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BLACK-TAILED, GUNNISON'S, AND UTAH PRAIRIE DOGS REPRODUCE SLOWLY

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Long-term research with marked individuals shows that black-tailed, Gunnison's, and Utah prairie dogs (Sciuridae: *Cynomys ludovicianus, C. gunnisoni,* and *C. parvidens*) all reproduce slowly, despite claims of ranchers and early naturalists. Five factors are responsible for the slow reproduction. First, survivorship in the 1st year is <60% for all 3 species, and it remains low in later years. Second, even under optimal conditions, females of all 3 species produce only 1 litter/year. Third, the percentage of males that copulate as yearlings is only 6%, 24%, and 49% for black-tailed, Gunnison's, and Utah prairie dogs, respectively. The percentage of females that copulate as yearlings is only 35% for black-tailed prairie dogs, but it is 100% for both Gunnison's and Utah prairie dogs. Fourth, the probability of weaning a litter each year is only 43%, 82%, and 67% for female black-tailed, Gunnison's, and Utah prairie dogs, respectively. Fifth, for those females that wean offspring, mean litter size at 1st juvenile emergence from the nursery burrow is 3.08, 3.77, and 3.88 for black-tailed, Gunnison's, and Utah prairie dogs, respectively.

Key words: *Cynomys gunnisoni, C. ludovicianus, C. parvidens,* litter size, prairie dog, reproduction, sexual maturity

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Mainly because ranchers view them as pests, prairie dogs (Rodentia: Sciuridae: *Cynomys*) have been targets of intensive eradication programs that involve shooting, poisoning, drowning, and destruction of habitat (Cincotta et al. 1987; Clark 1989; Marsh 1984; Roemer and Forrest 1996; Uresk et al. 1986; Vosburgh and Irby 1998). Sylvatic (bubonic) plague (*Yersinia pestis*), an introduced bacterial disease to which prairie dogs are highly susceptible (Barnes 1982, 1993; Cully 1993), also has killed millions of prairie dogs (Clark 1977; Cully et al. 1997; Eskey and Haas 1940; Lechleitner et al. 1962, 1968; Rayor 1985a; Ubico et al. 1988). Consequently, all 5 species are now rare. Mexican prairie dogs (*C. mexicanus*) are on the list of endangered species, Utah prairie dogs (*C. parvidens*) are on the list of threatened species but are under consideration for the list of endangered species (Roberts et al. 2000), and black-tailed prairie dogs (*C. ludovicianus*) are under consideration for the list of threatened species (Biodiversity Legal Foundation et al., in litt.; Miller et al. 2000; National Wildlife Federation, in litt.).

Ranchers disdain prairie dogs for 2 reasons (Chace 1976; Costello 1970; Jameson 1973; Petzal 1993; Randall 1976a, 1976b; Swenk 1915; Zinn and Andelt 1999). First, they worry that livestock (*Equus caballus* and *Bos taurus*) will step into prairie dog burrows and break a leg. Second, they believe that prairie dogs compete with livestock for food. Ranchers also fret that prairie dogs are prolific breeders from which they are not safe until every single one is gone. Livestock do sometimes incur broken legs after stepping into prairie dog burrows, but such fractures are rare (Aschwanden 2001; Hoogland 1995). Prairie dogs do eat some of the same plants that horses and cat-

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tle eat, but competition is minimal. Specifically, prairie dogs avoid numerous plants that livestock prefer, and prefer many plants that livestock avoid (Coppock et al. 1983a, 1983b; O'Meilia et al. 1982; Uresk 1984). Presence of prairie dogs also improves quality of certain plants, so that American bison (*Bos bison*), elk (*Cervus elaphus*), pronghorn antelope (*Antilocapra americana*), and livestock commonly forage at colony sites (Coppock et al. 1983a, 1983b; Knowles 1986a; Koford 1958; O'Meilia et al. 1982).

Brief Natural History of Prairie Dogs

Prairie dogs are herbivorous, colonial, ground-dwelling squirrels that inhabit western North America (Hollister 1916; Pizzimenti 1975). Territorial, harem-polygynous family groups are found within colonies. For Gunnison's (*C. gunnisoni*) and Utah prairie dogs, which hibernate for 4–6 months/year, these groups are called clans (Fitzgerald and Lechleitner 1974; Hoogland 1999; Travis et al. 1995, 1996; Wright-Smith 1978). For black-tailed prairie dogs, which do not hibernate, family groups are called coteries (Halpin 1987; Hoogland 1995; King 1955).

