

*Spermophilus richardsonii*. By Gail R. Michener and James W. Koepl

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*Spermophilus richardsonii* (Sabine, 1822)

Richardson's Ground Squirrel

*Arctomys richardsonii* Sabine, 1822:589. Type locality Carlton House, Saskatchewan.

*Spermophilus richardsonii* Cuvier, 1831:323.

**CONTEXT AND CONTENT.** Order Rodentia, Family Sciuridae, Genus *Spermophilus*, Subgenus *Spermophilus*. Formerly included the subspecies *aureus*, *elegans*, and *nevadensis* (Hall, 1981:385), but now considered monotypic (Nadler et al., 1971, 1982; Robinson and Hoffmann, 1975).

**DIAGNOSIS.** *S. richardsonii* is one of five species in the subgenus *Spermophilus* that lack pronounced spotted or mottled dorsal pelage (Hall, 1981; Howell, 1938). It is distinguished from *S. townsendii* by having a hindfoot length greater than 39 mm, by a longer tail (65 to 100 as opposed to 32 to 72 mm), and by the cinnamon buff rather than creamy white underparts. *S. richardsonii* is distinguished from *S. beldingi* by a longer tail (55 to 76 mm in the latter) and by the cinnamon buff or clay color rather than hazel color of the underside of the tail. *S. richardsonii* differs from *S. armatus* by lacking gray coloration on the underside of the tail.

Live *S. richardsonii* and *S. elegans* cannot be distinguished reliably by pelage color (Fagerstone, 1982), but the longer, higher pitched churr calls and monosyllabic, piercing chirp calls of the former are diagnostic (Fagerstone, 1982; Koepl et al., 1978). *S. richardsonii* differs from *S. elegans* by having a body length greater than 275 mm, hindfeet 43 mm or longer, a maxillary toothrow greater than 10 mm, nasal length greater than 16 mm, and a maximum skull length greater than 45 mm (Howell, 1938). The baculum of *S. richardsonii* has a slightly twisted shaft and lacks distinct projections on the distal expansion, whereas that of *S. elegans* has a markedly twisted shaft and 8 to 11 tooth-like projections (Burt, 1960). The diploid chromosome number of *S. richardsonii* is 36, whereas  $2n$  for *S. elegans* is 34 (Nadler et al., 1971).

**GENERAL CHARACTERS.** *S. richardsonii* is a stout-bodied, semi-fossorial species, with relatively short but dense pelage (Fig. 1). The upperparts are pinkish buff or cinnamon buff shaded with fuscous, with the posterior part of the back showing a dappled effect (Howell, 1938). The eye ring is light buff, and the sides of the head and neck and the fronts of the forelegs are cinnamon buff or clay. The tail is fuscous black above, cinnamon buff or clay below, and edged with pinkish buff.

Howell (1938:74) listed the following mean (range) measurements (in mm) of 16 adults (seven males and nine females) taken from the type locality: total length, 285.4 (277 to 306); tail length, 73.8 (65 to 83); hindfoot length, 44.9 (43 to 47). Skull measurements for each sex were: greatest skull length, 47.7 (47.3 to 48.0) for males, 46.5 (45.1 to 48.4) for females; palatilar length, 23.7 (23.0 to 25.0), 23.1 (22.5 to 24.0); zygomatic breadth, 31.9 (30.5 to 33.5), 30.4 (29.5 to 31.2); cranial breadth, 20.2 (19.9 to 20.8), 19.6 (19.0 to 20.9); interorbital breadth, 9.9 (9.5 to 10.6), 9.5 (8.8 to 10.0); postorbital constriction, 11.4 (10.8 to 11.9), 11.1 (10.8 to 11.5); length of nasals, 17.4 (17.0 to 18.0), 16.9 (16.0 to 18.1); length of maxillary toothrow, 10.4 (10.2 to 10.7), 10.4 (10.0 to 10.9). The dental formula is  $i\ 1/1, c\ 0/0, p\ 2/1, m\ 3/3$ , total 22. The upper toothrows are slightly convergent posteriorly (Fig. 2).

Five pairs of mammae are spaced uniformly from the axillary to the inguinal region (Moore, 1961).

