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Spermophilus elegans.

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Spermophilus elegans Kennicott, 1863

Wyoming Ground Squirrel

Spermophilus elegans Kennicott, 1863:158. Type locality Ft. Bridger, Uinta County, Wyoming.

CONTEXT AND CONTENT. Order Rodentia, Family Sciuridae, Genus *Spermophilus*, Subgenus *Spermophilus*. *Spermophilus elegans* is divided into three subspecies (Davis, 1939; Howell, 1928):

S. e. aureus (Davis, 1939:177). Type locality Double Springs, 16 mi NE Dickey, Custer County, Idaho.
S. e. elegans Kennicott 1863:158, see above.
S. e. nevadensis (Howell, 1928:211). Type locality Paradise, Humboldt County, Nevada.

Burnett (1931) and Howell (1938) described type localities, collectors, circumstances of collection, and gave taxonomic revisions.

DIAGNOSIS. Total length of adult *Spermophilus elegans* ranges from 253 to 307 mm (Armstrong, 1972; Howell, 1938; Long, 1965) making *S. elegans* similar in size to *S. armatus* (280 to 303 mm) and *S. beldingi* (254 to 300 mm), larger than *S. townsendii* (167 to 271 mm), and smaller than *S. columbianus* (327 to 410 mm) (Hall, 1981). Where sympatric with *S. beldingi*, *S. elegans* can be distinguished by its longer tail, more intense cinnamon coloration on nose and underparts, and buff rather than reddish color on underside of tail. Where sympatric with *S. townsendii*, *S. elegans* can be recognized by cinnamon rather than whitish underparts, tail with buffy white borders, and larger size. Where sympatric with *S. armatus*, *S. elegans* is distinguishable by buff rather than gray underside of tail (Hall, 1981); in addition, *S. elegans* exhibits character displacement, being slightly smaller and paler than *S. armatus* where the two species are allopatric (Long, 1965). Where sympatric with *S. richardsonii*, *S. elegans* can be recognized by a hindfoot length less than 275 mm, a maxillary toothrow less than 10 mm, nasal length less than 17 mm, a greatest skull length 42 to 45 mm, and a zygomatic breadth less than 30 mm (Howell, 1938). In total body length, 11 of 16 cranial measurements, and 11 of 19 measurements of the axial skeleton, *S. elegans* is significantly smaller than *S. richardsonii* (Fagerstone, 1982). Although the dorsal side sometimes is more grayish or brownish and less buffy, the head and shoulders are paler and the tail is darker with paler edgings than in *S. richardsonii* (Howell, 1938), pelage color is not consistently different between *S. elegans* and *S. richardsonii* (Fagerstone, 1982). Five pairs of mammae are spaced uniformly from the upper pectoral region into the inguinal region (Burnett, 1920). Bacula have 8 to 11 distinct tooth-like projections on the distal expansion, whereas those of *S. richardsonii* have projections reduced or absent. The shaft of the baculum of *S. elegans* is twisted pronouncedly, whereas the shaft in *S. richardsonii* is twisted only slightly (Neuner and Schultz, 1979). The diploid number is 34 compared with 36 in *S. richardsonii*; the X chromosome is smaller with the centromere more medially placed; and the Y chromosome is acrocentric (rather than subtelocentric) and larger than in *S. richardsonii* (Nadler et al., 1971). *S. elegans* lacks the Tf_2 allele typical of *S. richardsonii* (Nadler et al., 1974).

GENERAL CHARACTERISTICS. *Spermophilus elegans* is a big-eared ground squirrel (*sensu* Nadler, 1966) of small to medium size with a relatively long tail (Fig. 1). The dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22. Measurements (in mm) for eight male and five female adults were: greatest length of skull 43.0 to 46.8 and 43.3 and 45.3, respectively; zygomatic breadth 27.4 to 30.8 and 28.7 to 30.0; postorbital constriction 10.2 to 11.2 and 10.0 to 11.0; length of nasals 14.7 to 17.1 and 14.7 to 15.8; and maxillary toothrow 10.0 to 11.1 and 9.9 to 11.1 (Long, 1965). Lengths of tails and hindfeet for the same specimens ranged from 59 to 79 and 38 to 45, respectively (Long, 1965). Tail vertebrae for 10 *S. e. elegans* and 9 *S. e. nevadensis* measured 66 to 78 and 76 to 100, respectively. Upperparts are light drab and flecked with light pinkish buff, clay color, or pinkish cinnamon. The tail is edged with pale buff or white; the underside of the tail is clay colored, buff, or light brown (Hall, 1981; Howell, 1938).

When viewed from the dorsal side the braincase appears broad and the rostrum short (Fig. 2). The temporal ridges and sagittal crest are indistinct. Postorbital processes of the frontals are well developed and pointed. The slit-like infraorbital canals are small and their foramina are not visible when the skull is viewed laterally. The tympanic bullae are not well inflated; however, the paroccipital processes are conspicuous. Hamular processes of the pterygoids are elongate. Also well developed are the angular and coronoid processes of the dentary. Crowns of the cheekteeth have distinct cusps and valleys.