For black-tailed prairie dogs in South Dakota, the breeding season (i.e., the period when copulations occur) starts in mid-February and extends into early April (Hoogland 1995). For Gunnison's prairie dogs in Arizona and Utah prairie dogs in Utah, the breeding season extends from mid-March through early April (Hoogland 1999).

A keystone species has a large overall effect on an ecosystem (Mills et al. 1993; Paine 1969, 1980; Power et al. 1996). Prairie dogs of all species, and especially black-tailed prairie dogs, qualify as keystone species for several reasons (Kotliar et al. 1999; Miller et al. 1994, 2000; Sharps and Uresk 1990). Their foraging decreases height of vegetation, changes floral composition, and increases landscape heterogeneity (Cid et al. 1991; Cincotta et al. 1989; Weltzlin et al. 1997; Whicker and Detling 1988). Prairie dog excavations increase mixing of topsoil and subsoil, and also promote uptake of nitrogen by plants (Holland and Detling 1990; King 1955). Further, colonies increase biological diversity and species richness (Agnew et al. 1986; Clark et al. 1982; Hansen and Gold 1977; O'Meilia et al. 1982; Reading et al. 1989) because they attract myriad invertebrates and vertebrates (Hoogland 1995; Kotliar et al. 1999; Miller et al. 1994). Burrowing owls (*Athene cunicularia*), mountain plovers (*Charadrius montana*), and black-footed ferrets (*Mustela nigripes*) are among vertebrates that are especially dependent on prairie dog colonies for survival (Clark et al. 1982; Desmond and Savidge 1996; Knowles et al. 1982; Kotliar et al. 1999).

Here I deal with the concern that prairie dogs are prolific breeders. By documenting 5 factors that impede reproduction, I show that black-tailed, Gunnison's, and Utah prairie dogs replace themselves slowly under natural conditions.

Materials and Methods

For the last 26 years, I have investigated the ecology and social behavior of black-tailed, Gunnison's, and Utah prairie dogs. I studied black-tailed prairie dogs at Wind Cave National Park, South Dakota, in February–June 1975–1988 (Hoogland 1982, 1985, 1995, 1996a). I studied Gunnison's prairie dogs at Petrified Forest National Park, Arizona, in March–June 1989–1995 (Hoogland 1996b, 1997, 1998a, 1998b, 1999). My research with Utah prairie dogs at Bryce Canyon National Park, Utah, began in 1996 and has continued through 2001 in March–June of each year.

For permanent identification of individuals, I used fingerling eartags (National Band and Tag Company, Newport, Kentucky). For identification from a distance, I applied unique markers to each animal with Nyanzol-D black fur dye (J. Belmar Inc., North Andover, Massachusetts). Field assistants and I observed marked individuals from 4-m-high towers with binoculars and a 60-power telescope (Hoogland 1995).

Like females of Belding's (*Spermophilus beldingi*), Columbian (*S. columbianus*), round-tailed (*S. tereticaudus*), and Uinta (*S. armatus*)

ground squirrels (Balph 1984; Dunford 1977; Festa-Bianchet and Boag 1982; Sherman 1980), female prairie dogs reared their offspring in separate nursery burrows. Except when mothers of Gunnison's or Utah prairie dogs shared the same nursery burrow (Hoogland 1999; Rayor 1988), maternity was thus easy to establish. When about 5–6 weeks old, juveniles first emerged from the nursery burrow. By surrounding nursery burrows with traps shortly after juveniles first appeared aboveground (Hoogland 1995), I determined litter size by capturing, eartagging, and marking all littermate siblings before they mixed with juveniles from other litters.

I identified a male as breeding if I observed him copulate or if he had a black scrotum and descended (scrotal) testes during the breeding season. Nonbreeding males had gray or whitish scrotums with no descended testes. I identified a female as breeding if I observed her copulate or if she was lactating (i.e., with long, turgid teats) in May or June.

For black-tailed prairie dogs, I tallied positive annual survivorship if an individual survived from April (for adults and yearlings) or May (for juveniles) of 1 year until April of the following year (Hoogland 1995). For Gunnison's and Utah prairie dogs, I tallied positive survivorship if an individual survived from April (for adults and yearlings) or June (for juveniles) of 1 year until it emerged from hibernation in March or April of the following year (Hoogland 1999).

