THE ANNUAL CYCLE OF WYOMING GROUND SQUIRRELS IN COLORADO

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ABSTRACT.—Annual activity patterns and changes in mass of Wyoming ground squirrels (Spermophilus elegans elegans) were studied in Colorado from 1978 to spring 1981. Dates of emergence differed among years and among sex and age cohorts, and were dependent both on endogenous rhythms and on exogenous factors such as temperatures and snow cover. Adult males emerged during March, 16–18 days before females. Females were bred within 1–4 days after emergence. Both yearling males and females bred during 1979 and 1981, but yearling females did not wean litters during 1980 when ground squirrels emerged late and at low body mass because of low temperatures and deep snow cover. Parturition occurred in late April or early May, and juveniles appeared aboveground in late May or early June. In contrast to most other ground squirrel species, adult females submerged 1–1.5 weeks before adult males (late July and early August, respectively). Juvenile females submerged before juvenile males. An endogenous rhythm of consumption interacted with high body-fat levels to induce immersion in adults, and with low temperatures and low food availability to induce immersion in juveniles. Mean masses for males were significantly greater than for females upon emergence and through the breeding season. Breeding males lost mass after emergence, gained mass at a rapid rate from May through mid-July, then gained little extra mass until immersion. Breeding females gained mass after emergence, lost mass for 1 month after parturition, then gained mass again before immersion. Loss of mass during hibernation averaged 42% for adult and yearling males, 41% for adult and yearling females, 38% for juvenile males, and 37% for juvenile females. Because adults are aboveground for a short period, the amount of temporal contact between adults and juveniles is small and this species is classified as one of the least social ground squirrels.

The annual cycle of most North American ground squirrels (Spermophilus) consists of a hibernation season and an active season characterized by spring emergence, reproduction, emergence of juveniles, prehibernatory fattening, and late summer or autumn immersion. The date of spring emergence from hibernation differs from year to year, and the annual rhythm appears to be synchronized with environmental conditions at that time (Heller and Poulson, 1970; Michener, 1979). The timing of the reproductive sequence is set by the timing of emergence by females from hibernation; males usually emerge from hibernation before females and begin breeding as soon as females emerge (Knopf and Balph, 1977; McKeever, 1964; Michener, 1983a; Morton and Sherman, 1978; Murie and Harris, 1982). Variation in dates of immersion has been correlated with sex, age, reproductive history, and fat deposition (Dorrance, 1974; Michener, 1977, 1978, 1979; Morton, 1975; Murie, 1973).

Several early investigators described the annual cycle of Wyoming ground squirrels (Spermophilus elegans; Burnett, 1913; Howell, 1938; Warren, 1942) but their studies were incomplete and did not include variation between and within sex and age cohorts. More recent studies included dispersal (Hansen, 1962; Pfeifer, 1980), energy dynamics (Zegers and Williams, 1977, 1979), and time budgets (Zegers, 1981) of populations of S. e. elegans. The objectives of this research was to determine the timing of events and accompanying changes in mass of the Wyoming ground squirrel during the annual cycle in Colorado.

METHODS

The study was conducted from 1978 to spring 1981 in Middle Park, 9 km NW Kremmling, Grand Co., Colorado (elev. 2,350 m). Middle Park is an unforested intermountain basin where maximum air temperatures average 25°C and minimum temperatures average 3°C during May to September (National Oceanic and Atmospheric Administration, Climatological Record, 1979, 1980 for Kremmling, Colorado). Wyoming ground squirrels have established a nearly continuous series of colonies throughout the area. This study was conducted on 5 ha of human-modified pasture surrounded by sagebrush (Artemisia tridentata)-dominated rangeland.
The ground-squirrel population was censused by mark-recapture techniques. Squirrels were systematically trapped (Fagerstone, 1982) on a 1-ha area during four periods in 1978 (13–18 May, 28 May–2 June, 27 July–1 August, and 8–14 August) and at 2- to 3-week intervals during 1979 (beginning 29 June and ending 20 September) and 1980 (beginning 15 April and ending 16 September), and once during 1981 (25–30 April) using National live traps (15 by 15 by 41 cm; reference to trade names does not imply endorsement by the Federal Government). One hundred traps were placed near numbered stakes at 10-m intervals on a 90- by 90-m trapping grid. Traps were wired open and baited with sorghum for 2 days before each 5- or 6-day trapping period. Age of each trapped squirrel (juvenile, yearling, adult), based on previous trapping history, and its sex, body mass to the nearest 1 g, and reproductive condition were recorded. Squirrels were marked with numbered eartags (Monel #1 fingerling fish tags). Colored 1-cm-wide plastic strips were attached as neck collars to identify animals by sex and age groups, and each squirrel was dyed with Nyanzol D dye for individual recognition at a distance (Fagerstone, 1982).

