

## SEXUAL DIMORPHISM OF PRAIRIE DOGS

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Body mass is sexually dimorphic and varies seasonally for all 5 species of prairie dogs (Sciuridae: *Cynomys*), as shown by data from live individuals over a period of 28 years (1974–2001;  $n = 16,447$  body masses). Sexual dimorphism (i.e., body mass of males as percentage of body mass of females) during the breeding season is 105% for black-tailed prairie dogs, 127% for Utah prairie dogs, 131% for Gunnison's prairie dogs, and 136% for white-tailed prairie dogs. Sexual dimorphism is minimal at the end of the breeding season, when exhausted males are thin and early-breeding females are heavy with pregnancy. Sexual dimorphism is maximal at weaning, when rested, well-fed males are heavy and females are emaciated from lactation. The most likely ultimate causation for sexual dimorphism among prairie dogs is sexual selection.

**Key words:** *Cynomys gunnisoni*, *C. leucurus*, *C. ludovicianus*, *C. mexicanus*, *C. parvidens*, prairie dog, sexual dimorphism, sexual selection

Sexual dimorphism in body size can evolve in at least 3 contexts. The 1st context involves sexual selection (Alexander et al. 1979; Andersson 1994; Darwin 1871; LeBoeuf and Reiter 1988; Ryan 1985; Weckerly 1998). Via intrasexual sexual selection, sexual dimorphism might evolve when larger (or smaller) members of one sex compete better with members of the same sex. Via intersexual sexual selection, sexual dimorphism might evolve when larger (or smaller) members of one sex are more attractive to members of the opposite sex. Second, sexual dimorphism might result if natural selection exaggerates the different parental roles of males and females (i.e., division of parental labor). For example, sexual dimorphism might reduce competition between mates by making it easier for mothers and fathers to exploit different types of food, so that offspring will get more nutrition (Przybylo and Merila 2000; Ralls 1976; Selander 1966, 1972). Similarly, sexual dimorphism might result

because large females can produce more eggs (Howard 1988; Rahn et al. 1975; Wiklund and Karlsson 1988) or larger litters (Leitch et al. 1959; Millar 1977; Sauer and Slade 1987), or, for bats, because large females are better able to fly with fetuses (Myers 1978). Finally, sexual dimorphism might evolve in response to intersexual competition for food during the nonbreeding season (Amadon 1959; Peters and Grubb 1983; Schoener 1967; Temeles 1986). Of these 3 possibilities, sexual selection is probably the most common ultimate causation for sexual dimorphism (Dunn et al. 2001; Fairbairn 1997; Fisher and Owens 2000; Hedrick and Temeles 1989; Jehl and Murray 1986; Price 1984).

Sexual dimorphism in body size is ubiquitous among animal species. Biologists are perhaps more familiar with cases of male-biased sexual dimorphism, but female-biased sexual dimorphism also is common, especially among invertebrates, fish, amphibians, and reptiles (Ralls 1976). Even though robust sample sizes might show that 1 sex is statistically larger than the other,

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overlap is usually extensive in most sexually dimorphic species (Ipana and Durand 2000).

For reasons that are not clear, sexual dimorphism in body size is usually more conspicuous within taxonomic groups with large absolute body size (Abouheif and Fairbairn 1997; Payne 1984; Reiss 1986). Among mammals, for example, sexual dimorphism is pronounced in orders such as Artiodactyla, Pinnipedia, Primates, and Proboscidea (Clutton-Brock and Harvey 1977a, 1977b; Jarman 1974; Loison et al. 1999; Ralls 1977; Weckerly 1998).

One common way to determine sexual dimorphism is to compare linear skeletal measurements such as total length, foot length, and so forth. Linear measurements require immobilization and therefore are difficult to obtain from live animals, but they remain relatively constant for the same individuals from day to day and season to season (Amadon 1943, 1959; Ralls 1976). Another common way to assess sexual dimorphism is to compare body masses. Body masses show more daily and seasonal variation for the same individuals than do linear measurements, but their formidable advantage is that researchers can quickly, easily, and accurately weigh live animals. All my research on sexual dimorphism of prairie dogs concerns body mass. As a measure of sexual dimorphism, I use body mass of males as a percentage of body mass of females.

Prairie dogs (*Cynomys*) are large, diurnal, colonial rodents of the squirrel family (Sciuridae). The 5 species are black-tailed (*C. ludovicianus*), Mexican (*C. mexicanus*), Gunnison's (*C. gunnisoni*), Utah (*C. parvidens*), and white-tailed (*C. leucurus*) prairie dogs. All 5 species live in western North America and are similar in morphology and appearance. Black-tailed and Mexican prairie dogs have long, black-tipped tails and comprise the subgenus *Cynomys*. The other 3 species have short, gray- or white-tipped tails and comprise the subgenus *Leucocrosumys* (Hollister 1916; Pizzimenti 1975).