DISTRIBUTION. *Spermophilus e. elegans* is found in northcentral and northwestern Colorado, southern Wyoming, extreme western Nebraska, and extreme northeastern Utah (Fig. 3); it occupies mountain meadows from about 1,500-m elevation to above timberline (Armstrong, 1972; Burnett, 1931; Lechleitner, 1969). *S. e. aureus* inhabits valley bottoms and foothills in southwestern Montana and contiguous areas of Idaho, where mountain meadows are occupied by *S. armatus*. Thus, the northern distributional limits may be set by both habitat availability and interspecific competition (Nadler et al., 1971). *S. e. nevadensis* is found in northcentral Nevada (Fig. 3) and formerly occurred in southeastern Oregon, but no records for the state since 1927 are available (B. J. Verts, pers. comm.). Efforts to confirm reports of *S. e. nevadensis* remaining in extreme southwestern Idaho have been unsuccessful (E. Yensen, pers. comm.).

Hansen (1962) documented a southward dispersal in the mountainous regions of Colorado of approximately 2.4 km/year between 1930 and 1962. Absence of physical barriers and natural competitors, abundance of suitable habitat, the ability of these squirrels to inhabit burrows of other large fossorial rodents, and not the actions of modern man, account for this natural expansion into areas occupied before the last Pleistocene glaciation (Hanson, 1962). Competition with *S. tridecemlineatus*, *S. spilosoma*, and *S. franklinii* may be preventing expansion of the range of *S. elegans* to the east and southeast (Hansen, 1962). Durrant and Hansen (1954) suggested that the disjunct *S. e. nevadensis* was a relict that was being outcompeted by *S. beldingi* in more mesic habitats and by *S. townsendii* in arid habitats.

FOSSIL RECORD. The oldest fossils of the *S. richardsonii* complex found in Canada are from the Medicine Hat (Sangamon interglacial) and Hand Hills (probably Irvingtonian or later) faunas of southern Alberta (Harington, 1978). Farther south in the Great Plains, fossil *Spermophilus* are known from the Nebraskan stage (Hibbard, 1970); specimens belonging to the *S. richardsonii* complex are present in the Kansan local faunas of Texas and southwestern Kansas (Dalquest, 1965; Hibbard, 1970, 1976) and the Illinoian local fauna of the Oklahoma panhandle (Hibbard, 1970). The baculum of a specimen from the "*Citellus* zone" of the late Quaternary is less derived than those of recent forms of *S. richardsonii* and *S. elegans* in the degree of twist in the shaft, development of teeth on the distal end, and expansion of the ventral keel (Neuner and Schultz, 1979). Comparison of skulls and mandibles of living and fossil *S. elegans* and *S. richardsonii* indicated that the two species may have diverged from a common ancestor perhaps as recently as 11,000 years ago (Neuner, 1975).

The recent *S. richardsonii* complex possibly originated when an ancestral population in the Great Basin was split by forest bar-

FIGURE 1. Photograph of adult *Spermophilus elegans* taken in Rocky Mountain National Park, Colorado by D. A. Zegers.

riers that developed in a glacial period, Wisconsin or earlier (Nadler et al., 1971). During this isolation the range of the northern population (*S. richardsonii*) was reduced severely, likely in response to changes in environmental conditions. Inbreeding and chromosomal reorganization in this population produced an isolating mechanism that was partially effective when secondary contact occurred with the southern population, *S. elegans* (Nadler et al., 1971). Alternatively, this northern founder population arose during early post-Wisconsin time from squirrels that came from the Great Basin and invaded the area north of the Yellowstone River (Nadler et al., 1971). Chromosomal reorganization in this small, newly established population could have been maintained because of isolation from the ancestral population. This founder population could then spread as northern areas of the Great Plains became ice-free (Nadler et al., 1971).

Neuner (1975) proposed a center of origin in the Great Plains. At the close of the Pleistocene, disappearance of suitable habitat eliminated the central population and left peripheral populations isolated. These peripheral populations gave rise to *S. richardsonii* and three subspecies of *S. elegans*.

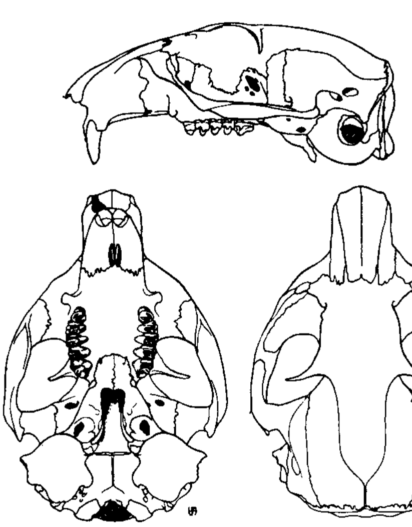

FIGURE 2. Cranium of *Spermophilus elegans nevadensis*, ×1, male, MVZ No. 70559, 4 mi S Romano, Nevada (from Hall, 1981; used with permission of John Wiley and Sons, New York).