The 5-ha study area was surveyed daily for newly emerged animals beginning on 15 March 1979, 15 March 1980, and 1 March 1981 (following ground-squirrel emergence on a lower-altitude site near Kremmling). Unmarked animals were trapped to determine sex. Daily surveys continued until most animals had emerged. From 19 June to 28 September 1979 and from 15 April to 14 September 1980, systematic surveys of ground-squirrel activity were conducted at hourly intervals for 2 days each week from a 5-m-high tower erected in the center of the trapping grid. During each survey, the area was scanned with a 15–45 x variable-power spotting scope and each squirrel was identified by its neck collar and dye marks. Activity surveys provided data on dates of spring emergence from hibernation, mating (by observation of aboveground copulations), litter emergence, and immergence.

Periodically throughout the active period, ground squirrels were collected from a nearby colony and their testes excised and weighed. Weights of the two testes were averaged for each male. Age of squirrels (yearling or adult) was not known.

Obtaining precise data on immergence dates is difficult because disappearance from the population by dispersal or death could be confused with immergence. Radiotelemetry was used to determine precise dates of immergence for individual ground squirrels. During 1979, 47 ground squirrels were equipped with 164 MHz neck-collar transmitters weighing 7–10 g (AVM Instrument Co., Wildlife Materials, or the Denver Wildlife Research Center’s Bioelectronics Unit). Fifteen yearling or adult males and 12 yearling or adult females were equipped with transmitters in June, and 10 male and 10 female juveniles were equipped in August. In April 1980, transmitters were attached to each of five yearling males, yearling females, adult males, and adult females. Locations of radioequipped squirrels were determined several times each week until hibernation. Because the battery life of transmitters averaged only 30–40 days, ground squirrels were fitted with new transmitters two or three times during the summer. For ground squirrels not radio equipped, the date of immergence was calculated to be half-way between the last date observed or trapped and the next observation or trapping period. Because ground squirrels that disappeared exceptionally early were unlikely to have hibernated, the earliest disappearance date of a known survivor was used as a critical date and disappearances of ground squirrels earlier than this date were not attributed to immergence.

Analysis of variance was used to test for differences in emergence dates, immergence dates, and mass between years and between sex and age cohorts. Length of time spent in hibernation and gains in mass were calculated for individuals rather than for cohorts before means were calculated. To avoid inclusion of transient animals in the data set, emergence dates were calculated for 1980 for only those individuals that hibernated on the study area in 1979 and emerged in 1980. Precise dates of emergence were not available for a sufficient number of animals to calculate mean dates for each cohort in 1979 and 1981.

Results

Emergence.—Dates of emergence from hibernation varied among years and among sex and age cohorts. Each year, males emerged on the 5-ha site before females. The first male emerged on 21 March 1979, 30 March 1980, and 9 March 1981. The first female emerged 16–18 days after the first male, on 6 April 1979, 17 April 1980, and 27 March 1981. Yearling ground squirrels (both males and females) emerged later than adult males, on about the same date as adult females. The mean dates of emergence for resident squirrels in 1980 were 20 April (n = 19; SE = 0.85 days) for adult males, 26 April (n = 16; SE = 1.31) for adult females, and 27 April for yearling males (n = 22; SE = 0.90) and females (n = 11; SE = 1.67). Adult males emerged significantly earlier (P < 0.01) than adult females or yearlings. Within the adult male cohort, heavier individuals emerged earlier than lighter ones (r = −0.64; P = 0.025). There was not a significant correlation for other cohorts.
Emergence was earliest in 1981 when temperatures had been above average for the 5 previous months (the mean daily departure from normal was 3.0°C for November through April), and mean March nighttime temperatures were persistently warm (7.0°C). Emergence was latest in 1980, when precipitation was above normal from November 1979 through March 1980 (19.4 mm as opposed to the 16-year normal of 14.4 mm), temperatures were below normal (mean daily departure from normal of −1.8°C for November through April), and snow melt occurred late.