**DISTRIBUTION.** *Spermophilus richardsonii* is a species of the northern plains and to a lesser extent the intermontane valleys (Fig. 3). Its range in Canada includes southern Alberta (except the Rocky Mountains), southern Saskatchewan, and southwestern Man-

itoba. In the United States it occurs in western Minnesota, north-eastern South Dakota, North Dakota (except the southwestern corner), and north central Montana (Howell, 1938; Swenson, 1981). In Montana, *S. richardsonii* is parapatric and locally syntopic with the sibling species *S. elegans* (Koepl et al., 1978; Koepl and Hoffmann, 1981; Nadler et al., 1971).

**FOSSIL RECORD.** *Spermophilus richardsonii* first appears in the fossil record in the Cudahy (late Kansan); specimens are known from the Illinoian Sandahl and Doby Springs faunas and Rancholabrean sites in Alberta, South Dakota, Colorado, Idaho, Kansas, New Mexico, and Wyoming (Kurtén and Anderson, 1980). Present distribution of this species does not include the latter five areas. The *S. richardsonii* complex presumably originated on the Great Plains, with subsequent isolation of peripheral populations in the late Pleistocene, giving rise to *S. richardsonii* and three subspecies of *S. elegans* (Nadler et al., 1971, 1982; Neuner, 1975; Neuner and Schultz, 1979).

**FORM AND FUNCTION.** Under constant conditions in captivity, *S. richardsonii* exhibits free-running cycles of food consumption, body mass, molt, testicular recrudescence, and hibernation (Melnyk, 1983; Scott and Fisher, 1970, 1978). Whereas periodicity of circannual cycles is 9 to 11 months for most species of *Spermophilus*, it is 6 to 8 months for *S. richardsonii* (Melnyk, 1983). The mechanism whereby free-living squirrels achieve synchrony with environmental conditions on an approximately 12-month schedule is not known.

Under natural conditions, winter torpor of Richardson's ground squirrels is interrupted at frequent intervals by rewarming to normothermic temperatures. In the 2 months after immergence, torpor episodes last 2 to 8 days. Thereafter, episodes increase to a mean of 19 days in January, then decrease to 14 days in February and 6 days in March (Wang, 1973, 1979). Intertorpor periods average less than 12 h throughout the hibernation season. From November to February, squirrels spend about 98% of the time in deep torpor. Although obligate hibernators under natural conditions, only 75% of captive juveniles maintained at 6°C and 2L:22D hibernated and none hibernated at 18°C and 12L:12D, though about 5% exhibited infrequent, brief bouts of torpor (Demeneix and Henderson, 1978). Captive squirrels invariably urinate, occasionally defecate, but rarely eat or drink during the intertorpor arousal (Demeneix and Henderson, 1978).

The thyroid gland exhibits an annual cycle of synthetic and resorptive activity, with least activity in early hibernation. However, serum levels of L-thyroxine and triiodo-L-thyronine are elevated in hibernating squirrels, seemingly because utilization (tissue uptake, urinary and fecal clearance) is reduced (Demeneix and Henderson, 1978; Winston and Henderson, 1981).



FIG. 1. Juvenile Richardson's ground squirrel, approximately 3 months old, from 9 km E Picture Butte, Alberta. Numbered metal tags in ears are used as a means of permanent identification of individuals. Photograph by Gail R. Michener.