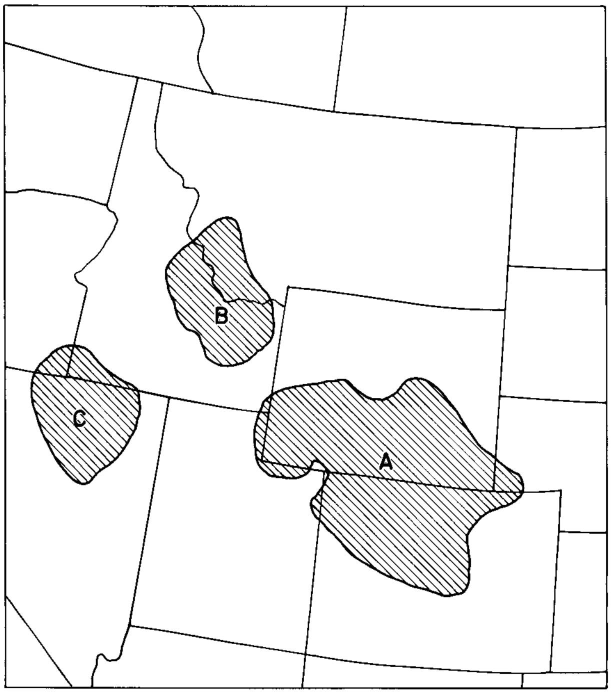

FIGURE 3. Distribution of *Spermophilus elegans*: A, *S. e. elegans*; B, *S. e. aureus*; C, *S. e. nevadensis*.

FORM AND FUNCTION. Multiple discriminant function analysis employing 36 cranial measurements of adult ground squirrels revealed that the three subspecies of *S. elegans* were more similar to each other than to *S. richardsonii* (Robinson and Hoffmann, 1975).

Mean values for the body composition of 15 summer-caught adults were: 32.7% dry weight, 66.8% water, 23.2% lean dry weight, and 9.9% fat (Zegers and Williams, 1979). Mean caloric value of body tissue for six adults was 5.4 kcal/gm dry weight.

Thermoneutrality for *S. elegans* extends from 27 to 38°C (Byman, 1979). Body temperature of nonhibernating squirrels varies between 36 and 40°C depending upon environmental conditions (Byman, 1979). Hudson et al. (1972) reported that mean resting metabolic rates (RMR) ranged from 0.4 to 0.5 ml O_2 g^{-1} h^{-1} at thermoneutrality and from 1.1 to 1.9 ml O_2 g^{-1} h^{-1} below thermoneutrality. Combining data from eight species of *Spermophilus*, they established the following relationship: RMR (ml O_2 g^{-1} h^{-1}) = $3.24W^{0.66}$ for body temperature of 35.7°C. Byman (1979) determined RMR for ambient temperatures (T_{mc}) of 0 to 40°C. Below thermoneutrality, RMR (ml O_2 g^{-1} h^{-1}) = $3.09 - 0.08T_{mc}$; in the thermoneutral zone RMR = 1.07; and above thermoneutrality, RMR = $6.25 + 0.19T_{mc}$. As for most mammals, thermal stability is maintained by the ability of the animal to adjust peripheral heat loss and intensify heat production (Hudson et al., 1972).

Pulmocutaneous water loss increases with ambient temperature; panting occurs when ambient temperatures are high (Hudson et al., 1972). Mean resting evaporative water loss below 26.5°C was 244 mg H_2O h^{-1}, and above 26.5°C was $8.15\ e^{0.129}T_{mc}$ (Byman, 1979).

The following analytical model of energy exchange with the environment was developed for models (statues) of *S. elegans*:

$$Q_{abs} = \epsilon\sigma A_t T_e + h_c(T_e - T_a)$$

where Q_{abs} is the absorbed radiation from all sources, ϵ is the squirrel's emissivity to long-wave infrared radiation, σ is the Stefan-Boltzmann constant, A_t is the total surface area of the statue available for radiative energy exchange with the environment, T_e is the operative environmental temperature of the statue, h_c is the convective heat transfer coefficient, and T_a is the average temperature of the air ambient to the statue (Byman, 1979). The energetic costs of thermoregulation predicted by use of this analytical model are greater for the time spent in the burrow than above ground because the squirrels spend approximately 21 h/day in their burrows during the "active" season. Estimates of water costs of thermoregulation based upon this model revealed that water costs are met easily by the water in green vegetation (Byman, 1979). Absorbed radiation (Q_{abs}) levels computed by this method during an idealized sunny midsummer day on a montane meadow varied by time of day and ranged from 8.4 to 26.3 watts (W) for a prostrate squirrel, from 10.7 to 29.0 W for a standing squirrel, and 12.3 to 26.4 W for a squirrel in the "alert" posture.

Males emerged from hibernation in late March or early April, and females appeared 1 to 2 weeks later (Clark, 1970*a*; House, 1964; Zegers and Williams, 1977). Within age and sex categories, heavier individuals emerged earlier than lighter ones; mean weight at emergence was 231 g and 189 g for males and females, respectively (Fagerstone, 1982). Fat deposits were not depleted at emergence but declined during April (Zegers and Williams, 1977); breeding females lost weight after parturition and continued to lose weight throughout lactation (Fagerstone, 1982). Adult fattening occurred through June and July. Fat deposition in adults was greater and more rapid for males than for females (Clark, 1970*a*; House, 1964; Zegers and Williams, 1977). Weights of adult males plateaued and sometimes declined slightly immediately before hibernation (Fagerstone, 1982; Zegers and Williams, 1977). Adults hibernate by late July. Because males tend to hibernate before females, the overall sex ratio in July was skewed in favor of males (Clark, 1970*a*); however, Zegers and Williams (1977) and Fagerstone (1982) reported that adult males entered hibernation after adult females. Juveniles first appeared above ground at 4 to 5 weeks of age (Zegers, 1977); they gained weight until they entered hibernation in late August to early September (Fagerstone, 1982; House, 1964; Lechleitner, 1969).