Figures show means ± 1 *SE*. All levels of significance (*P*-values) resulted from 2-tailed nonparametric statistical tests.

Results

Prairie dogs did not live long. Survivorship of females in the 1st year was <50% for Gunnison's and Utah prairie dogs and was 54% for black-tailed prairie dogs (Fig. 1). Survivorship of males in the 1st year was <50% for all 3 species (Fig. 2). Survivorship also was low for older black-tailed, Gunnison's, and Utah prairie dogs (Figs. 1 and 2).

Female black-tailed, Gunnison's, and Utah prairie dogs came into estrus and were sexually receptive for several hours on only 1 day during the breeding season. Consequently, female prairie dogs weaned a maximum of only 1 litter/year. Females of all 3

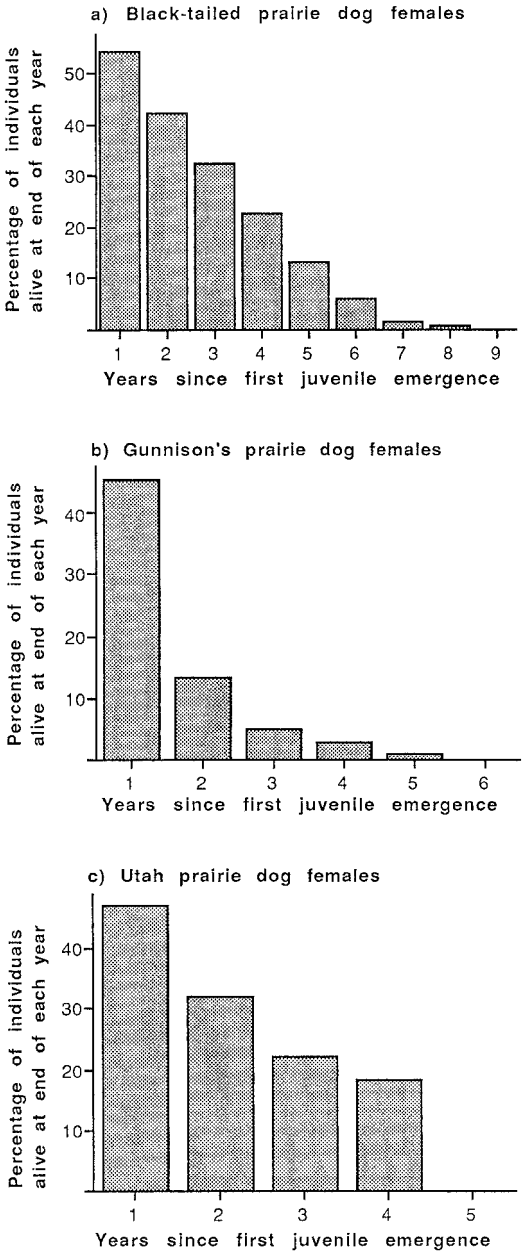

FIG. 1.—Survivorship of females for a) black-tailed, b) Gunnison's, and c) Utah prairie dogs. Each female was 1st marked soon after she 1st emerged from the natal burrow, when she was about 6 weeks old. Numbers of juvenile females marked at 1st emergence were 523, 715, and 272 for black-tailed, Gunnison's, and Utah prairie dogs, respectively. Female Utah prairie dogs sometimes live >5 years, but data shown here are from a 5-year study.