Prairie dogs of all species live in territorial family groups called either coteries for black-tailed and Mexican prairie dogs (King 1955; Trevino-Villarreal 1990) or clans for the other 3 species (Clark 1977; Fitzgerald and Lechleitner 1974; Rayor 1988; Tileston and Lechleitner 1966; Travis et al. 1996; Wright-Smith 1978). Females usually remain in the natal territory for life, but males usually disperse before reaching sexual maturity. Variance in lifetime reproductive success is greater for males than for females for at least 4 species (Hoogland 1995, 1998b, 2001, 2003), and probably for all 5 species. Thus, prairie dogs are appropriately classified as polygynous (Alexander et al. 1979; Clutton-Brock et al. 1982; Trivers 1972).

Sexual dimorphism varies seasonally for some animals (Ralls 1976), but documentation of seasonal variation is arduous. Here I quantify seasonal variation in sexual dimorphism for all 5 prairie dog species. I also investigate sexual dimorphism versus operational sex ratio (OSR), which is the number of fertilizable females divided by the number of sexually active males (Birkhead and Moller 1992; Emlen and Oring 1977; Westneat et al. 1990). A high OSR indicates polygyny, whereas an OSR near unity suggests monogamy. Because larger body mass promotes male reproductive success for black-tailed, Gunnison's, Utah, and white-tailed prairie dogs (Hoogland 1995, 1999, 2003), I predicted that an interspecific comparison would show that sexual dimorphism during the breeding season varies directly with OSR; that is, the most dimorphic species should be most polygynous and the least dimorphic species should be least polygynous.

#### MATERIALS AND METHODS

I have studied the ecology and social behavior of prairie dogs since 1974 (Hoogland 1979, 1981, 1985, 1999, 2001). I captured individuals with single- or double-door Tomahawk livetraps (Tomahawk, Wisconsin) baited with whole oats or sunflower seeds, to insert ear tags (National

Band and Tag, Newport, Kentucky), to mark the pelage with dye (Albanil Dye, Jersey City, New Jersey), or to check reproductive condition (Hoogland 1995). For handling and weighing, I transferred captured adults to a homemade conical canvas bag; for juveniles, I used a plastic sandwich bag (Glad, Oakland, California). I used a spring balance (Pesola AG, Baar, Switzerland) to determine body mass to the nearest gram.

After first emerging from burrows at about dawn, prairie dogs of all species usually forage aboveground for most of the day before submerging for the night at about sunset. Consequently, individuals usually have higher body mass in late afternoon (with full stomachs) than in early morning, with mass sometimes differing by as much as 150 g (Fitzgerald and Lechleitner 1974; see also Tileston and Lechleitner 1966). To reduce biases from daily variation in body mass, I weighed prairie dogs before noon. Weighings later in the day sometimes occurred when prairie dogs first emerged from their burrows later than usual (e.g., on cold days or on a female's day of parturition—Hoogland 1995).

Black-tailed prairie dogs of both sexes at Wind Cave National Park, South Dakota, usually do not copulate until they are 2 years old (Hoogland 1995; King 1955). By contrast, females of the other 4 species copulate as yearlings, and males of these species commonly copulate as yearlings as well (Bakko and Brown 1967; Clark 1977; Hoogland 1999, 2001; Rayor 1985, 1988; Tileston and Lechleitner 1966; Trevino-Villarreal 1990; Wright-Smith 1978). For Mexican, Gunnison's, Utah, and white-tailed prairie dogs, I have considered only 2 age-classes in my analysis of sexual dimorphism: adults ( $\geq 8$  months since 1st emergence from the natal burrow) and juveniles ( $< 3$  weeks, and usually  $< 1$  week, since 1st emergence from the natal burrow). For black-tailed prairie dogs, I have considered 3 age-classes: adults ( $\geq 20$  months since 1st emergence), yearlings ( $\geq 8$  months, but  $< 20$  months, since 1st emergence), and juveniles ( $< 3$  weeks, and usually  $< 1$  week, since 1st emergence).

For black-tailed prairie dogs, all body masses are from animals from Wind Cave National Park from 1975 through 1989. For Gunnison's prairie dogs, all body masses are from animals from Petrified Forest National Park, Arizona, from 1989 through 1995. For Utah prairie dogs, all body masses are from animals from Bryce Can-

yon National Park, Utah, from 1991 through 2001. For white-tailed prairie dogs, all body masses are from animals from the Arapaho National Wildlife Refuge, Colorado, from 1974 through 1976. Body masses for Mexican prairie dogs, which I have not studied, come from the research of Trevino-Villarreal (1990) in Galeana County, Nuevo Leon, Mexico, from 1985 through 1988.

