DURATION OF GESTATION AND LACTATION FOR GUNNISON'S PRAIRIE DOGS

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The length of gestation is the number of days between fertilization and parturition, and the length of lactation is the number of days between parturition and weaning. Determination of these lengths is difficult for ground-dwelling squirrels such as prairie dogs, marmots, and ground squirrels that usually copulate, give birth, and nurse offspring underground. For Gunnison's prairie dogs (*Cynomys gunnisoni*), the mean ±1 *SD* length of gestation is 29.3 ± 0.53 days (n = 124). The approximate length of lactation, estimated from the mean ±1 *SD* duration between parturition and the first emergence of juveniles from the natal burrow, is 38.6 ± 2.08 days (n = 112).

Key words: *Cynomys gunnisoni*, Gunnison's prairie dog, gestation, lactation, litter size

Probably to escape predators or interference from other conspecifics (Davis, 1982; Moller and Birkhead, 1989; Schwagmeyer, 1990), mating pairs of most species of ground squirrels (*Spermophilus*), marmots (*Marmota*) and prairie dogs (*Cynomys*) copulate underground. For example, copulations usually occur underground for Alaska and black-capped marmots (*M. broweri* and *M. camtschatica*), black-tailed prairie dogs (*C. ludovicianus*), and Uinta, California, Idaho, Arctic, Richardson's, and rock ground squirrels (*S. armatus*, *S. beecheyi*, *S. brunneus*, *S. parryii*, *S. richardsonii*, and *S. variegatus*; Fitch, 1948; Hoogland, 1995; Kapitonov, 1960; Michener, 1985; Ortega, 1990; Rausch and Rausch, 1971; Sherman, 1989; Slade and Balph, 1974).

The length of gestation is the number of days between fertilization and parturition, and the length of lactation is the number of days between parturition and weaning. Even when copulations occur above ground for ground-dwelling squirrels, as they commonly do for white-tailed prairie dogs (*C. leucurus*) and Belding's and thirteen-lined ground squirrels (*S. beldingi* and *S. tridecemlineatus*; Erpino, 1968; Hanken and Sherman, 1981; Hoogland, 1995; Schwagmeyer, 1984, 1986; Schwagmeyer and Foltz, 1990), parturition invariably occurs underground. Further, females of ground-dwelling squirrels almost always nurse their offspring underground (Barash, 1989; Ferron, 1984; Hoogland, 1995; Michener, 1983, 1984*a*). Consequently, determining the lengths of gestation and lactation for ground squirrels, prairie dogs, and marmots is more difficult than for animals such as red deer (*Cervus elaphus*) and American bison (*Bison bison*) that are above ground and conspicuous not only for copulation, but also for parturition and nursing (Berger, 1992; Berger and Cunningham, 1991; Clutton-Brock et al., 1982). Using some new methods and some that have been used by other researchers (e.g., Michener, 1985; Sherman, 1976), I provide here the first accurate estimates of the lengths of gestation and lactation for Gunnison's prairie dogs (*C. gunnisoni*) living under natural conditions.

STUDY AREA AND METHODS

My study colony of Gunnison's prairie dogs was at Petrified Forest National Park, Arizona, at an elevation of ca. 1,700 m. I initiated research there in 1989, and continued through 1995. Using binoculars and a 60× telescope, field assistants and I watched marked individuals from 4-m-high observation towers.

Gunnison's prairie dogs are medium-sized (250-1,100 g for adults), hibernating, colonial rodents of the squirrel family (Sciuridae; Fitzgerald and Lechleitner, 1974; Longhurst, 1944; Slobodchikoff and Schulz, 1988; Waring, 1970). Colonies occur in Arizona, Colorado, New Mexico, and Utah (Pizzimenti, 1975; Pizzimenti and Hoffmann, 1973). Within colonies, Gunnison's prairie dogs live in territorial, harem-polygynous family groups called clans (Fitzgerald and Lechleitner, 1974; Rayor, 1985, 1988; Slobodchikoff et al., 1991). Clans typically contain one breeding male and three or four genetically related breeding females, as well as numerous juvenile offspring (Hoogland, 1996).