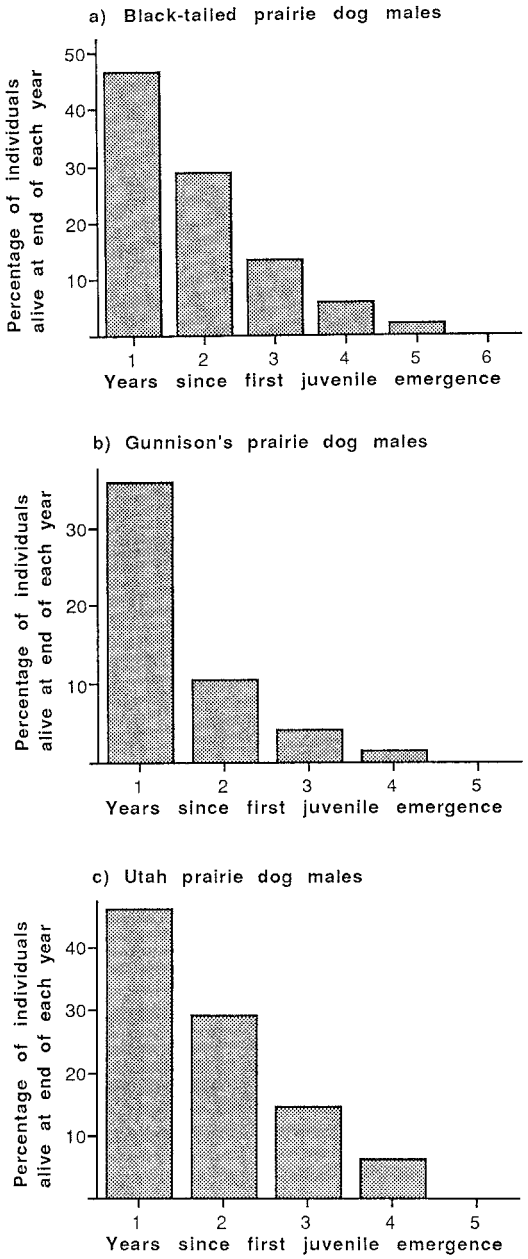

FIG. 2.—Survivorship of males for a) black-tailed, b) Gunnison's, and c) Utah prairie dogs. Each male was 1st marked soon after he 1st emerged from the natal burrow, when he was about 6 weeks old. Numbers of juvenile males marked at 1st emergence were 587, 692, and 242 for black-tailed, Gunnison's, and Utah prairie dogs, respectively. Male Utah prairie dogs sometimes live >5 years, but data shown here are from a 5-year study.

species sometimes came into estrus a 2nd time if they had failed to conceive in the 1st estrus (J. L. Hoogland, in litt.).

Probability of copulating in the 1st year was 6%, 24%, and 49% for males of black-tailed (n = 261), Gunnison's (n = 271), and Utah prairie dogs (n = 112), respectively. Probability of copulating in the 1st year was 35% for female black-tailed prairie dogs (n = 269), but was 100% for female Gunnison's (n = 358) and Utah prairie dogs (n = 128). Probability of weaning a litter each year was 43%, 82%, and 67% for female black-tailed (n = 821), Gunnison's (n = 216), and Utah prairie dogs (n = 168), respectively. Infanticide reduced or eliminated 39% of black-tailed prairie dog litters (n = 591 litters) and 15% of Utah prairie dog litters (n = 172). I detected no infanticide among Gunnison's prairie dogs (n = 358 litters—Hoogland 1999). For black-tailed and Gunnison's prairie dogs, the most common litter sizes at 1st juvenile emergence were 3 and 4. For Utah prairie dogs, the most common litter sizes were 4 and 5 (Fig. 3).

For black-tailed prairie dogs, males that copulated were heavier than males that did not copulate (770 g ± 10.1 *SD*, n = 120 versus 520 ± 11.4 g, n = 131; Mann–Whitney U-test, $P < 0.001$). Of copulating black-tailed prairie dogs, heavy males sired more offspring than lighter males (Fig. 4). These positive trends of male reproductive success versus male body mass also were evident among Gunnison's and Utah prairie dogs (J. L. Hoogland, in litt.). For all 3 species, litter size varied directly with maternal body mass (Fig. 5).

DISCUSSION

A long-lived individual has more opportunities to rear offspring than an individual that dies prematurely. Longevity thus has a major impact on lifetime reproductive success for animals such as lesser snow geese (*Anser caerulescens*—Cooke and Rockwell 1988), African lions (*Panthera leo*—Packer et al. 1988), and vervet monkeys (*Cerco-*