For juveniles, body masses determined by me were available for 1,251 black-tailed prairie dogs, 1,452 Gunnison's prairie dogs, 1,064 Utah prairie dogs, and 235 white-tailed prairie dogs. For adults, body masses determined by me were available for 3,917 black-tailed prairie dogs, 4,194 Gunnison's prairie dogs, 2,416 Utah prairie dogs, and 150 white-tailed prairie dogs. For black-tailed prairie dogs, body masses determined by me also were available for 1,455 yearlings. For Mexican prairie dogs, body masses determined by Trevino-Villarreal (1990) were available for 313 adults. With these large sample sizes, I decided not to include smaller sample sizes from previous investigators who used different methods, worked at different colonies, and did not specify exact dates of weighings (e.g., Bakko and Brown 1967; Clark 1977; Fitzgerald and Lechleitner 1974; Garrett and Franklin 1988; Garrett et al. 1982; King 1955; Rayor 1985; Tileston and Lechleitner 1966; Wright-Smith 1978).

Sample sizes from white-tailed and Mexican prairie dogs (both resulting from 3 years of research) are smaller than sample sizes for black-tailed (15 years), Gunnison's (7 years), and Utah (11 years) prairie dogs. Conclusions from the latter 3 species are thus more reliable.

For the black-tailed prairie dogs that I studied, copulations occurred from mid-February through early April, and periods of gestation and lactation were about 35 and 41 days, respectively (Hoogland 1995). For the Gunnison's prairie dogs that I studied, copulations occurred from mid-March through mid-April, and periods of gestation and lactation were about 29 and 39 days, respectively (Hoogland 1997, 1998a). For the Utah and white-tailed prairie dogs that I studied, timing for these reproductive events was similar to timing for Gunnison's prairie dogs (Hoogland 2001, 2003). For the Mexican prairie dogs studied by Trevino-Villarreal (1990), copulations occurred from December through April; most juveniles first emerged from

natal burrows in April and May. Juvenile prairie dogs of all species start to eat vegetation upon 1st emergence from the natal burrow, and completion of weaning occurs shortly thereafter (Hoogland 1995, 1999, 2003).

For black-tailed, Gunnison's, Utah, and white-tailed prairie dogs, I grouped body masses from half-month intervals (15–28 February, 1–15 March, 16–31 March, and so forth) during the reproductive season (i.e., 1st copulation through 1st emergences of all juveniles from natal burrows). Outside the reproductive season, I grouped body masses from longer time intervals. With the smaller sample sizes of Mexican prairie dogs, I grouped body masses into 2-month intervals.

To calculate OSR, I scored a male as sexually active during the breeding season if I observed him copulate (>90% of all scorings), or I did not see him copulate but he defended a territory containing breeding females and had a pigmented scrotum during the breeding season (Hoogland 1995). I scored a female as fertilizable if I observed her copulate or if she showed signs of either copulation (open vagina), gestation (increased body mass), or lactation (long, turgid nipples—Hoogland 1995).

For most marked individuals, I determined body mass at different stages of the same annual cycle. For example, for Gunnison's and Utah prairie dogs, I usually weighed the same female in late March or early April shortly after she emerged from hibernation, again in early May when she was in late pregnancy, and a 3rd time in June when her juveniles first appeared above-ground. However, I usually had only 1 body mass per individual within the same half-month interval, so estimates and tests of sexual dimorphism for each time interval involved single weights per individual per year. Body mass of the same individual varied across years, and I therefore considered body masses from the same individual in different years to be statistically independent.

Probably because of annual variation in factors such as precipitation, competition, and availability of food, body masses of males and females were higher in some years than in others for all 5 species. The observed trends in sexual dimorphism were nonetheless evident every year for all species. Combining data from different years generated sample sizes large enough for meaningful statistical analyses. All levels of

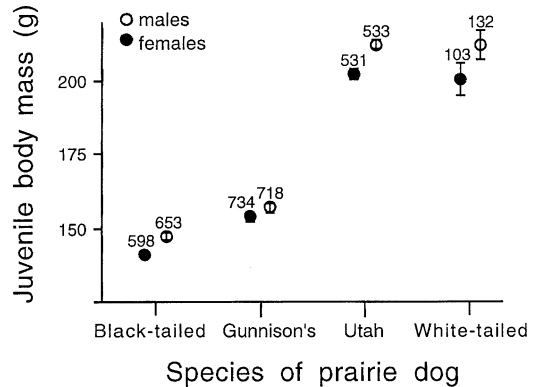


FIG. 1.—Sexual dimorphism in body mass of juvenile prairie dogs at 1st emergence from natal burrow. Intersexual differences were significant (Mann–Whitney *U*-test) for black-tailed and Utah prairie dogs ( $P < 0.001$ ), but not for Gunnison's ( $P = 0.137$ ) and white-tailed prairie dogs ( $P = 0.134$ ).

probability resulted from 2-tailed nonparametric statistical tests (Mann–Whitney *U*-test or Kruskal–Wallis analysis of variance). Symbols in graphs indicate means  $\pm 1$  SE; the number above each SE line indicates the number of weighings.

