniles, accurate measurements of annual fitness within natural populations are elusive. However, biologists often can accurately quantify components of annual fitness (Clutton-Brock 1988). Later-expressed components of fitness are more reliable than early-expressed components (Shaw et al. 2008). For prairie dogs, for example, litter size at weaning is a better predictor of annual fitness than the presence or absence of conception and parturition. The latest-expressed, and therefore most reliable, component of fitness that I could measure for prairie dogs was the number of yearlings produced by each female. Mating with ≥ 2 males significantly enhanced the production of yearlings by female Gunnison's, Utah, and white-tailed prairie dogs.

Polyandrous female Gunnison's and white-tailed prairie dogs were more likely than monandrous females to conceive and give birth. One or more of at least 5 reasons might explain this higher likelihood; in each scenario, copulation with a 2nd or 3rd male probably would increase the probability of conception. First, some males that copulate might be sterile (i.e., might not produce sperm, or might produce sperm that are incapable of fertilization—see Møller and Birkhead 1989; Torok et al. 2003; Uller and Olsson 2005). Second, sexually mature males sometimes might experience a temporary absence or shortage of sperm (Birkhead 1991, 2000; Preston et al. 2001; Schradin et al. 2009). For prairie dogs, this shortage might be especially likely late in the afternoon of a day when a male has already copulated with as many as 4 females earlier on the same day (this study). Third, sperm of certain males sometimes might be genetically incompatible with a female's ova (Kraaijeveld-Smit et al. 2002; Zeh and Zeh 2003; Mays and Hill 2004; Pryke et al. 2010). Fourth, semen might contain certain chemicals that help to induce ovulation at the optimal time for conception (Chen et al. 1985; Adams et al. 2005). Finally, the physical stimulation of copulation might help to induce ovulation at the optimal time for conception (Fernandez-Baca et al. 1970; Dewsbury 1975; Beach 1976).

If polyandry increases female ARS, then the frequency of polyandry should positively correlate with the number of fitness components ($n = 4$ that I measured for prairie dogs) that are favorably affected. In tepid support of this hypothesis, the frequencies of polyandry were higher for Gunnison's prairie dogs (frequency of polyandry = 65%, 4 fitness components enhanced) and Utah prairie dogs (73%, 3 components) than for white-tailed prairie dogs (30%, 2 components) and black-tailed prairie dogs (33%, 0 components).

Factors other than a female's number of sexual partners affect her survivorship and other components of her fitness (Olsson and Madsen 2001; Johnson and Brockmann 2010), and such factors might have obscured the specific effects of polyandry for female prairie dogs. Two obvious candidates were female age and female body mass. If middle-aged, heavy females were more likely to survive and had higher ARS (Clutton-Brock et al. 1982; Sherman and Morton 1984; Hoogland 1995), then this linkage might have rendered them more attractive to males—and therefore more likely to be polyandrous. Middle-aged, heavy females of all 4 species were indeed more likely than older and younger females of lower body mass to conceive, and they weaned larger litters. However, 6 of the 9 significant enhancements from polyandry of the 4 fitness components depicted in Figs. 2–5 were independent of the effects from female age and female body mass. These results indicate that polyandry per se was directly responsible in some species for the higher probability of conception and parturition, the larger litter sizes at weaning, the higher survivorship of offspring in the first 9 months after weaning, and the production of more yearlings.

Another factor that might have affected the frequency of polyandry among prairie dogs is OSR. A low OSR (i.e., a low ratio of sexually mature females to sexually mature males), for example, might induce females to be polyandrous (Emlen and Oring 1977; Clutton-Brock 2007). The frequency of polyandry varied inversely with OSR for Gunnison's prairie dogs, but not for any of the other 3 species. Further, OSR did not seem to explain interspecific differences in the frequency of polyandry.

Quality of the home territory also might have affected the frequency of polyandry among prairie dogs (Emlen and Oring 1977; Clutton-Brock 2007). Territories with copious resources, for example, might make it easier for a female to gain body mass and to improve personal condition, so that she can more easily maximize the benefits of polyandry and minimize the costs. I did not collect any information on the quality of the home territories (e.g., quantity and type of vegetation) for any species, and therefore could not investigate the possible importance of this variable on the frequency of polyandry.

If polyandry per se confers a payoff, then polyandrous females might have invested more time, energy, and resources in reproduction than monandrous females to capitalize further on the initial payoff (Sheldon 2000; Kozielska et al. 2004; Simmons 2005; Fisher et al. 2006). Increased parental investment by polyandrous females (e.g., by being more vigilant for predators or by collecting more mouthfuls of nest material for their nursery burrows) will confound any

comparison of polyandrous versus monandrous females, but presumably will not occur unless polyandry confers some initial advantage, however small. I detected no evidence for any species that polyandrous females invested more in their offspring, but I recognize that convincing evidence for (or against) increased maternal investment following polyandry is elusive.