Female Gunnison's prairie dogs at my study colony copulated in their first breeding season, when they were ca. 11 months old. Age of sexual maturation was more variable among males; in some years (when older males were rare) as many as 75% of males copulated as yearlings, but in other years (when older males were more common) as few as 10% of yearling males copulated (Hoogland, 1996; Rayor, 1985, 1988). Size of litters at my study colony when juveniles first appeared above ground at ca. 5 weeks of age ranged from one to seven (mean $\pm$ 1 *SD* = 3.71 $\pm$ 1.18; n = 204).

Like mothers of other species of sciurids such as black-tailed prairie dogs and Belding's, Columbian, (*S. columbianus*), round-tailed (*S. tereticaudus*), and Uinta ground squirrels (Balph, 1984; Dunford, 1977*a*, 1977*b*; Festa-Bianchet and Boag, 1982; King, 1955; Sherman, 1980), mothers of Gunnison's prairie dogs usually reared their offspring in separate nursery burrows (Hoogland, 1996). Maternity was thus easy to establish when the juveniles first appeared above ground.

At Petrified Forest National Park, Gunnison's prairie dogs hibernated from November through February. Individuals emerged from hibernation in early March, and the mating season (i.e., the interval during which copulations occurred) started in mid- or late March and extended through early April (Hoogland, 1996). Individual females were sexually receptive during an estrus period that spanned 4–10 h of a single day. Females usually copulated with more than one male, and sometimes with as many as four or five; precise assignment of paternity usually was impossible from behavioral observations alone (Hoogland, 1996).

Methods for studying Gunnison's prairie dogs were almost identical to those used in my long-term study of black-tailed prairie dogs (Hoogland, 1985, 1986, 1992, 1995). To capture individuals, I used Tomahawk, 15 by 15 by 60-cm, double-door livetraps baited with a mixture of whole oats and sunflower seeds. For permanent identification of individuals, I used National fingerling eartags. For visual identification from a distance, I used Nyanzol fur dye. Dye markings on the flank included combinations of numbers, stripes, and symbols, and were unique for each individual.

Exceptions sometimes occurred, but most Gunnison's prairie dogs copulated underground. I determined the date of copulation from either vulvar examinations or behavioral observations.

In 1989 and 1990, I systematically livetrapped female Gunnison's prairie dogs on a daily basis during each morning of the breeding season. Upon emergence from hibernation in March, a female's vulva was slightly swollen and seemed to be sealed shut by a thin layer of skin. The vulva continued to swell for several days until it appeared ready to burst, and on the next morning was wide open. Sometimes the open vulva had a conspicuous copulatory plug similar to that found in other species of sciurids (Hoogland, 1995; Michener, 1984*b*; Murie and McLean, 1980). I inferred copulation on the day before I first detected the open vulva.

In 1989 through 1995, I watched marked Gunnison's prairie dogs during the breeding season. Although most copulations occurred underground, six almost-diagnostic above-ground behaviors commonly occurred before or after an underground consortship, which was as short as 5 min or as long as 300 min (Hoogland, 1996). These behaviors included: 1) a female rarely submerged alone with a male during daylight hours unless she was in estrus; 2) a female was the recipient of unusually frequent anal sniffing on the day of her estrus and copulation, 3) just before consorting underground with an estrus female, a breeding male sometimes gave one or more unique mating calls not heard in any other context, 4) self-licking of the penis or the vulva commonly occurred after an underground consortship, but almost never under other circumstances, 5) just after consorting underground, the male or the female commonly rolled in the dirt; such "dustbaths" rarely occurred at any other time, 6) on the day that she consorted under-

ground, an estrus female sometimes remained above ground as much as 60 min after nonestrous females had submerged for the night. Several independent lines of evidence indicate that these unusual behaviors really did indicate estrus and copulation. For example, those rare copulations (n = 24) that occurred above ground showed the same diagnostic behaviors. Further, in those years when I recorded vulvar condition, the diagnostic behaviors consistently occurred only on the day before I first recorded the open vulva. Many of these same behaviors also are diagnostic of underground copulations of other species of sciurids such as Richardson's and Idaho ground squirrels and black-tailed prairie dogs (Davis, 1982; Hoogland, 1995; Michener, 1985; Sherman, 1989). Finally, dates of parturitions and dates of first appearances of their offspring above ground for females of Gunnison's prairie dogs varied directly with dates of underground consortships for the same females (for both, $r \geq 0.811$ and $P < 0.001$ each year, Spearman-rank correlation test). For example, the first female to consort underground with breeding males each year was invariably the first to give birth and the first to produce emergent offspring.