During most year, snow covers parts of the study area at the time of emergence. Each year, ground squirrels appeared first on areas with the least snow. In 1980 (a year of late snows), emergence on the study area followed snow melt, beginning on 30 March on a southwest-facing slope 100 m west of the trapping grid where 10 cm of snow were present compared to 60–100 cm on the grid itself. On 10–15 April, ground squirrels emerged on bare ground west of the grid but the grid was still snow covered. The first male emerged within the grid on 15 April, and the first female on 17 April. By 19 April, ground squirrels had emerged only on the half of the trapping grid without snow. By 26 April, no snow remained on the grid and ground squirrels had emerged on all areas.

**Breeding.**—Upon emergence, male ground squirrels had enlarged testes \( n = 2, \bar{X} \pm SE = 0.67 \pm 0.01 \text{ g} \), indicating that testicular development occurs before spring emergence (as in Uinta ground squirrels, *S. armatus*; Ellis et al., 1983). Testes regressed to \( \frac{1}{10} \) of their emergence mass \( n = 12; 0.07 \pm 0.011 \text{ g} \) within 2 weeks after emergence. However, breeding may have continued for a short period thereafter, because in many small mammals sperm reserves are retained after spermatogenesis has declined in the testes (Racey, 1985; Racey and Tam, 1974). Testes remained small through June, then enlarged to \( 0.24 \pm 0.04 \text{ g} (n = 6) \) before adult males entered hibernation.

Ten instances of aboveground copulatory behavior were observed, and all occurred within 4 days after the female emerged, 7–11 April 1979, 18–22 April 1980, and 30 March–3 April 1981. Adults and yearlings of both sexes were observed breeding.

**Gestation length.**—A litter was born in the laboratory on 14 May 1980 to a female that emerged on 21 April and was trapped on 22 April, giving a gestation period for *S. elegans* in Colorado of 22 or 23 days.

**Lactation period and emergence of juveniles.**—For three of the 10 females observed to copulate, juvenile emergence dates were known, with juveniles appearing aboveground 29–33 days after birth (based on a 22–23-day gestation period). The first juveniles appeared on the surface on 31 May 1979, 9 June 1980, and 23 May 1981. Juveniles were first observed to eat grass between 4 and 6 weeks after birth. During 1979 and 1980, all reproductive females had nipples indicative of lactation during the last week of May and the first 2 weeks of June. One female in 1979 and two females in 1980 still had nipples indicative of lactation during the last week of June.

**Immergence into hibernation.**—Entry into hibernation was gradual for *S. elegans*. Immediately before immergence, radio equipped ground squirrels increased the percentage of time spent underground and fed little (Fagerstone, 1982). Squirrels sometimes spent several days underground at the nest then reappeared for 1 or 2 days. Radio equipped *S. elegans* did not enter torpor immediately even after final immergence, but moved underground in an area 0.3–0.9 m in diameter; arousal was frequent but squirrels remained belowground. About 2 weeks after entering their hibernacula, squirrels no longer showed movement and probably entered torpor.

Most adult and yearling males immerged during late July and early August. Mean dates of immergence were 4 August 1979 (\( n = 32; SE = 5 \text{ days} \); range, 26 June–29 September) and 2 August 1980 (\( n = 33; SE = 3 \); range, 24 June–1 September), a difference not significant \( (P > 0.1) \). Mean dates of immergence for radioequipped ground squirrels were 17 August 1979 (\( n = 10; SE = 8 \); range, 5 July–29 September) and 28 July 1980 (\( n = 6; SE = 9 \); range, 24 June–1 September). During both years, 30% of adult and yearling males immerged by 15 July, and 55%
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by 1 August. Mean dates of immersgence in 1980 were later for yearlings (12 August; n = 12) than for adults (29 July; n = 8) but were not significantly different (P > 0.1). Adult and yearling males that survived the winter of 1979–1980 and were retrapped the following spring remained in hibernation for a mean of 249 days (n = 17; SE = 7.7; range, 202–300).