The tables of Trevino-Villarreal (1990) for Mexican prairie dogs allowed me to calculate accurate means, but not standard errors, for different time intervals. Without the raw data, statistical testing of sexual dimorphism in Mexican prairie dogs was not possible.

## RESULTS

At 1st emergence from the natal burrow, juvenile males were heavier than juvenile females for all 4 species for which I have data, but the intersexual difference was only significant for black-tailed and Utah prairie dogs (Fig. 1). The statistical insignificance for white-tailed prairie dogs probably resulted from small sample sizes.

Adult males were heavier than females for black-tailed, Gunnison's, and Utah prairie dogs for most time intervals (Figs. 2 and 3). The same was true for Mexican and white-tailed prairie dogs, but small sample sizes often precluded statistical significance (Fig. 4).

Even during the period when most fe-

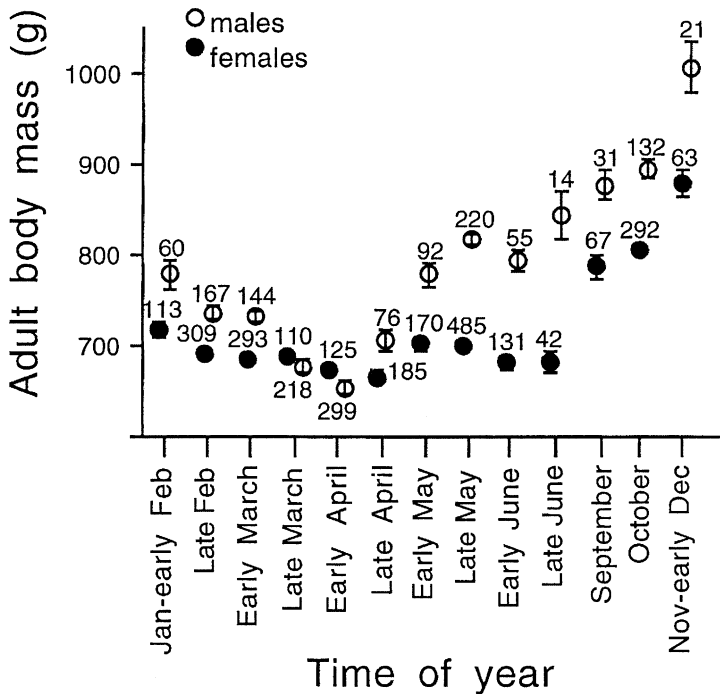


FIG. 2.—Sexual dimorphism in body mass of adults at different stages of the annual cycle for black-tailed prairie dogs. Intersexual differences were significant for most stages (Mann–Whitney *U*-test):  $P = 0.380$  for late March,  $P = 0.041$  for early April, and  $P \leq 0.004$  for all other stages.

males were in late pregnancy (late April), adult male Gunnison's prairie dogs were always significantly heavier than adult females. For Utah prairie dogs during the period of late pregnancy (late April), by contrast, adult males were insignificantly lighter than adult females. For black-tailed prairie dogs during the period of late pregnancy (early April), adult males were significantly lighter than adult females.

For yearling black-tailed prairie dogs, males were heavier than females during certain time intervals (late January and early February and early May through early November), but females were heavier during other time intervals (late February through late April). Most of these intersexual differences among yearlings were not significant.

For black-tailed prairie dogs, body mass varied curvilinearly with age: middle-aged

individuals were heavier than younger and older individuals (Fig. 5). Similar variation in body mass versus age also occurs for Gunnison's and Utah prairie dogs (Hoogland 2003).

Regarding body mass of females, Mexican prairie dogs were the heaviest and Gunnison's prairie dogs were the lightest (Fig. 6a). Regarding body mass of males, Mexican prairie dogs were the heaviest in February–March and April–May, but white-tailed prairie dogs were the heaviest in June–July (Fig. 6b). Gunnison's prairie dog males were the lightest for all 3 time periods.

Contrary to expectation, sexual dimorphism during the breeding season did not vary directly with OSR in an interspecific comparison involving black-tailed, Gunnison's, Utah, and white-tailed prairie dogs; no data on OSR were available for Mexican prairie dogs. For example, the most dimor-