In the laboratory, hibernating squirrels (mean live weight = 184 g) lost 0.7 ± 0.0 ($\bar{X}$ ± S.E.) g/day (Hansen and Reed, 1969). In the field four hibernating males lost an average of 0.8 g/day (Zegers and Williams, 1977). Mean weight loss during hibernation was 0.4 and 0.7 g/day for juveniles and adults, respectively (Fagerstone, 1982).

Spermophilus elegans showed an endogenous rhythm in food consumption and weight gain (Fagerstone, 1982). For captive juveniles that averaged 133 ± 4.3 g, daily energy consumption was 72.5 ± 0.5 kcal, fecal energy was 20.1 ± 0.4 kcal, and production was 31.5 ± 0.2 kcal per squirrel (Hansen and Reed, 1969). Daily maintenance metabolic rate (RMR + activity) for captive *S. richardsonii* averaged 0.24 ± 0.04 kcal/g; the ratio of maintenance metabolic rate to basal metabolic rate was 2.57 ± 0.39 (Johnson and Groepper, 1970). Assimilation efficiencies for three *S. richardsonii* were 82.2 ± 0.2% (Johnson and Groepper, 1970).

Although few physiological studies of hibernation in *S. elegans* are available, the sibling species, *S. richardsonii*, was studied extensively (Scott et al., 1974; Wang, 1978). In *S. elegans* arousal from hibernation appeared to be under endogenous control, but timing of emergence seemed to be effected primarily by snow depth and secondarily by air temperature (Fagerstone, 1982). Hibernation probably is stimulated by reduced food consumption. Juveniles reduce intake when food availability declines at the end of the growing season; hence, they hibernate in September (Fagerstone, 1982). For adults, however, the decline in consumption (hypophagia) is not related to food availability but to reduced activity resulting from excessive fat deposition. By mid-July, adults are so obese they often have difficulty walking; to hibernate then probably is more energy efficient than to attempt to maintain optimal weight while avoiding predators (Fagerstone, 1982). Although an obligate hibernator in the wild (Michener, 1983), *S. elegans* does not hibernate when kept under a constant temperature and light : dark regime (Fagerstone, 1982).

Melatonin occurs in retinas, pineal glands, and Harderian glands; nocturnal levels of melatonin rise in pineals (Reiter et al., 1981). Splenic weight, relative to total body weight, increased from March to April, peaked in May for adult males, and peaked in June for adult females; adrenal weights, relative to total body weight, peaked in June for male and female adults (Clark, 1970*a*).

ONTOGENY AND REPRODUCTION. Timing of breeding varies with climatic conditions and latitude (Clark, 1970*b*; House, 1964; Michener, 1973). Male and female yearlings breed (Clark, 1970*a*; Fagerstone, 1982; Pfeifer, 1982*a*). Although female yearlings bred in 1979, they did not in 1980 in the same population; this probably was related to greater snow cover, cooler air temperatures, and the poorer condition of yearlings (flea-covered and emaciated) at emergence in 1980 (Fagerstone, 1982). Males tended to emerge from hibernation approximately 1 week before females (House, 1964) and developed scrotal testes within 9 days (Clark, 1970*a*). Mean (ranges in parentheses) masses of testes were 1.8 g (1.1 to 2.7) in March, and 0.2 g (0.1 to 0.2) May through July (Clark, 1970*a*). Length of testes showed the same trend (Clark, 1970*a*; House, 1964). For *S. richardsonii*, and perhaps for *S. elegans*, behavioral estrus lasts less than 24 h, and mating occurs within 5 days of emergence of the females from hibernation (Michener, 1980). Estimates of the length of gestation range from 17 days (Denniston, 1957) to 28 to 32 days (Howell, 1938). Because matings between *S. elegans* and *S. richardsonii* produce viable hybrids, length of gestation in *S. elegans* probably is similar to the 22.5-day period for *S. richardsonii* (Michener, 1980).

One litter per season is produced (Burnett, 1920; Clark, 1970*a*; Lechleitner, 1969). Litters born in captivity averaged 7.0 young (Denniston, 1957; Koeppl and Hoffmann, 1981). Clark (1970*a*) reported a mean litter size of 6.0 based on litters born in captivity, 6.1 based on placental scars, and 5.3 based on embryos *in utero*. Zegers (1977) calculated mean litter size of 5.9 at time of emergence of young (approximately 4 to 5 weeks old). Pfeifer (1982*b*) found that size and sex composition of litters differed between years. Litters of yearling females were not significantly smaller than those of adult females (Pfeifer, 1982*a*).

In the laboratory, mean body mass at birth was 6.2 g (Koeppl and Hoffmann, 1981) and 6.0 g (Denniston, 1957). At 2 days, neonates are hairless and reddish in color. Some blood vessels and internal organs are visible beneath the skin. The digits are fused; the tail is short and tapered. Small vibrissae are located on the snout. Sex can be distinguished by position of genital papillae. Pups can produce audible squeaks and can roll, but they cannot crawl or right themselves when placed on their backs (Clark, 1970*b*).