Adult and yearling females immersger about 1.5 weeks earlier than adult and yearling males during 1979 (P < 0.01) and 1980 (P < 0.05). Mean dates of immersgence were 25 July 1979 (n = 19; SE = 4; range, 1 July–23 August) and 25 July 1980 (n = 22; SE = 4; range, 2 July–31 August); there was no significant difference between years. Mean dates of immersgence for radioequipped ground squirrels were similar, 28 July 1979 (n = 7; SE = 5; range, 7 July–23 August) and 5 August 1980 (n = 6; SE = 6; range, 16 July–31 August). During both years, 50% of adult and yearling females entered hibernation by mid-July and 70% by 1 August. Mean dates of immersgence of yearlings in 1980 (3 August; n = 7; SE = 5; range, 23 July–31 August) were later than for adults (22 July; n = 8; SE = 6; range, 2 July–19 August) but were not significantly different. Adult and yearling females remained belowground an average of 278 days (n = 13; SE = 5; range, 241–298). Dates of immersgence were not significantly different for females that weaned a litter (31 July; n = 10; SE = 4; range, 10 July–19 August) than for nonreproductive females (4 August; n = 5; SE = 3; range, 24 July–31 August) during 1980.

Juvenile Wyoming ground squirrels immersger after adults. The mean dates of immersgence in 1979 were 9 September for juvenile females (n = 22; SE = 1.3; range, 3–22 September) and 16 September for juvenile males (n = 52; SE = 1.1; range, 2–24 September). Juveniles immersger significantly (P < 0.01) earlier during 1980: 1 September for females (n = 30; SE = 2.2; range, 10 August–20 September) and 8 September for males (n = 49; SE = 1.3; range, 18 August–20 September). In 1979, only 1% of juveniles entered hibernation before September compared to 24% in 1980. Females immersger significantly earlier than males during both years (P < 0.01). Juveniles remained in hibernation for a mean of 223 days (n = 21; SE = 1.6; range, 210–240) for males and 230 days (n = 12; SE = 1.2; range, 227–240) for females. There was a difference in overwinter survival between juvenile ground squirrels that hibernated early, before 7 September (50% survival for 12 females and 29% for 14 males), and those that hibernated later (70% for 10 females and 50% for 40 males).

Seasonal changes in mass.—Trapping was first conducted during the last week of May in 1979, at which time males (n = 30) had a mean mass of 280 ± 5.9 g. Because only a few animals in the population were of known age, sample sizes were insufficient to compare yearling and adult masses. Males gained mass slowly between 28 May and 10 June at the rate of 1.2 g/day (n = 13) then gained more rapidly between 10 June and 3 August at the rate of 2.4 g/day (n = 15), attaining a mean mass of 394 ± 18.2 g (n = 8) by 3 August, after which mass stabilized until immersgence at 388 ± 11.1 g (n = 18; Fig. 1). In 1980, male ground squirrels emerged from hibernation in mid-April. During May and early June mean mass was significantly lower (P < 0.01) than in 1979. However, gain of mass was faster during 1980, and by late June ground squirrels had a higher mass than during a comparable period in 1979. In 1980, 13 adult males (X ± SE = 226.2 ± 9.2 g) emerged 27.7 g heavier (P < 0.01) than 17 yearlings (198.5 ± 8.8 g) and remained heavier throughout the summer. Gain in mass differed between adult and yearling males. Individual adult males (n = 4) lost 1.0 g/day during the breeding season (15–29 April), whereas yearlings (n = 3) gained 2.4 g/day during the same period. Both adults and yearlings then gained mass at the rate of 1.9 g/day (n = 24) between 29 April and 6 June. Gain in mass was more rapid after 6 June, at 3.1 g/day (n = 22). After 15 July, mean gain in mass of adults slowed to 0.3 g/day (n = 3), whereas yearlings continued to gain 1.6 g/day (n = 8) through August. Seven adult males had a mass of 426 ± 16.5 g during the week before hibernation in the yearlings compared to 414 ± 15.1 g for seven yearlings. Adult and yearling males (n = 8) lost a mean of 171 ± 12.3 g during hibernation (41.5% of their body mass). The mean rate of loss of mass during hibernation was 0.74 ± 0.05 g/day (n = 8; range, 0.53–0.91).