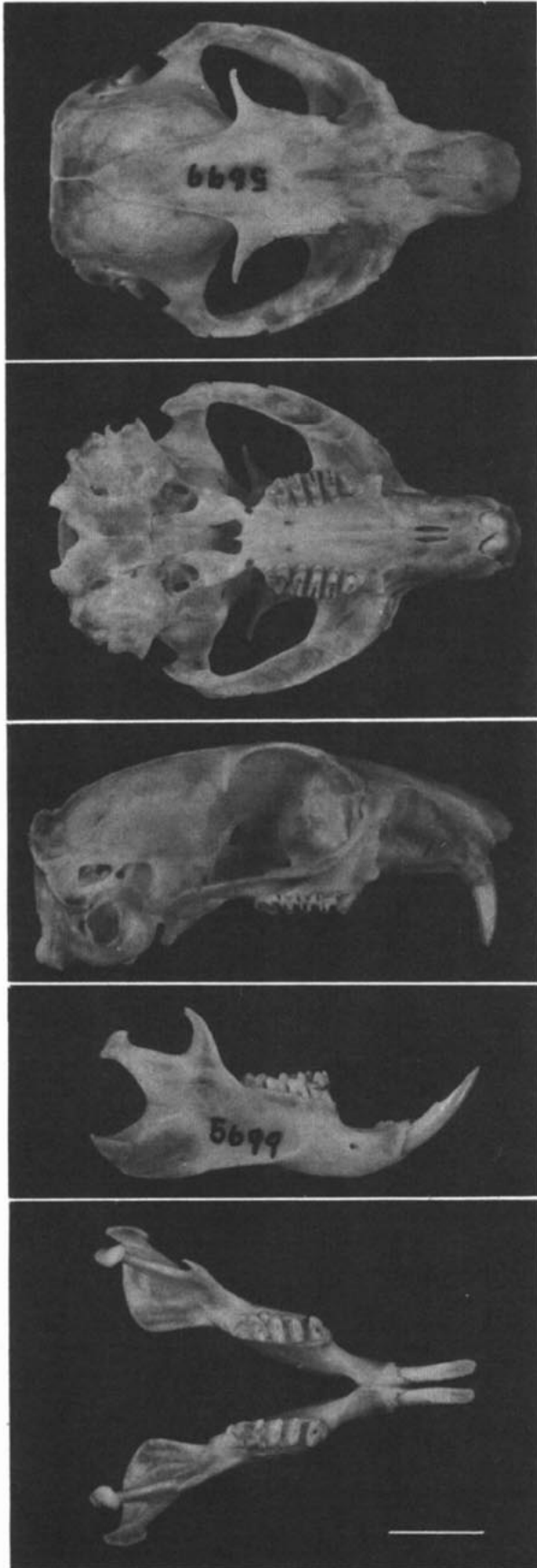


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral and occlusal views of lower jaw of an adult male *Spermophilus richardsonii* collected between Cooking Lake and Hastings

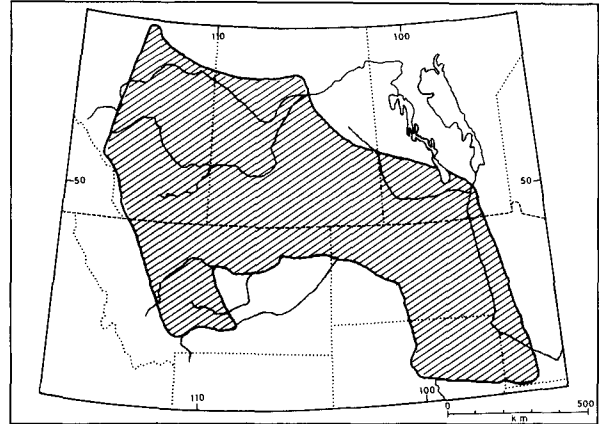


FIG. 3. Geographic distribution of *Spermophilus richardsonii* (modified from Hall, 1981; Nadler et al., 1982; Soper, 1964; and Swenson, 1981) presented on a Lambert zenithal equal-area projection.

Free-ranging, normothermic squirrels have a mean abdominal temperature of 38.2°C in the day and 37.9°C at night (Wang, 1972). Similar body temperatures were recorded for captive animals maintained at 13°C (Wang, 1972) and 7°C (Scott et al., 1974). Body temperature drops as low as 2 to 3°C in torpid squirrels in the field. Rewarming from torpid to normothermic temperatures requires 1.5 to 6 h depending on the individual and its initial body temperature. Wang (1979) estimated that, of the energy expended during hibernation, 70.6% is used during the brief intertorpor re-warming and arousal period with the remainder used during entry into and maintenance of deep torpor.

Richardson's ground squirrels store lipid in white and brown adipose tissues (Dolman and Michener, 1983). Brown adipose tissue is located in axillary, intermuscular (primarily neck and shoulder), and intrathoracic regions. The proportion of brown adipose tissue in the intrathoracic deposit increases from birth to prehibernation; deposits on the heart and aortic arch probably contribute to efficient re-warming of the body core during periodic arousals from torpor.