At 5 days, gray pigment covers the dorsal and lateral areas of the body; the underparts remain pink (Burnett, 1920; Clark, 1970*b*). The area of the eyes is darkly pigmented. Claws are present. Young squirrels eliminate yellow feces. They can pull themselves forward with their forelimbs and can right themselves when placed on their backs (Clark, 1970*b*).

At 6 days, short hairs appear on snout and cheeks. Lower incisors are visible below the surface of the gums on day 11, and they perforate the gums on day 12. On day 14, hair on the base of the nose has the rust-reddish color of the adult. The tail is covered with short, fine hairs, and the toes are separated fully. When disturbed, young give a half-muted trill (Clark, 1970*b*).

By day 24, the eyes are open. By day 26, the upper incisors have erupted and the external auditory meatus is open. At 4 weeks pups have the coloration of adults. They run well. When handled, they urinate and attempt to bite. At 5 weeks, pups eliminate dark fecal pellets and exhibit tail-flicking (Clark, 1970*b*). Weaning occurs at 4 to 6 weeks (Clark, 1970*a*, 1970*b*; Fagerstone, 1982).

During the first week after birth, the rate of increase in body mass was 11.4% per day and declined each week to 2.0% per day during week 10 (Clark, 1970*b*). Hindfoot length achieved adult size at 42 days; tail length and total length required 56 and 63 days, respectively, to reach 100% of adult length (Clark, 1970*b*). Koeppl and Hoffmann (1981) determined postnatal growth by measuring total length, tail length, body length, length of left hindfoot, and body mass from birth through approximately 3 months of age for *S. elegans*, *S. richardsonii*, *S. armatus*, and *S. columbianus*. Mean instantaneous growth rates for the four species combined were correlated negatively with litter size during the preweaning period, but correlated positively with litter size after weaning. The only sexual dimorphism found in developing *S. elegans* involved hindfoot length and body mass of older individuals.

Juvenile activity is restricted to the burrow entrance during the first week after emergence; at 6 to 7 weeks of age they follow their mother up to 50 m from the maternal burrow (Fagerstone, 1982).

Minimum body mass of adult females was the most significant factor determining reproductive effort for a group of 18 species of burrowing sciurids that included *S. elegans* (Armitage, 1981). On the basis of minimum body mass of adult females, *S. elegans*, in addition to *S. lateralis*, *S. richardsonii*, *S. tereticaudus*, *S. townsendii*, and *S. tridecemlineatus*, had a high reproductive effort (mean litter size times juvenile body mass at weaning; Armitage, 1981).

ECOLOGY. Predators include coyotes, *Canis latrans*; dogs, *C. familiaris*; badgers, *Taxidea taxus*; weasels, *Mustela* spp.; felids, *Felis* spp.; foxes, *Vulpes fulva* and *Urocyon cinereoargenteus*; goshawks, *Accipiter gentilis*; and red-tailed hawks, *Buteo jamaicensis* (Burnett, 1913, 1924; Fagerstone, 1982; Pfeifer, 1980*a*, 1980*b*; Zegers, 1977). Pfeifer (1980*b*) determined that aerial predation alone did not skew the sex ratio among juveniles (biased toward females) and hypothesized a combination of differential dispersal and mortality as agents producing the sex ratio imbalance seen in adults. Ground predators may be a significant source of mortality (Fagerstone, 1982; Pfeifer, 1980*a*; Zegers, 1977).

Adult males disperse in April; juvenile males disperse in August (Fagerstone, 1982). Retention of juvenile females is higher than that of males (Pfeifer, 1982*b*). Dispersal of juvenile males is related to absolute number of yearling and adult male competitors for mates and the adult sex ratio; dispersal of juvenile females is determined more by the extent of competition with female littermates for suitable maternity burrows that are limited in number and vary in quality (Pfeifer, 1982*b*). In comparison with those that occupied less frequently reused maternity burrows, females that occupied frequently reused maternity burrows weaned significantly more young that, in subsequent years, were more likely to reproduce. Therefore, females that inhabited frequently reused burrows had more surviving descendants than those that occupied other maternity burrows (Pfeifer, 1982*a*).

Clark (1970*a*) reported overwinter survival (July to April) of 67% and summer survival (April to July) of 75%. Zegers and Williams (1979) calculated survival for all cohorts at 54% (n = 68) for the summer of 1974 and 31% (n = 67) for 1975; survivorship was 65% (n = 37) and 100% (n = 21) for the following winters, respectively. In 1974, summer survival rates for adult males and females and juvenile males and females were 78, 65, 38, and 29%, and, in 1975, 31, 32, 33, and 30% respectively (Zegers and Williams, 1979). Fagerstone (1982) found winter survival to be 53, 64, 44, and 59%, respectively, for the same age and sex cohorts.

Pfeifer (1980*b*) determined sex ratios (female : male) of juveniles to be 1.4:1 at emergence (late May to early June) and 5.6:1 in late July. Differential dispersal apparently caused the skewed ratio. Clark (1970*a*) found overall sex ratios of 0.2:1 in March, 1.7:1 in April, 1.1:1 in May, 0.8:1 in June, and 0.4:1 in July at the end of the "active" season. These differences were attributed to differential times of arousal and entry into hibernation between the sexes.