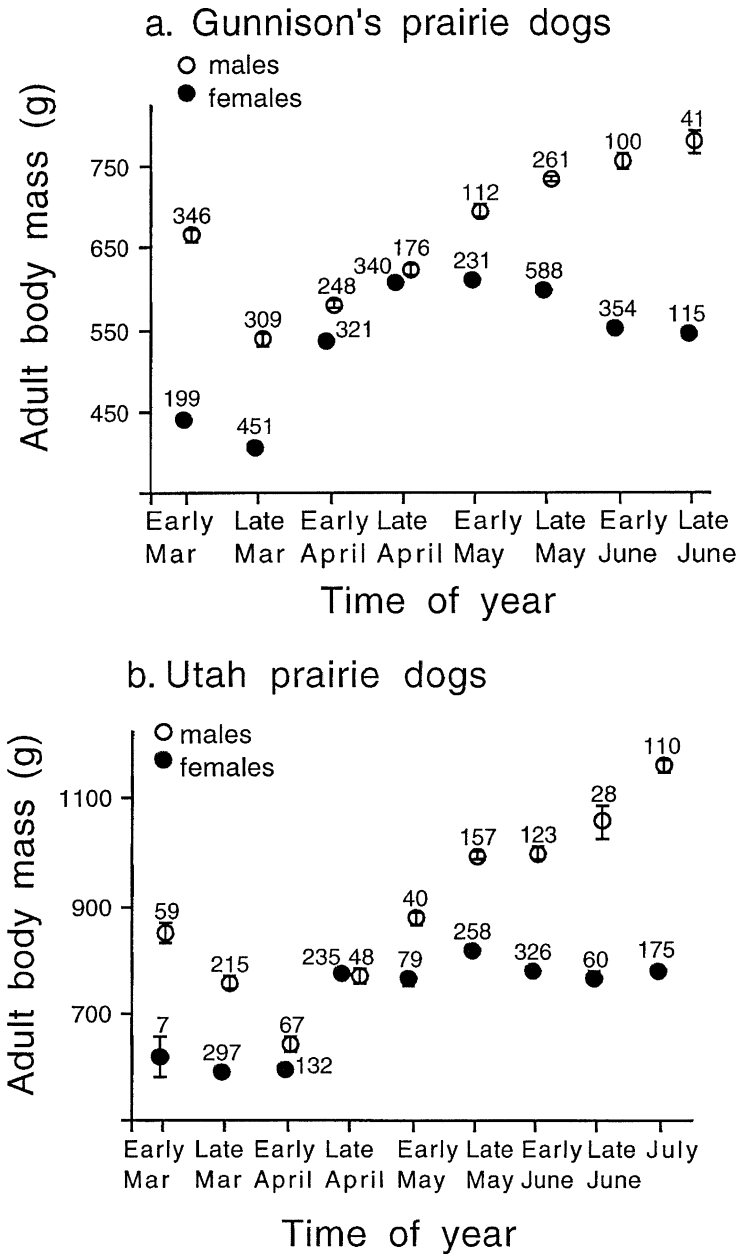


FIG. 3.—Sexual dimorphism in body mass of adults at different stages of the annual cycle for a) Gunnison's and b) Utah prairie dogs. Intersexual differences were significant for most stages (Mann–Whitney *U*-test). For Gunnison's prairie dogs,  $P = 0.026$  for late April and  $P < 0.001$  for all other stages. For Utah prairie dogs,  $P = 0.964$  for late April and  $P \leq 0.009$  for all other stages.

phic species (white-tailed prairie dogs) had the lowest OSR, and the least dimorphic species (black-tailed prairie dogs) had the 2nd-highest OSR.

## DISCUSSION

All 5 prairie dog species showed male-biased sexual dimorphism at most stages of the