Richardson's ground squirrels depend on body fat for energy during hibernation and exhibit an annual weight cycle of maximum mass shortly before entry into hibernation and minimum mass at or shortly after emergence in spring (Harding and Rauch, 1981; D. Michener, 1974). Masses of squirrels vary between years, between locations, and with age and sex. In southern Alberta, mean mass of yearling females at emergence is typically about 200 g and that of older females is about 250 g (Michener, 1984a). Minimum body mass for adult females occurs at emergence from hibernation; females gain mass between emergence and insemination (ca. 23 g) and between insemination and late pregnancy (ca. 139 g), but lose mass (ca. 54 g) at parturition (Michener, 1984a). Although females increase their total mass after hibernation, lipid stores decline and remain small during late pregnancy and lactation (Dorrance, 1974). Body mass stabilizes during lactation and mothers do not commence prehibernation weight gain until about 40 days postpartum. Females that do not wean litters start prehibernation weight gain earlier and immerse earlier than females that wean a litter (Michener, 1978). Females attain prehibernation masses of about 350 to 435 g.

Mean mass of adult males at emergence from hibernation is about 360 to 425 g in central and southern Alberta (Davis, 1982a; Dorrance, 1974; Michener, 1984a) and about 300 g in the foothills of Alberta and in Saskatchewan (Davis, 1982a; D. Michener, 1974). Older males are slightly heavier than yearling males at emergence (Michener, 1984a). Minimum body mass for males occurs during the mating season, several weeks after emergence, when males lose an average of 8 to 18% of their prebreeding mass (Dorrance, 1974; Michener, 1984a). Males begin to gain weight when most females have emerged and mated; they continue to increase in mass until

← Lake, Alberta. Specimen UAMZ 5699 from the Museum of Zoology, University of Alberta. Scale represents 10 mm.

they enter hibernation. Adult males attain prehibernation masses of 450 to 500 g in southern Saskatchewan and central Alberta (Dorrance, 1974; D. Michener, 1974) and 500 to 655 g in southern Alberta (Michener, 1984b).

In southern Alberta, one of us (GRM) recorded a mean mass for newly emerged juveniles (28 to 30 days old) of 76 g ( $n = 361$ , range 45 to 120, 90% of individuals weigh 60 to 95 g). Juveniles gain mass steadily following emergence from the natal burrow, and males exceed females in mass within 2 weeks of emergence. Average prehibernation masses of juvenile females and males in southern Alberta are 365 and 459 g, respectively (Dolman and Michener, 1983). Males divert more energy to growth than to fat deposition in their first summer of life. Although juvenile males are about 25% heavier than juvenile females at entry into hibernation, they store less lipid (46 g as opposed to 91 g) and have a lower fat content (10% as opposed to 24% of body mass) and a greater lean-body mass than females (Bintz and Strand, 1983; Dolman and Michener, 1983).

Richardson's ground squirrels have an anal gland of three evertible papillae that protrude from the orifice and pulsate when the animal is handled (Sleggs, 1926). Apocrine glands located at the oral angle, on the dorsum from the scapular region to the pelvic region, and ventral to the ears (Kivett et al., 1976), probably function in identification and marking.

Oxygen consumption (resting metabolic rate plus limited activity) recorded for captive squirrels at 22–24°C averaged 0.97 ml  $O_2$   $g^{-1}$   $h^{-1}$  for control animals, 1.23 for animals starved for 7 days, and 1.67 for animals starved and water deprived for 7 days (Bintz and Mackin, 1980). During starvation and water deprivation, normothermic squirrels maintain water balance by catabolizing protein-containing tissues with high water content in addition to adipose tissue (Bintz et al., 1979). Over a 5-day period of starvation and water deprivation, squirrels exhibited an evaporative water loss of 3.10 ml water  $100$   $g^{-1}$   $day^{-1}$  compared with 3.61 for control squirrels (Bintz and Roesbery, 1978).