If copulation with ≥ 2 males clearly enhanced the production of yearlings for female Gunnison's, Utah, and white-tailed prairie dogs, then why weren't all females of these species polyandrous? For 2 species, examination of my data suggests that the answer stems from a serious cost: polyandrous female Gunnison's and white-tailed prairie dogs were less likely than monandrous females to survive until the next mating season. For Gunnison's prairie dogs, for example, females that copulated with ≥ 3 males were 36% less likely than monandrous females to survive until the next mating season. This lower survivorship probably resulted because polyandrous females paid higher costs of reproduction (Olsson and Madsen 2001; Johnson and Brockmann 2010; Madsen 2011) than monandrous females. Specifically, polyandrous females were more likely to conceive and to wean larger litters, and therefore were more likely to pay the costs of pregnancy and lactation (Sherman and Morton 1984; Clutton-Brock et al. 1989; Hoogland 1995), including increased susceptibility to predation (Hoogland et al. 2006; Madsen 2011). Other factors that might have contributed to the lower survivorship of polyandrous versus monandrous females include significantly less time for foraging on the day of estrus, and tendencies for polyandrous females to engage in more hostile interactions, from which they tended to incur more wounds and injuries.

Mate-guarding (Sherman 1989; Westneat 1994; Kempenaers et al. 1995) is another factor that might have prevented certain females from copulating with more than 1 male. Immediately after copulation with a female, the 1st-copulating male attempted to prevent additional copulations by chasing away other males trying to invade the female's home territory, or by chasing the female back into her home territory when she began to roam into adjacent territories in search of other males (Hoogland 1995, 1998a, 2007). As for other animals (Orlans 1969; Armitage 1986; Birkhead and Møller 1992; Simmons 2005; Gowaty 2012), male and female prairie dogs thus had a conflict of interest regarding the optimal number of sexual partners for each female. A female frequently increased 1 or more components of her fitness by being polyandrous. A male, by contrast, maximized his ARS with a particular female when he was able to monopolize her via mate-guarding, so that she remained monandrous and he sired all her offspring. Neither sex in any of the 4 species was completely "winning" the conflict of interest regarding the optimal number of sexual partners per female (Fig. 1).

Mate-guarding is easier in some habitats than in others (Emlen and Oring 1977; Westneat 1994; Westneat and Mays 2005). Males can more easily see and guard females when the visibility within the habitat is high (i.e., for prairie dogs, when vegetation is short), for example (Sherman and Morton 1988;

Mays and Ritchison 2004). Mate-guarding also is easier when reproductive synchrony is low—so that a male can guard 1 sexually receptive female at a time without missing opportunities to copulate with, and then guard, other receptive females (Emlen and Oring 1977; Sherman 1989; Hoogland 1995). Might interspecific differences in the ability of males to guard females explain interspecific differences in the frequency of polyandry? The answer here is unclear. On one hand, the black-tailed prairie dog, which showed the 2nd-lowest frequency of polyandry, has a higher visibility within the habitat and lower reproductive synchrony than the other 3 species (King 1955; Hoogland 1995, 2007). On the other hand, the white-tailed prairie dog, which showed the lowest frequency of polyandry, resembles Gunnison's and Utah prairie dogs and typically has low visibility within the habitat (Tileston and Lechleitner 1966; Clark 1977; Hoogland 1981, 2003a, 2007). Further, white-tailed prairie dogs reproduced more synchronously than any of the other 3 species (this study).

For all 4 species, a female prairie dog that has copulated with 1 male on the single day when she is sexually receptive can immediately and decisively preclude copulations with additional males by simply remaining underground after copulating with the 1st male, or by submerging alone into 1 of the 20+ burrow systems within her home territory for the remainder of the single day after reappearing aboveground following copulation with the 1st male. Some females did resort to one or the other of these strategies after copulating with a single male (Hoogland 1995, 1998a), and these options indicate that males cannot easily impose polyandry on unwilling females. The majority of females for all 4 species reappeared and remained aboveground after the 1st copulation, however, and once-mated females often deliberately searched for additional males with which they had not yet copulated (Hoogland 1995, 2007). Further, probably to increase the probability of copulation with additional males, an estrous female typically remained aboveground later than other, nonestrous females at the end of the day. Polyandry was thus an intentional choice for females. Monandry and polyandry probably represent alternative mating strategies (Oliveira et al. 2008; Schuster 2010; Neff and Svensson 2013) for female prairie dogs, with natural selection favoring monandry (low ARS, high survivorship) for some females and polyandry (higher ARS, lower survivorship) for other females.