As for black-tailed prairie dogs and Belding's and Richardson's ground squirrels (Hoogland, 1995; Michener, 1985; Sherman, 1976), vulvar examinations in combination with changes in body mass pinpointed the day of parturition for Gunnison's prairie dogs. About 4 weeks after copulation, each pregnant female consistently showed a white vagina each morning with no visible blood. She then abruptly showed a distinctly pink or red vagina, often with fresh blood; in addition, the peri-vaginal fur often showed fresh bloodstains. On the same day that the vagina was first pink or red, body mass suddenly dropped a mean ± 1 *SD* of 75.9 ± 19.1 g (range = 37-110 g, n = 43). I inferred parturition on the first day that maternal body mass plummeted and the vagina was pink or red, rather than white.

Pregnant females usually emerged early in the morning, spent the entire day foraging above ground, and were among the last to submerge for the night. However, like female black-tailed prairie dogs (Hoogland, 1995), female Gunnison's prairie dogs radically altered their behaviors on the day of parturition. Specifically, on the first day of the pink or red vagina the female was usually one of the last to appear above ground in the morning, sometimes first emerging as much as 4 h after all the other colony residents. Further, the female usually made one or more lengthy visits to the home nursery burrow, often for as long as 3–4 h, on the first day of the pink or red vagina, and she was one of the first to submerge for the night. These striking changes in behavior were presumably indicative of parturition and maternal care of neonates. The altered behaviors usually continued for 2 weeks or so, after which most mothers resumed the routine typical of pregnant females. All significance levels (P-values) resulted from two-tailed nonparametric statistical tests.

Results

I had two estimates for length of gestation for Gunnison's prairie dogs. First, from changes in vulvar condition coupled with drastic loss of maternal body mass, I estimated length of gestation ($\bar{X}$ ± 1 *SD*) to be 29.3 ± 0.45 days (range = 29-30 days, n = 43). Second, from radical changes in a mother's pattern of first appearance above ground each morning, I estimated length of gestation ($\bar{X}$ ± 1 *SD*) to be 29.3 ± 0.57 days (range = 28–31 days, n = 81). These two estimates, almost identical, did not differ statistically (P = 0.724, Mann-Whitney U test). The overall estimate of length of gestation for Gunnison's prairie dogs ($\bar{X}$ ± 1 *SD*) was 29.3 ± 0.53 days (n = 124).

I estimated length of lactation ($\bar{X}$ ± 1 *SD*) to be 38.6 ± 2.08 days (Fig. 1). Technically, Fig. 1 shows the number of days between parturition and the first emergence of juveniles from the natal burrow.

For certain females, I was able to determine both date of copulation and date of first emergence of juveniles, but not the date of parturition. Size of samples for the cumulative duration of both gestation and lactation (Fig. 2) was larger than samples for either gestation or lactation alone.

Discussion

The pink or red vagina coupled with loss in body mass identified parturition for 43 females. However, this method required live-trapping and, therefore, was disruptive

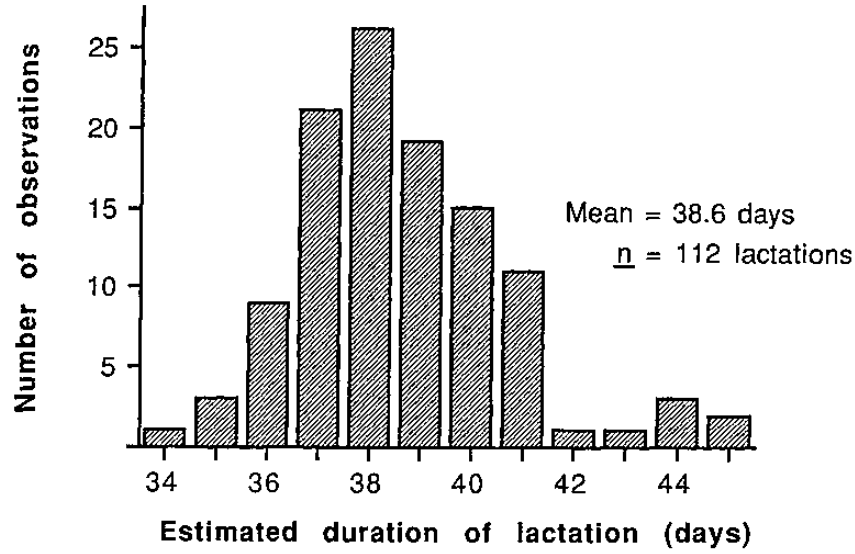

FIG. 1.—Length of lactation for Gunnison's prairie dogs, estimated by counting the number of days between parturition within a burrow and the first emergence of juveniles at that burrow.

and time-consuming. The late first appearance above ground of the mother ca. 4 weeks after copulation provided a simpler, equally accurate, alternative method for identifying parturition, and hence length of gestation when I also knew the date of copulation, for 81 additional females.