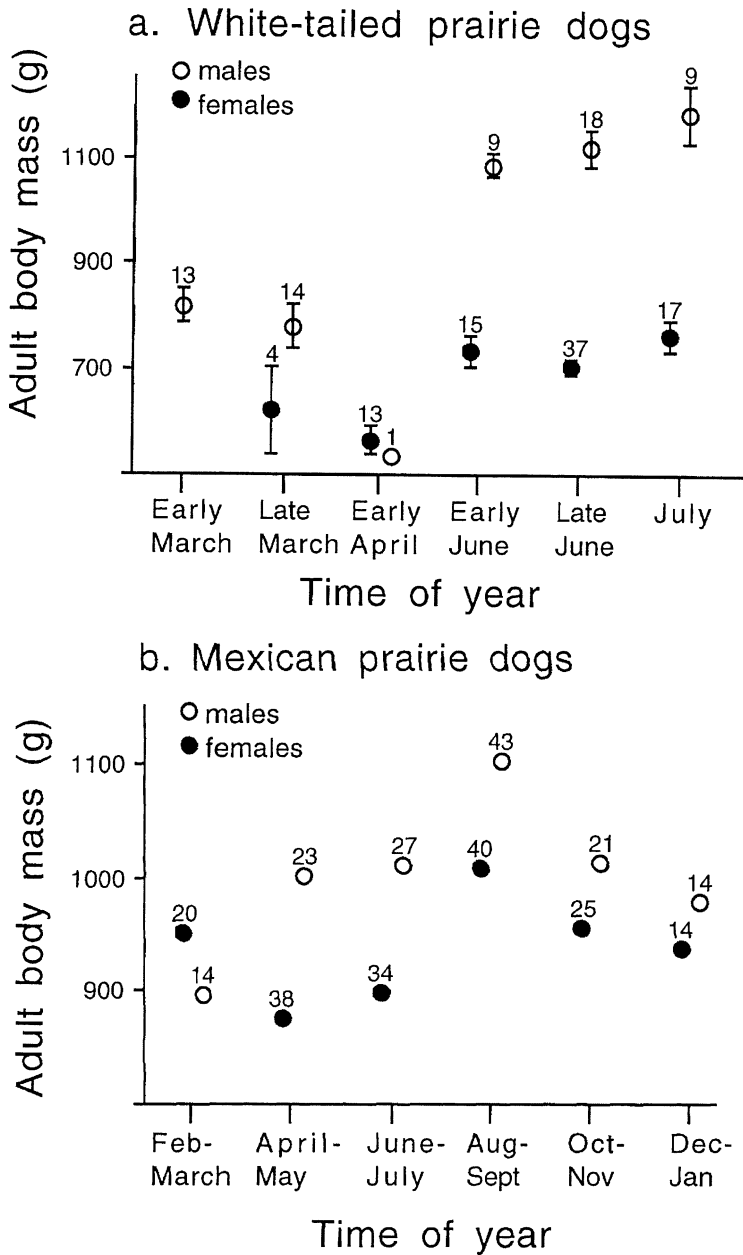


FIG. 4.—Sexual dimorphism in body mass of adults at different stages of the annual cycle for a) white-tailed and b) Mexican prairie dogs. For white-tailed prairie dogs,  $P \geq 0.137$  for intersexual differences in late March and early April, and  $P < 0.001$  for all other stages (Mann-Whitney  $U$ -test). For Mexican prairie dogs, statistical testing of sexual dimorphism was not possible.

annual cycle. Except when females were in late pregnancy or when sample sizes were small, most of the intersexual differences in body mass were statistically significant.

Despite large sample sizes for black-tailed, Gunnison's, and Utah prairie dogs, in particular, information on sexual dimorphism was unavailable or minimal for cer-

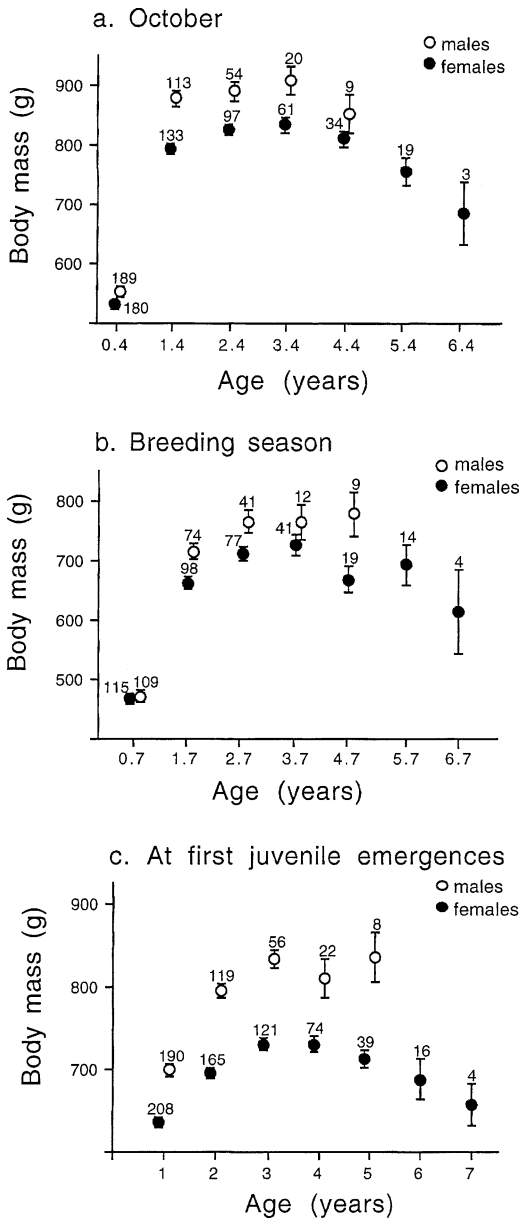


FIG. 5.—Sexual dimorphism in body mass at different ages for black-tailed prairie dogs a) in October, 4 months before the breeding season; b) during the breeding season of February and March; and c) at 1st juvenile emergences in May and June. In October,  $P = 0.199$  for intersexual differences at age 4.4, and  $P \leq 0.012$  for all earlier ages (Mann–Whitney  $U$ -test). During the breeding season,  $P = 0.575$  at age 0.7;  $P = 0.457$  at age 3.7; and  $P \leq 0.022$  for ages 1.7, 2.7, and 4.7. At 1st juvenile emergences in May

and June,  $P \leq 0.003$  for all ages. Male black-tailed prairie dogs at the study colony did not live longer than 5 years.

tain stages of the annual cycle. Each year I initiated livetrapping just before the breeding season (late February or early March), and continued until the capture of the last juvenile (late June). Livetrapping at other times of the year was irregular. More information on prairie dog body masses from July through January would be valuable.