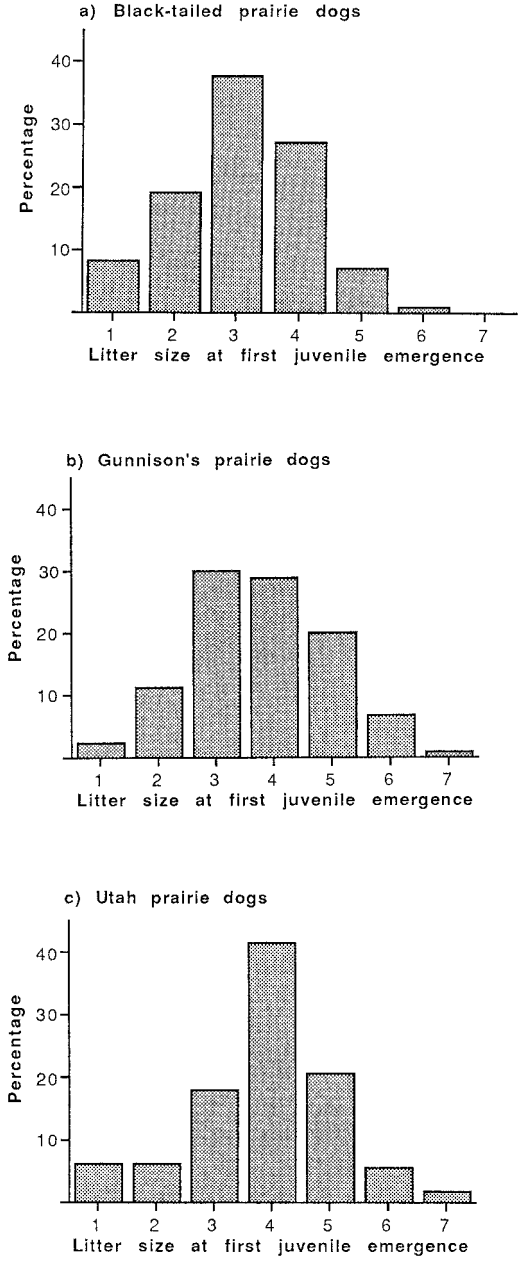

FIG. 3.—Litter size at 1st juvenile emergence for a) black-tailed, b) Gunnison's, and c) Utah prairie dogs. Mean litter sizes are 3.08 (n = 361), 3.77 (n = 340), and 3.88 (n = 161), respectively.

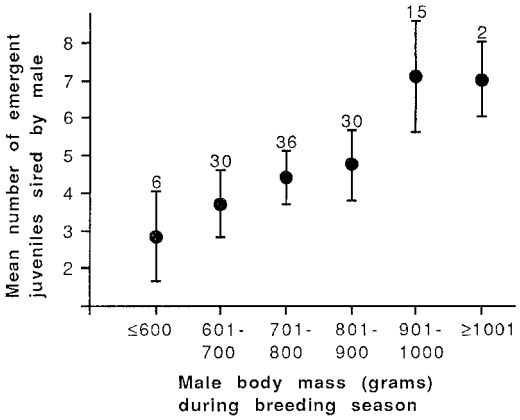

FIG. 4.—Reproductive success increases with body mass for male black-tailed prairie dogs. The number above each *SE* indicates the number of males assessed for reproductive success and is restricted to males that copulated at least once (r_s = 0.229, P = 0.014). I determined siring success from behavioral observations and electrophoresis of blood samples (Hoogland 1995).

pithecus aethiops—Cheney et al. 1988). Less than 50% of weaned black-tailed, Gunnison's, and Utah prairie dogs live long enough to copulate. Survivorship also is low among older prairie dogs. Such low survivorships severely limit prairie dog reproduction.

For myriad species of small rodents, females commonly wean >2 litters/year (King 1968; Tamarin 1985). Even under optimal conditions, by contrast, female black-tailed, Gunnison's, and Utah prairie dogs resemble females of other ground-dwelling squirrel species and rear a maximum of only 1 litter/year (Armitage 1991; Boellstorff et al. 1994; Hanken and Sherman 1981; Murie 1996; Schwagmeyer 1984; Sherman 1989). This univoltine habit is another key factor that limits reproduction. Delayed sexual maturation also inhibits prairie dog reproduction. This delay is especially pronounced for black-tailed prairie dogs, for which only 6% of yearling males and 35% of yearling females copulate.

For those female prairie dogs that live long enough and reach sexual maturity, many do not wean a litter after copulating.