For some animals such as mountain ca-

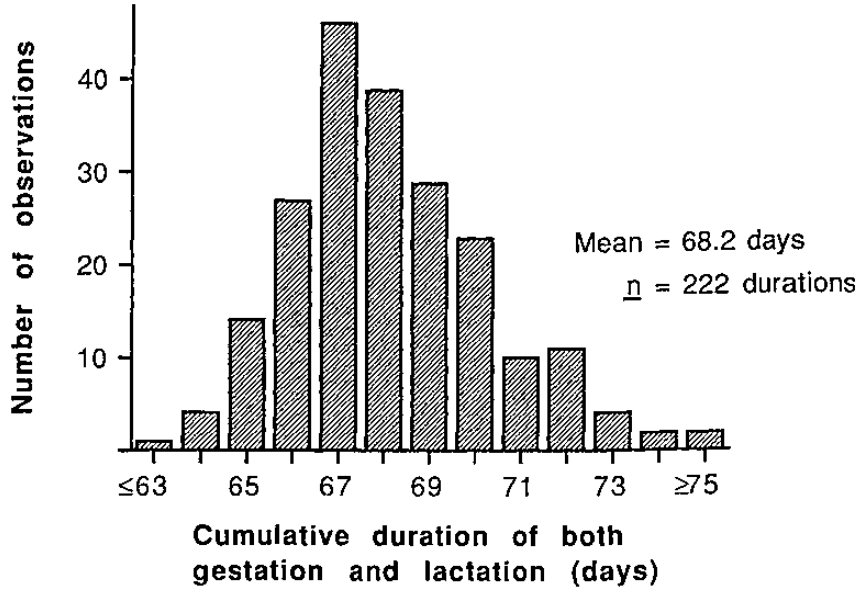

FIG. 2.—Cumulative length of both gestation and lactation, estimated by counting the number of days between copulation by a female and the first emergence of that female's offspring from the natal burrow. Sample sizes are larger here than in Fig. 1 because I could not always specify the date of parturition for many females that I saw copulate.

vies (*Microcavia australis*), parturition almost always occurs in the morning (Rood, 1972). For other animals such as Richardson's ground squirrels, however, parturition commonly occurs in late afternoon or early evening (Michener, 1985). I assigned parturition to a female Gunnison's prairie dog on the morning of the first day when I observed either her pink or red vagina coupled with a precipitous loss in body mass, or her delayed first emergence in the morning. The freshness of the blood in most vaginal examinations indicated that parturition really had occurred on the assigned morning. However, parturition occasionally might have occurred in the late afternoon or evening of the day before I detected the diagnostic signs. If so, then some of my estimates of the length of gestation were too long by 1 day, and some of my estimates of the length of lactation (Fig. 1) were too short by 1 day.

Not every female Gunnison's prairie dog that copulated gave birth. As for female black-tailed prairie dogs (Anthony and Foreman, 1951; Knowles, 1987), failure to give birth might have resulted either from failure to conceive or from abortion of all embryos (with or without resorption) after conception. Females that did not give birth showed no pink or red vagina, no sudden loss in body mass, and no radical change in time of first emergence from the home nursery burrow ca. 4 weeks after copulation. Most females that failed to give birth had vaginas sealed shut by a thin layer of skin at the expected time of parturition, but others had open, white vaginas that never turned pink or red.

At the expected time of parturition, some female Gunnison's prairie dogs that failed to give birth after copulating had atrophied mammary glands that were hard to find. I surmise that these females, like female black-tailed prairie dogs showing similar atrophy (Hoogland, 1995), either never achieved fertilization or aborted their embryos almost immediately after conception. Other females that failed to give birth after copulating had larger, more visible mammary glands at the expected time of parturition. I surmise that these latter females conceived and were pregnant for ≥1 week before abortion.