Peak density of local concentrations reached 44/ha in short grass prairie (House, 1964). Clark (1970*a*) found densities of 0.2/ha in March to 1.2/ha in June for residents of a short grass meadow. Densities in a montane meadow ranged from 20/ha in late April to 14/ha in May to 48/ha in early June, when both juveniles and adults were active, to 20/ha in late July, when most adults had retreated into hibernacula and many juveniles either had dispersed, been killed by predators, or hibernated (Zegers, 1977, 1981*a*).

Zegers and Williams (1979) estimated summer daily energy budget for an adult of mean weight (291.3 g) at 35.5 kcal; 8.6 kcal were spent above ground (3.2 h), and 26.9 kcal were spent in the burrow (20.8 h/day).

Analysis of stomach contents revealed that forbs (and to a lesser extent grasses) were primary foods of this squirrel (Burnett, 1924; Clark, 1968; Hansen and Johnson, 1976; Hansen and Ueckert, 1970; House, 1964). Seasonal variation in plants consumed may be related more to changes in availability than to changes in dietary selection (Clark, 1968; House, 1964). Protein and fat content of food were highest and cellulose content lowest during gestation and lactation; fat content also was high during the period of fat storage and growth before hibernation (House, 1964). Caloric values of oven-dried plant material removed from the stomachs of 25 squirrels was 4.4 kcal ± 0.1 in April, 4.4 ± 0.1 in May, 4.3 ± 0.1 in August (Hansen and Reed, 1969). The diet of *S. elegans* contained no significant quantity of C_4 vegetation (Caswell et al., 1973). No significant differences in diet or mass of stomach contents between sexes were noted (Hansen and Johnson, 1976). Individuals feed on carcasses of road-killed conspecifics (Hansen and Ueckert, 1970; Zegers, 1977) and other carrion (Clark, 1968). Because *S. elegans* and orthopterans are major primary consumers in montane grasslands, Hansen and Ueckert (1970) assessed the level of competition for food among those animals and found the diet of only one of seven orthopterans, *Melanoplus infantilis*, more generalized than that of *S. elegans*.

Latitudinal replacement in habitat utilization between *Ochotona princeps*, *Marmota flaviventris*, and *S. elegans* was interpreted as evidence of interspecific competition (Barash, 1973). Carey et al. (1980) found *S. elegans* restricted to areas with deep soils, whereas *S. lateralis* was limited to areas with shallow soils. Hansen (1962) reported that, outside the range of *S. elegans*, *S. lateralis* occupied both meadows and rocky areas, but where sympatric with *S. elegans*, *S. lateralis* was restricted to rocky areas. Apparently these species compete for suitable habitat.

Spermophilus elegans occupies a variety of sage plain and grassland habitats such as valley bottoms and foothills, montane meadows, subalpine talus slopes (Armstrong, 1972; Barash, 1973; Hoffmann et al., 1969), and reclaimed surface-mined areas (Pentacost, 1978). Burrows were found at edges of open marsh (Burnett, 1931), along borders of cultivated fields, along railway embankments (Howell, 1938), on rocky hillsides (Burnett, 1913), and in horse pastures (Zegers, 1977). Pfeifer (1980*a*) found maternity burrows concentrated on knolls and ridges that were the first to be clear of snow in the spring.

With the method of greatest distance between captures as the diameters of circles, Clark (1970*a*) calculated home range area of males from 0.2 to 0.7 ha ($\bar{X} = 0.4$ ha) depending upon age of the individual. With minimum area polygons, Clark (1970*a*) calculated home ranges of 0.1 to 0.5 ha (mean = 0.2 ha) for the same males.

During the breeding season males hold territories (Fagerstone, 1982). During the gestation and lactation periods males no longer defend territories, but females do. Female territoriality appears to function to protect the burrow entrance (thus, the young) against intrusion by conspecifics rather than to defend an area of open ground (Zegers, 1981*b*).

Common ectoparasites include fleas, *Cropsylla idahoensis* (Jellison, 1945), and ticks, *Dermacentor andersoni*, *Ixodes sculptus*, and *I. spinipalpus* (Carey et al., 1980). Ecke and Johnson (1950) reported *Opisocrotis labis* as the most common flea on *S. e. elegans*, although *Oropsylla idahoenis* and *Opisocrostis tuberculatus tuberculatus* also were present. Although trypanosomes and helminth parasites were not studied in *S. elegans*, similar endoparasites to those in *S. richardsonii* (Hilton and Mahrt, 1972; McGee, 1980) likely are present. At times, sylvatic plague can be widespread and exert heavy mortality on *S. elegans* (Ecke and Johnson, 1950; Fitzgerald and Lechleitner, 1970). *S. elegans* is a host of Colorado tick-fever virus (Bowen et al., 1981*a*; Carey et al., 1980) and is relatively resistant (≤ 50% viremic) following experimental inoculation of Colorado tick virus (Bowen et al., 1981*b*).