Sexual dimorphism varied with stage of the annual cycle for all 5 prairie dog species. For example, sexual dimorphism in Gunnison's prairie dogs was 143% in late June, but was only 103% in late April. For Utah prairie dogs, sexual dimorphism ranged from 153% in late June to 99% in late April. For black-tailed prairie dogs, sexual dimorphism ranged from 124% in late June to 97% in early April.

Despite large sample sizes, all body masses for each species were from a single geographic area (e.g., Wind Cave National Park, Petrified Forest National Park, or Bryce Canyon National Park). Most body masses for each species were from a single colony. However, body size varies across the geographic range for all 5 species of prairie dogs (Pizzimenti 1975). Skeletal measurements increase with latitude for Utah prairie dogs, for example, but decrease with latitude for white-tailed and Mexican prairie dogs (Pizzimenti 1975). Further, body mass can vary substantially between 2 nearby colonies, mainly because of differences in competition and availability of forage (Cully 1997; Garrett et al. 1982; Rayor 1985; Wright-Smith 1978). Data from other colonies and from more geographic areas would be valuable, and might change some of my conclusions (e.g., the ranking of prairie dog species by body mass of females). With so much intraspecific variation, speculation about reasons for interspecific differences in body mass

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and June,  $P \leq 0.003$  for all ages. Male black-tailed prairie dogs at the study colony did not live longer than 5 years.



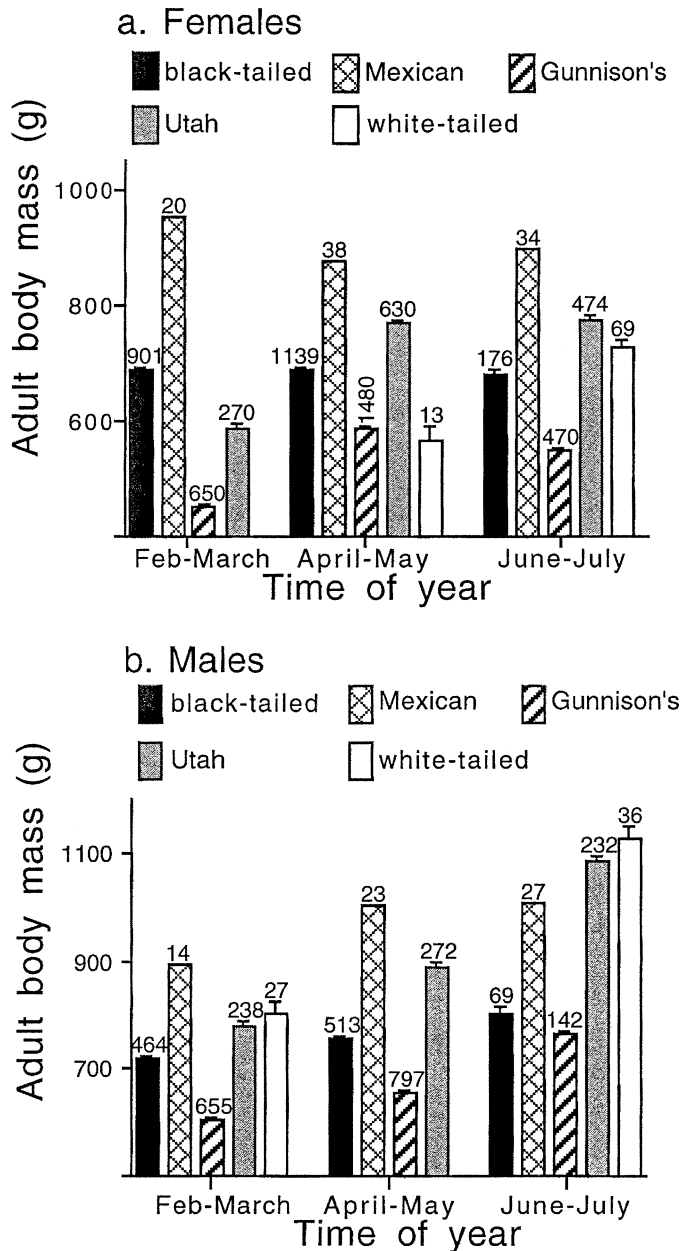


FIG. 6.—Body masses of a) adult females and b) adult males for all 5 species of prairie dogs at different stages of the annual cycle. Interspecific differences were significant for both sexes ( $P < 0.001$  for each stage, Kruskal–Wallis analysis of variance, which does not include data from Mexican prairie dogs).

and sexual dimorphism would be premature.

Competition for food during the non-breeding season or at any other time prob-

ably has not been important in the evolution of sexual dimorphism among prairie dogs. For example, for black-tailed prairie dogs, males and females of the same coterie eat

the same plants within the same small home territory throughout the year (Hoogland 1995; King 1955). Males and females within the same family group of the other prairie dog species also routinely consume the same plants in the same home territory (Clark 1977; Hoogland 1999, 2003; Rayor 1988; Travis et al. 1995; Trevino-Villarreal 1990; Wright-Smith 1978).