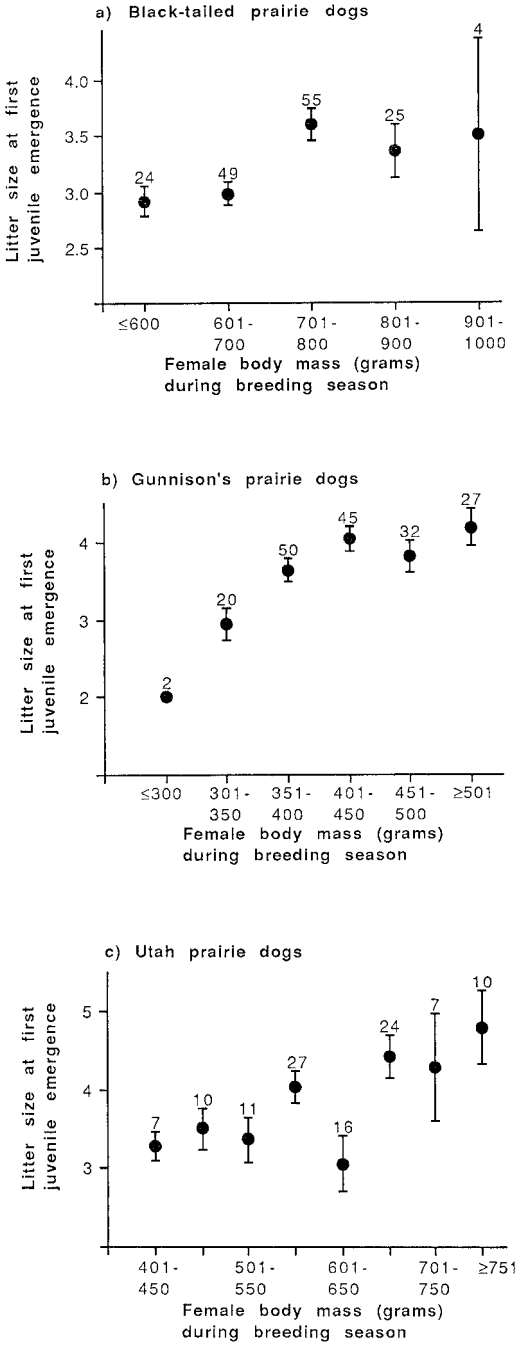

FIG. 5.—Mean litter size at 1st juvenile emergence increases with maternal body mass for a) black-tailed ($r_s = 0.269$, $P < 0.001$), b) Gunnison's ($r_s = 0.273$, $P < 0.001$), and c) Utah prairie dogs ($r_s = 0.351$, $P < 0.001$). The number above each *SE* indicates the number of females evaluated for litter size and is restricted to females that reared ≥1 offspring to 1st emergence.

Even though 100% of Gunnison's and Utah prairie dog females at my study colonies copulated, for example, only 82% and 67%, respectively, weaned a litter (cf. Rayor 1985b; Wright-Smith 1978). Some of the unsuccessful females never conceive, others conceive and then abort before parturition, and still others lose their young sometime after parturition. Genetic defects and diseases sometimes eliminate unweaned offspring in the nursery burrow (Hoogland 1995). Predators such as long-tailed weasels (*Mustela frenata*), American badgers (*Taxidea taxus*), prairie rattlesnakes (*Crotalus viridis*), and black-footed ferrets also kill unweaned young (Clark 1976; Halpin 1983; Hoogland 1981; Loughry 1987). At my study colony of Utah prairie dogs in 1998, for example, long-tailed weasels killed >40 unweaned juveniles.

Infanticide, the killing of juveniles by adult conspecifics (Hrdy and Hausfater 1984), is another important cause of mortality for prairie dogs. For example, at my study colonies of black-tailed and Utah prairie dogs, infanticide partially or totally eliminated 39% and 15%, respectively, of all litters born. In contrast, I did not detect a single unequivocal case of infanticide at my study colony of Gunnison's prairie dogs (Hoogland 1999).

Even though infanticide occurs commonly in colonies of both black-tailed and Utah prairie dogs, circumstances are remarkably different. Whereas almost all infanticides among black-tailed prairie dogs occur underground, marauding Utah prairie dogs bring their victims aboveground before or after killing them. More important, the most common killers among black-tailed prairie dogs are lactating females. In contrast, the most common killers among Utah prairie dogs are breeding males, who sometimes kill offspring of females with whom they copulated. Female black-tailed prairie dogs and male Utah prairie dogs usually consume their victims after infanticide. This cannibalism suggests that increased sustenance for the killer is the ultimate reason

for infanticide (Hrdy 1979; Sherman 1981). Female black-tailed prairie dogs probably use the nutrition from cannibalism to enhance personal survivorship and the probability of successful weaning (Hoogland 1995). Male Utah prairie dogs use the nutrition from cannibalism to increase body mass, which varies directly with male reproductive success.