Because of the diseases harbored by *S. elegans* and possible competition with humans and livestock for food, this species has been the object of extensive control efforts (Burnett, 1913, 1924; Record, 1978). Strychnine-grain baits applied at 6.7 to 11.1 kg/ha on 6.1-m swaths with 6.1 or 30.5 m between swaths reduced squirrel activity 73 to 97%; 6.2 g of strychnine-grain bait placed at burrow entrances reduced activity by 94% (Record, 1978). Steam-rolled, whole oats treated with 2% zinc phosphide were an effective, short-term population control measure (Matschke et al., 1982). After prebaiting, 4 g of the oat bait placed at each burrow entrance reduced density estimates 59.5 and 95.0% at the end of May and beginning of August, respectively. However, density returned to pretreatment levels the following June.

Spermophilus elegans can be captured with treadle-type wire mesh traps (about 15 by 15 by 45 cm) placed at burrow entrances (Zegers, 1982); peanut butter, lettuce, apples, and carrots are effective baits. For identification at a distance, marks produced by either dark hair dye, or freeze-brands applied with a banding tool (Hadow, 1972) or with liquid freon (Russell, 1981) are effective. Toe clipping and ear tabs also are adequate marking techniques. Radiotelemetry is useful to determine movements, home ranges, and dates of hibernation (Fagerstone, 1982). Squirrels can be tranquilized with 0.1 cc ketamine hydrochloride; recovery takes 0.5 to 1 h during which they are susceptible to hyperthermia (Fagerstone, 1982). Direct counts and capture-mark-release provide comparable estimates of density (Zegers, 1981*a*). However, Fagerstone (1982) found no significant correlation between the number of squirrels determined by visual count and the number trapped on the same day; a good index of abundance may be provided by use of the highest visual count during a 5-day period.

Wire suspension-type rat cages are appropriate for housing individual ground squirrels (Marsh and Howard, 1971). Cages with minimum dimensions of 21 by 28 by 21 cm with mesh floors are adequate to keep individuals for up to 6 months. Positive catch-type latches with harness-type back-up latches are necessary because others are not sufficiently secure. Pelleted food should be supplemented with "greens" and whole grains. Because ground squirrels often host large numbers of ectoparasites, squirrels should be dusted periodically with carbaryl (Marsh and Howard, 1971).

BEHAVIOR. *Spermophilus elegans* is completely diurnal (House, 1964), retreating below ground for the night. Typically they show bimodal activity patterns; they are most active in mid-morning and early evening (Fagerstone, 1982). Snowstorms, hail, and heavy rains cause above-ground activities to cease (Clark, 1970*a*), although specific behaviors generally are not affected by air temperature and degree of cloudiness (Zegers, 1981*b*). On cold, sunny days squirrels use postures to maximize heat gain from the sun (Zegers, 1977). Under hot conditions *S. elegans* does not use postures to thermoregulate (Byman, 1979); excessive hyperthermia is avoided by retreating into the burrow. Operative temperatures greater than 39°C limit above-ground activity bouts to less than 10 min (Byman, 1979).

Postures and individual behaviors include: fighting, digging, self- and allogrooming, hay-gathering, running, chasing, walking, two feeding postures, three "alert" postures, and tail-flicking (Clark and Denniston, 1970; Zegers, 1981*b*). Agonistic and other social interactions include: growling, whistling, chasing, and fighting (Burnett, 1924; Clark and Denniston, 1970).

Although time budgets of adults and juveniles were similar, adults spent significantly more time in the upright feeding posture and less time in the down feeding posture than juveniles; no differences in budgets were found between males and females (Zegers, 1981*b*). Feeding was the most protracted activity, consuming 39.3% of all time spent above ground. Individuals spent approximately 36% of their time above ground in "alert" postures and less than 5% of their time chasing or fighting (Zegers, 1981*b*). Agonistic behavior was most common during breeding and gestation (Fagerstone, 1982). Toward the end of the active season adults became more sedentary and spent less time feeding than earlier in the season (Zegers, 1977). In another population, time spent feeding increased throughout the season for adults but decreased at the end of the season for those individuals that hibernated later than average (Fagerstone, 1982).

The feeding activity of juveniles declined in early August during the time of juvenile male dispersal, but increased again before hibernation. Agonistic behavior was most common among juveniles in July and August and was practically nonexistent after mid-August. Time spent by juveniles in alert postures increased from late July to hibernation (Fagerstone, 1982).

Mating was observed in the laboratory but not in the field (Clark and Denniston, 1970). In the laboratory, males approached receptive females by first sniffing noses then sniffing and nibbling the nape of the neck and shoulders of the females. Then, males sniffed and nibbled down the dorsal midline to the anogenital region (nuzzling). Females responded by either raising the tail and slight lordosis or by growling, whistling, and kicking sawdust toward the male. Sometimes receptive females responded to nuzzling by taking the male's tail in the mouth and pulling him around the cage. During copulation a single intromission typically was maintained until ejaculation. At that time, pelvic thrusts ceased, the male released his clasp of the female, and he remained quiescent for at least 1 min. Second copulations within the hour were not observed when motile sperm were found in vaginal smears (Clark and Denniston, 1970).