Adult and yearling females emerged from hibernation significantly lighter than adult and yearling males (P < 0.01) in both years. Mean mass of adult and yearling females (n = 28) was
262 ± 5.9 g during the last week of May 1979 before weaning and juvenile appearance above-ground (Fig. 1). Both adult and yearling females lost 0.7 g/day \( (n = 17) \) through mid-June. During this period, females still had enlarged nipples indicative of lactation. After weaning young, females then began to gain mass at 1.4 g/day \( (n = 13) \) through June. Gain in mass was more rapid (3.7 g/day) through mid-July, when they attained a mean of 353 ± 11.3 g. Mean mass at imnersion in 1979 was 350 ± 14.1 g \( (n = 12) \). During 1980, adult and yearling females \( (n = 30) \) emerged at a mean mass of 196 ± 7.2 g, with yearling females \( (n = 11; 164 ± 9.8 g) \) emerging at a significantly lighter \( (P < 0.01) \) mass than adult females \( (n = 4; 223 ± 6.1 g) \). Both adult and yearling females gained mass rapidly between 15 April and 1 May \( (5.0 \text{ g/day for six adults and 3.6 \text{ g/day for two yearlings})} \). In 1980, gain in mass by adults differed from that of yearlings during and after May because few yearling females bred. Adult females \( (n = 9) \) gained 1.2 g/day during gestation in May then lost mass after parturition in late May and continued to lose mass throughout lactation at the rate of 0.76 g/day \( (n = 5) \). From late June until emergence adults \( (n = 3) \) gained 4.0 g/day. In contrast, yearlings \( (n = 7) \) gained 1.4 g/day from 29 April to 16 July, then gained 2.2 g/day \( (n = 2) \) before emergence. Adults hibernated in 1980 at a mean mass of 313 ± 22.2 g \( (n = 6) \) and yearlings hibernated at 295 ± 8.5 g \( (n = 13) \). Mean masses of adult and yearling females were lower in 1980 from mid-July through hibernation than in 1979 \( (P < 0.01) \). Mean loss of mass by seven adult and yearling females during hibernation was 152 g (40.7% of their body mass). The mean rate of loss of mass during hibernation was 0.57 ± 0.56 g/day \( (n = 7; \text{ range, 0.53–0.91}) \).

Juveniles were first trapped the last week of June during 1979 and 1980, about 3 weeks after emergence. Mass of juvenile males was significantly lower during June 1980 \( (n = 20; 118 ± 4.8 g; \text{ Fig. 1}) \) than during June 1979 \( (n = 17; 138 ± 8.1 g) \). However, gain in mass was more rapid between 23 June and 16 July 1980 \( (3.4 \text{ g/day, } n = 8) \) than in 1979 \( (2.9 \text{ g/day, } n = 12) \), so by mid-July 1980 there were no significant differences in mass of juveniles between years. From mid-July through August, juveniles gained mass at 1.7 g/day \( (n = 32) \) in 1979 compared to 2.7 g/day \( (n = 19) \) in 1980, so by the end of August 1980, juvenile males were significantly heavier than in 1979. Those ground squirrels that remained aboveground after August gained little extra
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mass (1.1 g/day in 1979, n = 15, and 0.5 g/day in 1980, n = 5). Mean mass at hibernation was
272 ± 5.6 g (n = 46) in 1979 and 292 ± 3.3 g (n = 45) in 1980. Juvenile males (n = 12) lost
a mean of 112 g (38% of their body mass) during hibernation, a mean rate of mass loss of 0.50
± 0.04 g/day (n = 12; range, 0.31–0.82).