Litter sizes are small for those females that successfully defend against predators and infanticide. Mean litter sizes at 1st juvenile emergence for black-tailed, Gunnison's, and Utah prairie dogs are 3.08, 3.77, and 3.88, respectively.

Despite the 5 factors that curtail reproduction, certain prairie dogs do succeed at rearing offspring. Of numerous possibilities that might enhance reproductive success (Clutton-Brock 1988; Newton 1989), body mass is the most conspicuous for black-tailed, Gunnison's, and Utah prairie dogs. Heavy males are more likely than lighter males to copulate. Further, among copulating males, heavy males sire more offspring than lighter males. For females, litter size varies directly with maternal body mass.

Prairie dogs are probably better able to attain large body mass, and therefore to survive and reproduce, when food and other resources are plentiful. For example, compared with conspecifics at an old colony with limited forage, black-tailed prairie dogs at a younger colony survived better, showed faster juvenile growth rates, reached sexual maturity sooner, and had larger litters (Garrett et al. 1982). Gunnison's and Utah prairie dogs from favorable versus unfavorable colony sites show the same trends (Cully 1997; Rayor 1985b; Travis and Slobodchikoff 1993; Wright-Smith 1978). These results indicate the importance of high-quality habitats for the conservation and long-term survival of prairie dogs.

If black-tailed, Gunnison's, and Utah prairie dogs, and presumably Mexican and white-tailed (*C. leucurus*) prairie dogs, reproduce slowly, why have ranchers and early naturalists labeled them as prolific breeders? Three considerations are relevant. First, prairie dogs do reproduce more successfully under certain conditions. For example, prairie dogs reproduce more rapidly in young, expanding colonies where resources are plentiful (Rayor 1985b; Travis and Slobodchikoff 1993; Wright-Smith 1978). Reproduction also increases dramatically in years after a population crash caused by shooting, poisoning, or sylvatic plague (Cully 1997; Cully et al. 1997; Knowles 1986b, 1987; Radcliffe 1992; Turner 2001). Second, juvenile prairie dogs from different litters mingle and cluster shortly after 1st emergences from natal burrows. They aggregate not only aboveground, but also spend the night in groups with ≥ 1 of their mothers in the same burrow, where communal nursing occurs (Hoogland 1995; Hoogland et al. 1989). When ranchers and early naturalists saw as many as 7–10 juveniles on the same burrow mound, they mistakenly equated these numbers with inflated litter size. In reality, such conglomerates contain juveniles from 2, 3, or even 4 different litters. Third, because of competition for forage that sometimes occurs between prairie dogs and livestock (Collins et al. 1984; Knowles 1986a; O'Meilia et al. 1982), ranchers probably find it difficult to view prairie dogs objectively.

I have argued that 5 factors slow reproduction of black-tailed, Gunnison's, and Utah prairie dogs. Does this viewpoint result because my study colonies were old and in unfavorable habitats where reproductive success of prairie dogs was low (Garrett et al. 1982; Rayor 1985b)? The answer might be affirmative for my study colony of black-tailed prairie dogs, which was >20 years old, had a stable population size, and had little room for expansion (Garrett et al. 1982; Hoogland 1995). However, the answer is probably negative for my study colonies of Gunnison's and Utah prairie dogs. These colonies were young and appeared to be in favorable habitats, as indi-

cated by the steady increase in colony size (i.e., the number of adult and yearling residents each spring) during my research (Hoogland 1999).

I have investigated factors that inhibit, or enhance, reproduction for black-tailed, Gunnison's, and Utah prairie dogs living under natural conditions. Unnatural factors pose a greater problem than do natural factors for the conservation of black-tailed, Gunnison's, and Utah prairie dogs. Poisoning, destruction of habitat, and sylvatic plague, in particular, are unnatural forces that threaten the long-term survival of prairie dogs (Biodiversity Legal Foundation et al., in litt.; McNulty 1971; Miller et al. 1994, 2000; Roberts et al. 2000).

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