Studies of numerous species have demonstrated a significant positive effect of multi-locus heterozygosity on the survivorship of offspring (Parsons and Bodmer 1961; Brown 1997; Foerster et al. 2003; Smith et al. 2005). High levels of heterozygosity among offspring might be difficult to generate in populations suffering from low genetic diversity, however. Further, inadequate genetic diversity can increase the levels of abnormality and incompatibility of sperm (Packer et al. 1991). Polyandry should offer more opportunities than monandry for females to obtain and select sperm that are viable, more compatible, and more likely to produce offspring with multilocus heterozygosity (Zeh and Zeh 1997; Thiel and

Hinojosa 2003; Simmons 2005; Pryke et al. 2010). If so, then the frequency of polyandry should be higher, and the benefits from polyandry should be more pronounced, for species with low genetic diversity than for species with higher genetic diversity. I could not test these predictions with my own data, because I did not collect any information about genetic diversity within and among the 4 species of prairie dogs. However, from a study of 29 allozyme loci, McCullough (1991) showed that 34% and 17% of loci were polymorphic for Gunnison's and Utah prairie dogs, respectively, but 41% of the same loci were polymorphic for both black-tailed and white-tailed prairie dogs. In other allozyme studies, 5% (2/40) and 3% (1/32) of loci were polymorphic for Gunnison's and Utah prairie dogs, respectively (Chesser 1984; Benedix 1988; see also Travis et al. 1997), but 44% (7/16) were polymorphic for black-tailed prairie dogs (Chesser 1983; Daley 1992). The combination of genetic data from these latter studies and my information on polyandry supports the predictions listed above: polyandry was more common, enhancements to fitness components were more common and of higher magnitude, and genetic diversity was lower for Gunnison's and Utah prairie dogs than for black-tailed and white-tailed prairie dogs. The lower genetic diversity for Gunnison's and Utah prairie dogs might have resulted because these species have smaller overall population sizes and smaller geographic ranges than black-tailed and white-tailed prairie dogs (Hollister 1916; Hoogland 2003a; United States Fish and Wildlife Service 2008).

The evidence for the hypothesis that interspecific differences in the frequency and consequences of polyandry result from interspecific differences in the amount of genetic diversity is preliminary, for 2 reasons. First, sample sizes for estimates of genetic diversity are small. Even though McCullough's (1991) estimates come from the same 29 loci for all 4 species, for example, sample sizes for the number of individuals per species ($n = 21$ for 1 species, $n = 15$ for the other 3 species) and the number of collection sites per species ($n = 5$ for 1 species, $n = 2$ or 3 for the other 3 species) are small. Larger sample sizes from more collection sites would be valuable for a better understanding of interspecific differences in the amount of genetic diversity. Second, even though my estimates of the frequency and consequences of polyandry come from recording both the total number of sexual partners for each female and 4 fitness components for each female for a minimum of 190 females per species, all my data for each species come from a single colony. Because intraspecific, intercolonial variation in social behavior can be substantial (Hoogland 1981, 1995; Clutton-Brock et al. 1982; Lott 1991; Brown and Brown 1996), information on polyandry from several colonies per species would be valuable for a better understanding of how the frequency and consequences of polyandry vary within and among species.

What is the mechanism by which polyandry enhances components of fitness for female Gunnison's, Utah, and white-tailed prairie dogs? I do not have biochemical assignments of paternity for most of the females that weaned litters and for

which I had good information on the number of sexual partners; my best information on paternity comes from black-tailed prairie dogs (Hoogland 1995), for which neither costs nor benefits of polyandry were evident (Table 2). Further, I have no information on cryptic female choice (Eberhard 1996; Solomon and Keane 2007; Pryke et al. 2010; Firman and Simmons 2012; Kvarnemo and Simmons 2013) for any species. Consequently, I cannot rigorously evaluate the 5 mechanisms regarding indirect benefits from polyandry in Table 1 that require information on paternity. I was able, however, to evaluate several mechanisms regarding direct benefits from polyandry in Table 1. Polyandrous females were more likely than monandrous females to conceive for 2 species, for example. I detected no evidence for other direct benefits that females might reap from polyandry, and I also detected no evidence for “convenience polyandry.” A study with good information from each female on the number of her sexual partners, estimates of the 4 components of her fitness, and the paternity of her offspring would be a valuable next step in our understanding of polyandry among the 4 species of prairie dogs.

My study underscores the value of long-term comparative research for animals living under natural conditions. If I had studied only black-tailed prairie dogs, I would have concluded that costs and benefits of polyandry are minimal. If I had studied only Gunnison's prairie dogs, on the other hand, I would have concluded that both costs and benefits of polyandry dramatically affect female survivorship and 4 components of female ARS. For most animals, including Utah and white-tailed prairie dogs, the truth about polyandry probably lies somewhere between these 2 extremes.

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