Body masses of juvenile females were not significantly different from those of males after
emergence from natal burrows; however, by mid-July juvenile males were significantly heavier
than juvenile females (P < 0.01). Mean mass of juvenile females was not significantly different
between years (Fig. 1). When first trapped in late June, juvenile females averaged 128 ± 16.1
g (n = 5) in 1979 and 124 ± 6.8 (n = 16) in 1980, then gained mass steadily at 2.2 g/day in
1979 (n = 9) and 2.6 g/day in 1980 (n = 7) until immersgence. Juvenile females hibernated at
a mean mass of 240 ± 6.9 g (n = 18) in 1979 and 261 ± 5.5 g (n = 19) in 1980 and lost a mean
of 89 g (37% of their body mass; n = 8) during hibernation, a mean rate of loss of mass of 0.39
g/day.

DISCUSSION

Variation in dates of emergence observed between years in this study was similar to that
observed for most other ground squirrel species (Michener, 1984). Burnett (1913) was the first
to document wide variation in dates of emergence between years for the Wyoming ground
squirrel; emergence in Colorado and Wyoming occurred as early as 13 February or as late as
15 April. The most commonly reported dates of emergence (without regard to sex or age) were
the last week of March and the 1st week of April (Burnett, 1913; Cary, 1911; Clark, 1968; Clark

Several hypotheses have been proposed to account for variation in dates of spring emergence
of hibernating ground squirrels, including endogenous rhythms (Davis, 1976; Knopf and Balph,
1977) and exogenous factors such as spring temperatures and snow cover (Michener, 1984;
Quanstrom, 1968). Both exogenous and endogenous factors played a role in this study of S.
elegans. Air temperature influenced emergence dates, with emergence latest in 1980 when March
and April temperatures were below normal and earliest in 1981 when temperatures were un-
seasonably warm. The sequence of emergence on the study area also was influenced by snow
depth, with squirrels emerging earliest on south-facing slopes and latest on north-facing slopes,
an observation also made by Shaw (1925) for Columbian ground squirrels (S. columbianus).

In ground squirrels, an endogenous temporal threshold apparently exists that precludes animals
from emerging early despite weather conditions that would favor emergence (Michener, 1984).
In 1981, light snow cover and high average maximum daily temperatures (10.9°C) should have
favored early emergence during the last 2 weeks of February, yet emergence did not occur until
the 2nd week of March. A temporal threshold also probably exists that forces ground squirrels
to emerge within 2–3 weeks after their normal emergence period even when winter weather
persists, as in this study in 1980. An endogenous rhythm, therefore, appears to control both the
minimum and maximum number of days that ground squirrels spend in hibernation (Davis,
1976). Within that temporal range, exogenous factors probably determine the actual dates of
emergence.

The emergence sequence of S. elegans was typical of that of most ground squirrels, with males
emerging 1–2 weeks before females (Michener, 1984). Because breeding immediately followed
emergence, dates of observed breeding varied between 30 March and 22 April in the 3 years of
this study and between 20 March and 15 April in a Wyoming study of S. elegans (Clark, 1970b;
Clark and Denniston, 1970). In Uinta, Belding's (S. beldingi), and Columbian ground squirrels,
yearling males typically are not sexually mature and emerge later than adult males (Knopf and
Balph, 1977; Morton and Sherman, 1978; Murie and Harris, 1982; Walker, 1968). For species
in which yearlings are reproductively mature upon emergence from hibernation at 11 months
of age (S. parrity, S. richardsonii), yearlings normally emerge and breed at the same time as
adults (Dorrance, 1974; McLean and Towns, 1981; Michener, 1983a). In S. elegans, yearling
males are reproductively mature at 11 months but, depending on climatic conditions, may or
may not emerge with adult males and breed. During 1979, yearlings emerged from hibernation at the same time as adult males and were observed to breed. Both yearling and adult males lost mass during the 1979 breeding period as they competed with other males for access to females. In 1980, when spring emergence was delayed by low temperatures and heavy snow cover, yearling males emerged significantly later and at significantly lower mass than adults. Although yearlings had descended testes, they did not lose mass after emergence as adults did and may not have expended as much energy in breeding. Because females were bred within 1–3 days after emergence (Michener, 1983a), the late emergence of yearling males may have resulted in reduced breeding opportunities. During years with normal weather conditions (1979 and 1981), yearling males emerged at the same time as adults and competed with adults for breeding opportunities.