Although intersexual competition for food is not obviously related to sexual dimorphism among prairie dogs, evidence for the importance of sexual selection is compelling (Hoogland 1995, 1998b, 2003). Specifically, large prairie dog males are more likely than smaller males to secure breeding territories (intrasexual sexual selection), and to be chosen for copulation by estrous females (intersexual sexual selection). Large males consequently sire more offspring for at least 4 of the 5 species. Larger body mass also promotes female reproductive success for 4 of the 5 species, but the effect of body mass on reproductive success is always more pronounced for males (Hoogland 1995, 1998b, 1999, 2003).

In theory, male and female prairie dogs probably would benefit from maximal body mass throughout the year. In practice, however, individuals sometimes must sacrifice body mass to achieve other goals. For example, males of all species are obsessed with defending territories and courting estrous females during the breeding season, and therefore do little foraging (Hoogland 1995, 1999, 2001). Consequently, body mass of males plummets during the breeding season until all females have copulated. Thus, the most stressful period for males (in terms of body mass) is the breeding season. After the breeding season, males concentrate on foraging once again and slowly regain body mass. For females, the most stressful period is lactation. Body mass of females drops steadily during lactation (or rises only slowly), and does not rise again until after the weaning of offspring. These different schedules and requirements for

males and females help to explain why sexual dimorphism varies seasonally for prairie dogs.

Division of parental labors also helps to explain seasonal variation in sexual dimorphism among prairie dogs. For example, only females increase body mass via pregnancy and lose body mass via lactation. On the other hand, male black-tailed and Utah prairie dogs are more likely than females to defend offspring against invading infanticidal males, and large males defend better than smaller males (Hoogland 1995, 2001).

Male-biased sexual dimorphism among prairie dogs is typically minimal at the end of the breeding season: exhausted males are emaciated, but early-breeding females are heavy because they are in late pregnancy. For black-tailed and Utah prairie dogs at the end of the breeding season, sexual dimorphism is actually female-biased. By contrast, sexual dimorphism is typically maximal after the 1st emergences of juveniles from their natal burrows, when rested, well-fed males are heavy and females depleted from lactation are thin.

With so much seasonal variation, how should biologists specify sexual dimorphism for prairie dogs? Perhaps the answer for prairie dogs and other animals should depend on causation. For prairie dogs, as noted above, the most likely ultimate explanation for sexual dimorphism is sexual selection. Consequently, the most appropriate time to measure sexual dimorphism probably is at the beginning of the breeding season, when intra- and intersexual sexual selection—but not necessarily sexual dimorphism—should be most intense. Male-biased sexual dimorphism during the breeding season is 105% for black-tailed prairie dogs, 127% for Utah prairie dogs, 131% for Gunnison's prairie dogs, and 136% for white-tailed prairie dogs. Levels of sexual dimorphism at other stages probably are mostly secondary consequences of sexual selection for sexual dimorphism during the breeding season.

Because larger body mass enhances male

reproductive success for prairie dogs (Hoogland 1995, 2003), I predicted that an interspecific comparison would show a positive correlation between sexual dimorphism during the breeding season and OSR; that is, the most dimorphic species (white-tailed prairie dogs) should be most polygynous and the least dimorphic species (black-tailed prairie dogs) should be least polygynous. Curiously, I detected no correlation, even though 3 aspects of my analysis are noteworthy. First, my estimates of both sexual dimorphism and OSR result from large sample sizes collected over many years. Other studies have relied on smaller sample sizes. Second, my most reliable estimates of sexual dimorphism result from body masses of males and females during the breeding season. In other studies, estimates of sexual dimorphism result from body masses recorded throughout the year. Third, my estimates of OSR result from numbers of males and females that were sexually mature, and I observed most of them copulate. In other studies, estimates of OSR usually result from simple counts of males and females, many of whom do not copulate. The major shortcoming of my analysis, obviously, is that I have data on both sexual dimorphism and OSR for only 4 species.

Previous comparative research has indicated that sexual dimorphism correlates positively with the degree of polygyny within taxonomic groups such as pinnipeds, primates, and ungulates (Alexander et al. 1979; Clutton-Brock et al. 1977; Jarman 1974; Perez-Barberia et al. 2002). However, these correlations resulted from rough estimates of OSR and from body masses measured throughout the year. As for prairie dogs (Hoogland 1995, 2001), do many full-size pinnipeds, primates, and ungulates fail to mate—and thereby bias estimates of OSR based merely on counts of adults rather than on counts of adults that actually copulate? Do pinnipeds, primates, and ungulates show seasonal variation in sexual dimorphism similar to the variation among

prairie dogs? If the answer is affirmative for either of these questions, then the observed positive correlations between polygyny and sexual dimorphism require further scrutiny.

Precise causation for sexual dimorphism is usually unknown, and evidence for seasonal variation in sexual dimorphism is elusive. More information on both issues will lead to a better understanding of sexual dimorphism within natural populations.

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