Alarm calls include chirps (sharp, short, bird-like sounds similar to the sound of a cricket) and churrs (longer than chirps and consisting of a large number of notes similar in frequency and duration); threat sounds include growls of low frequency and intensity and teeth chatters in which the upper and lower incisors are rapidly (≅ 13 times/s) struck together (Fagerstone, 1982). Squeals are emitted only when the squirrels are held and are composed of either many continuous harmonics that waver in frequency or sharp peaks rising rapidly in frequency, then falling immediately (Fagerstone, 1982). Acoustical analysis classified differences among these five types of sound (Koeppl et al., 1978). Audiospectrograms revealed that calls are different from those of *S. armatus*, *S. columbianus*, and *S. richardsonii*. Chirps and churrs of *S. elegans* are significantly different from those of *S. richardsonii* in number and duration of notes and in starting frequency (Fagerstone, 1982). *S. elegans* × *S. richardsonii* hybrids produce chirps and churrs slightly different from those of either parent (Koeppl et al., 1978). Because of the weak harmonic structure of calls, and because calls often are given from the burrow entrance with only the head above ground, it is difficult to locate calling squirrels. A special call for aerial predators was not recorded (Koeppl et al., 1978).

Armitage (1981) included *S. elegans* among those relatively asocial ground squirrels in which individuals aggregate in favorable habitat but members of the colony live individually. Other asocial species include *S. tridecemlineatus*, *S. tereticaudus*, *S. townsendii*, *S. beldingi*, *S. richardsonii*, *S. armatus*, and *S. beecheyi*. Among these and 10 other species of burrowing sciurids, degree of sociality is related to body size, seasonality, maturity, and reproductive effort (Armitage, 1981). On a scale of 1 (asocial) to 5 (egalitarian polygynous harems), Michener (1983) placed *S. elegans* at social grade 2: "single-family female kin clusters." In this grade of sociality, males and females occupy individually distinct ranges after breeding. Male offspring disperse from the natal area, whereas females often remain in or near their mother's range throughout their lives. Juveniles from different litters do not intermingle. Females and their offspring form a moderately cohesive group that is not sociable with adjacent groups (Michener, 1983). Social behavior is not a prominent component of the behavior of *S. elegans*. Intraspecific agonistic behaviors other than those related to reproduction are uncommon (Clark and Denniston, 1970). Adult males defend territories by chasing and occasionally fighting conspecific males. Likewise, adult females defend their maternity burrows (therefore, their young) from intrusion by other adults and juveniles (Zegers, 1981*b*). Sniffing, nibbling, and mutual grooming, except among mating adults or between females and their young, were not reported.

GENETICS. The diploid number is 34, with 32 biarmed autosomes, a submetacentric X chromosome, and an acrocentric Y chromosome (Nadler et al., 1971). Karyotypes of *S. e. elegans* (Nadler, 1964*a*), *S. e. nevadensis* (Nadler, 1964*b*), and *S. e. aureus* (Nadler, 1968*a*) are indistinguishable. In the zone of geographic contact between *S. e. aureus* and *S. richardsonii* ($2n = 36$) some individuals with hybrid karyotypes of $2n = 35$ are produced. Such individuals have 15 sets of biarmed autosomes, 2 acrocentric autosomes from the *S. richardsonii* parent, an unmatched metacentric from the *S. elegans* parent, and a set of sex chromosomes (Nadler et al., 1971). Nadler (1966) proposed Robertsonian centric fusion and a pericentric inversion for the divergence of karyotypes of *S. richardsonii* and *S. elegans*. By use of G- and C-banding, Stupca et al. (1978) implicated the telocentric pairs 1 and 2 from *S. richardsonii* in the formation of metacentric pair 7 of *S. elegans*.

As revealed by starch-gel electrophoresis, *S. elegans* shows transferrin polymorphism and is characterized by Tf_4; some populations in Colorado have a low frequency of Tf_6 (Nadler et al., 1974). In serum protein patterns *S. elegans* lacks Tf_2 (Nadler, 1968*b*).

From serum collected from *S. elegans* and four other species, Gerber and Birney (1968) determined that subgenera *Ictidomys* and *Spermophilus (S. elegans)* were related more closely to each other than to *Otospermophilus* or *Callospermophilus*. The latter two subgenera showed highest immunological affinities for each other. These precipitin tests support the concept that *Spermophilus* and *Ictidomys* evolved as separate lineages at least since the Pliocene (Gerber and Birney, 1968).

Burnett (1920) described white individuals with traces of gray on the dorsum as albinos. No other anomalous colormorphs have been reported.

REMARKS. I use the generic name *Spermophilus* in preference to *Citellus* on the basis of the Law of Priority.

Before Howell (1938) grouped them together as *Citellus richardsonii*, *S. elegans* and *S. richardsonii* were considered distinct species. Differences in bacula (Burt, 1960), cranial morphology of living and fossil forms (Neuner, 1975; Robinson and Hoffmann, 1975), axial skeleton (Fagerstone, 1982), blood proteins (Nadler et al., 1974), fleas (Jellison, 1945), alarm calls (Fagerstone, 1982; Koeppl et al., 1978) and diploid number (Nadler et al., 1971) indicate that the two should be considered separate species. I have attempted herein to exclude information gathered only for *S. richardsonii* except where similar information about *S. elegans* is not published and data from *S. richardsonii* may shed light on the biology of *S. elegans*.

Because *S. elegans* and *S. richardsonii* long were considered conspecific, both are commonly referred to as "Richardson's ground squirrel." Other vernacular names include "picket pin" and "flickertail."

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