Yearling female S. elegans do not always breed their 1st year (Burnett, 1920). In this study, seven of eight adult and all 12 yearling females bred and had litters during 1979. In 1980, all nine adult females but only one of 11 yearling females had litters. The yearly difference probably was related to the poor condition of yearlings at emergence in 1980, when snow depth was great and no green vegetation was available upon emergence. Females emerged emaciated, flea-covered, and at significantly lighter masses in 1980 than in 1979, and yearling females emerged at lighter masses than adults. Three female deaths during April and May 1980 were attributable to starvation and hypothermia. By not breeding in 1980, yearling females were able to add mass throughout the summer whereas adults lost mass after parturition then had to gain mass rapidly during the latter part of the summer in preparation for hibernation.

The gestation period for one female with a known date of emergence was 22–23 days, similar to that reported for the sibling species S. richardsonii (Michener, 1985). Denniston (1957) reported a gestation period of only 17–18 days for a female that both mated and gave birth in captivity. However, the female had been trapped recently before mating in captivity and she could have mated previously in the field.

Autumnal dates of immersgence varied by sex, age, and fat deposition. Female S. elegans immerged 2 weeks before males despite the energy drain of parturition and lactation. This immersgence pattern also occurs in S. armatus and S. parryii (Knopf and Balph, 1977; McLean and Towns, 1981) but is contrary to other ground squirrel species such as S. beldingi, S. franklinii, and S. richardsonii (Michener, 1984), for which the typical sequence of immersgence is adult males, adult females, subadults, and juveniles. Reproduction by female S. elegans did not delay dates of immersgence, as the mean date of immersgence for females that weaned litters was 4 days earlier than that of females that did not wean litters. In contrast, in Marmota olympus, M. flaviventris, S. richardsonii, and S. franklinii, adult females that do not bear litters or rear litters to weaning hibernate earlier than females that wean litters (Barash, 1973, 1976; Choromanski-Norris and Fritzell, 1986; Kilgore and Armitage, 1978; Michener, 1978, 1979). As in other ground-squirrel species (Michener, 1984), juvenile S. elegans immerged later than adults.

Spermophilus elegans entered hibernation gradually in this study and in a study by Burnett (1913), remaining in burrows for a day or two at a time at first, then for longer intervals until they no longer emerged at all. Quanstrom (1971) observed that adult S. richardsonii were active every other day by the end of July, then every 3rd day as the hibernation period approached.

Numerous factors have been postulated to influence dates of ground squirrel immersgence, including time of emergence, temperature, food shortages, endogenous rhythms, and photoperiod. Date of emergence did not influence date of immersgence for S. elegans. Despite late emergence in 1980, dates of immersgence of adult squirrels in 1980 did not differ from those in 1979. Because of the delay in emergence of adults in 1980, juveniles also appeared on the surface later and at significantly lower masses. However, the heavy accumulation of snow during 1980 provided a lush grass cover on the study area and allowed juveniles to accumulate fat at a faster rate and immerge earlier during 1980 than during 1979.

Torpor has been shown to be induced by low temperatures, lack of food, or a decrease in consumption of food and water (Davis, 1976). Hibernation of sciurids occurred when low food
consumption coincided with low temperatures. Davis (1976) found that sciurids entered torpor much faster in winter, when 3-4 h of food deprivation induced torpor, than in summer, when 3-4 weeks of food deprivation were required. In *S. elegans*, a combination of autumnal temperatures and reduced food availability induced hibernation even in juveniles without large fat reserves. Before hibernation, juveniles ranged between 175 and 290 g for females and 230 and 375 g for males; both fat and thin juveniles immerged in late September when food was absent, a result observed by Davis (1967) and Pengelley (1968) for other sciurids.