Like pre-emergent juvenile black-tailed prairie dogs (Hoogland, 1995), pre-emergent juvenile Gunnison's prairie dogs depended primarily on their mother's milk for nourishment, but probably ate plants brought underground by the mother as well. Conversely, emergent juveniles depended primarily on their own foraging for nourishment, but sometimes received additional nourishment from nursing (J. L. Hoogland et al., in litt.; L. S. Rayor, pers. comm.). To further complicate matters, almost all nursing occurred underground. With these problems in mind, and cognizant of the difficulty of trying to specify the exact day of weaning, I followed the example of previous research with other ground-dwelling squirrels (Barash, 1973; Davis, 1984; Holmes and Sherman, 1982) by estimating that weaning for Gunnison's prairie dogs coincides with the first emergence of juveniles from the natal burrow. The estimated length of lactation is thus the number of days between parturition and first emergence of juveniles (Fig. 1).

For black-tailed prairie dogs, the estimated length of gestation ($\bar{X} \pm 1\ SD = 34.6 \pm 0.73$ days, $n = 225$—Hoogland, 1995) is longer than for Gunnison's prairie dogs. The estimated length of lactation ($\bar{X} \pm 1\ SD$) for black-tailed prairie dogs (41.3 ± 2.46 days, $n = 149$—Hoogland, 1995) also is longer than for Gunnison's prairie dogs (Fig. 1). Comparable data are not yet available for white-tailed, Mexican (*C. mexicanus*), and Utah (*C. parvidens*) prairie dogs.

For black-tailed prairie dogs and Richardson's ground squirrels, length of gestation seems unrelated to size of litter (Hoogland, 1995; Michener, 1985). For humans (*Homo sapiens*) and some domestic animals such as goats (*Capra hircus*), pigs (*Sus scrofa*), cattle (*Bos taurus*), and sheep (*Ovis aries*), however, the length of gesta-

tion varies inversely with size of litter (Clegg, 1959; Dziuk, 1977). Gunnison's prairie dogs resemble the latter animals because length of gestation varied inversely with size of litter at first emergence of juveniles ($P = 0.015$, $r = -0.247$, Spearman-rank correlation test; $n = 101$). However, the mean difference in length of gestation between females that reared only one emergent offspring versus females that reared six or seven emergent offspring was only 1 day.

Juvenile Gunnison's prairie dogs might have emerged from the natal burrow because they were ready and large enough to obtain all their nourishment from their own foraging. If so, then females with small litters probably provided more milk per juvenile and were better able to accelerate weaning than were females with larger litters. The number of days between parturition and first emergence of juveniles, therefore, should have varied directly with size of litter. Conversely, first emergence might have occurred primarily because a mother had exhausted all her personal resources for producing milk, such as internal fat reserves and food in the defended territory around the home nursery burrow, although her offspring might not have been ready or large enough to obtain all their own nourishment. If so, then females with large litters presumably ran out of resources faster than females with smaller litters. The number of days between parturition and first emergence of juveniles in this latter scenario should have varied inversely with size of litter. Another possibility is that weaning occurred primarily when a mother had exhausted her personal resources, but mothers appropriately adjusted size of litter relative to personal resources; length of lactation should have been unrelated to size of litter, as occurs for animals such as Richardson's and Cascade golden-mantled ground squirrels (*S. saturatus*; Kenagy et al., 1990; Michener, 1985). With these arguments in mind, I examined size of litter versus the estimated length of lactation for *C. gunnisoni*. As for black-tailed prairie dogs (Hoogland, 1995), the number of days between parturition and first emergence of juveniles varied inversely with size of litter at first emergence of juveniles for Gunnison's prairie dogs, but this trend was not statistically significant ($P = 0.067$, $r = -0.190$, Spearman-rank correlation test; $n = 92$). These results, along with the smaller body mass of juveniles in larger litters, indicate that first emergence of juvenile Gunnison's prairie dogs resulted primarily from exhaustion of maternal resources.

Although ground squirrels, marmots, and prairie dogs have been the subjects of numerous longterm studies (e.g., Murie and Michener, 1984), reliable estimates of lengths of gestation and lactation under natural conditions are available for only a handful of species (Hoogland, 1995; Knopf and Balph, 1977; Michener, 1984*c*, 1985; Murie and Harris, 1982; Sherman, 1976). Perhaps the methods outlined here will lead to estimates from additional species.

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