The factors initiating hibernation of juveniles in autumn (dropping temperatures and food shortages) were not the same factors that initiated hibernation of adults; adults immerged during the hottest part of the summer when food was still green and available. McCarley (1966) stated that early hibernation allowed ground squirrels to avoid food shortages, but food was not a limiting factor for Wyoming ground squirrels in this study, particularly during 1980 when abnormal rainfall created a lush summer vegetation. Increasing temperatures in July and August have been postulated to stimulate prehibernation behavior (McCarley, 1966), allowing adults to avoid high temperatures. However, ground squirrels in this study avoided activity aboveground during midday and were active in morning and evening when temperatures averaged a moderate 13°C. Yeaton (1969) hypothesized that early disappearance of adults prevented competition for resources with juveniles and reduced adult male-female agonistic interactions. Neither of these hypotheses explain the early disappearance of adult *S. elegans*, because adult females hibernated before adult males and agonistic interactions between adult males and females were infrequent during mid-summer (Fagerstone, 1982). Fat accumulation probably controlled onset of hibernation in adult *S. elegans*. It has been stated frequently that animals must become fat to become torpid (Jameson, 1965; Mrosovsky, 1971) and, when fat, hibernate regardless of environmental stimuli (McCarley, 1966). *S. elegans* in this study underwent marked seasonal changes in mass characteristic of hibernating ground squirrels (Harding and Rauch, 1981); they entered a hyperphagic phase of rapid fattening before hibernation characterized by low activity and high food intake. Juveniles stopped increasing in length after 70 days of age (Clark, 1970a), so gains in mass of both adults and juveniles resulted primarily from increased storage of peritoneal and subcutaneous fat (House, 1964; Zegers and Williams, 1977). Adult *S. elegans* became so fat that they had difficulty running and entering small burrows (Fagerstone, 1982). To hibernate then may be more efficient energetically than to attempt to maintain optimal mass while avoiding predators. Stored fat not only maintained the animals through hibernation but also provided energy for a month after emergence when food was limited and animals expended energy in reproductive activities (House, 1964; Zegers and Williams, 1977).

Most Sciuridae show an endogenous rhythm in food consumption that occurs even in individuals that do not become torpid (Davis, 1976; Fagerstone, 1982; Pengelley and Fisher, 1963; Pengelley et al., 1976). All sex and age cohorts of Wyoming ground squirrels underwent a period of prehibernatory fattening preceding immersgence and spent more time feeding, fed farther from their burrows, and showed greater overlap in home ranges (Fagerstone, 1982). During the week immediately before immersgence individuals became less active, spent increased time close to their burrows, and reduced food consumption (Fagerstone, 1982). This endogenous rhythm of food consumption probably interacted with low temperatures and low food availability to induce immersgence in juveniles, and with high body-fat levels to induce immersgence in adults.

Michener (1984) proposed that the degree of sociality exhibited by each species is related to the timing of events in the annual cycle of ground squirrels, with the most social species having a temporal overlap >70% between the active seasons of adults and juveniles and the least social species having little or no temporal overlap. Adult:juvenile temporal overlap was postulated by Michener (1983b) to permit development of social tolerance and space sharing, leading to increased sociality. *S. elegans* shows little adult:juvenile temporal overlap. Only adults and yearlings were present aboveground for the first 2-2.5 months of the active season. After juveniles appeared aboveground in late May or early June, all sexes and ages were active simultaneously for about 1 month before adults began immersing. Adult and yearling females immerged in
late July, followed by adult and yearling males 1.5 weeks later, so juveniles spent the rest of the summer without contact with adults. Juvenile females hibernated a mean of 33 days after adult males and 46 days after adult females. Based on a mean date of emergence of 4 June for litters from 1979 to 1981, 64% and 50% of the active season of juvenile females coincided with the active seasons of adult males and females, and 60% and 47% of the active season of juvenile males coincided with active seasons of adult males and females. This is slightly more contact than S. richardsonii juveniles have with adults (33% and 52% of the active season of juvenile females and 23% and 36% of the active season of juvenile males coincided with aboveground activity of adult males and adult females; Michener, 1984). Based on the low degree of social contact between adults and juveniles, S. elegans would be predicted to fit into the less-social grades of ground squirrels (Michener, 1983b).

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