**ONTOGENY AND REPRODUCTION.** Female *S. richardsonii* produce one litter annually, commencing when they are 1 year old (Michener, 1985; Sheppard, 1972). Females typically mate 3 to 5 days after they emerge from hibernation (Michener, 1983a, 1985). The mating season is usually 3 to 5 weeks long in southern Alberta, but 50% of females are inseminated within a 3- to 9-day period (Michener 1983a, 1984a; Nellis, 1969; Sheppard, 1972). Peak breeding occurs in mid- to late March in southern Alberta (Michener, 1983a) and in mid-April in central Alberta and Saskatchewan (Dorrance, 1974; Nellis, 1969; Sheppard, 1972; conception dates given by these authors are about 6 days early as they used Asdell's [1964] erroneous report of a 28-day gestation to calculate the time of conception). Ninety to 100% of females breed and bear young each year (Dorrance, 1974; D. Michener, 1974; Michener, 1985; Nellis, 1969; Sheppard, 1972). Litters are born in underground burrows after a 22.5-day gestation period (Michener, 1980a, 1985).

From studies with a sample size of at least 14 (when data from different years within one study are combined; Dorrance, 1974; Nellis, 1969; Schmutz, 1977; Sheppard, 1972), minimum and maximum mean litter sizes based on counts of embryos or implantation sites are 5.2 ( $n = 23$ ) and 9.3 ( $n = 429$ ). Maximum counts of embryos (Pigage, 1975) and implantation sites (Nellis, 1969) are 14 and 15, respectively. Mean litter size at birth (Dolman, 1980; Michener, 1977a, 1985) ranges from a minimum of 4.9 ( $n = 15$ , range 3 to 6) to a maximum of 8.3 ( $n = 46$ , range 3 to 13). Mean litter size at first emergence from the natal burrow (Dorrance, 1974; Michener, 1979a, 1985; Schmutz, 1977; Wehrell, 1973) ranges from a minimum of 3.8 ( $n = 24$ , range 1 to 6) to a maximum of 7.2 ( $n = 210$ , range 1 to 13). In central Alberta, yearlings carried significantly fewer embryos than older females (Dorrance, 1974), whereas embryo counts for yearling and older females in southern Saskatchewan did not differ (Sheppard, 1972). Yearling females weaned significantly fewer young than older females at one site in Alberta (Michener, 1980b), whereas litter size at emergence did not vary with age at another location (Michener, 1985). Litter size is positively correlated with maternal body mass and fat index (Dorrance, 1974; Sheppard, 1972), suggesting that differences in litter size between yearling and older females may be more indicative of differences in body mass than of age.

Juveniles first leave the natal burrow when 26 to 33 days old

( $\bar{X} = 29.2$  days) (Michener, 1977b, 1985), and appear above ground from late April to mid-May in southern Alberta (Michener, 1985) and from late May to early June in eastern North Dakota, southern Saskatchewan, central Alberta, and the foothills of the southern Alberta Rocky Mountains (Dorrance, 1974; Michener, 1979a; D. Michener, 1974; Quanstrom, 1971; J. Schmutz et al., 1980; S. Schmutz et al., 1979).

Mean body length, mean tail length, and mean hindfoot length of captive-born neonates less than 24-h old are 55.7 mm, 9.3 mm, and 7.8 mm, respectively (Koepl, 1979). Minimum and maximum mean masses of neonates less than 24-h old are 6.5 g ( $n = 91$ ) and 7.4 g ( $n = 56$ ); extreme values for individual live neonates are 4.4 and 9.6 g (Dolman, 1980; Harper et al., in litt.; Koepl, 1979). Postnatal increase in mass occurs in three linear phases: at 13% per day from 1 to 10 days, at 6% per day from 11 to 45 days, and at about 1.5% per day thereafter to 70 days of age (Dolman, 1980).

At birth, young are naked with eyes and ears closed, teeth unerupted, and digits fused. Fine pelage appears at 4 to 7 days, foredigits separate at 13 days, ears open at 19 to 21 days, upper incisors erupt at 20 to 22 days, eyes open at 21 to 25 days ( $\bar{X} = 23.1$  days), and adult pelage develops at 22 to 28 days (Harper et al., in litt.). Feces are brown and solid (indicating consumption of solid food) by 25 days.

Neonates are essentially poikilothermic at birth. At 14 days, young can elevate body temperature 4 to 5°C above ambient for at least a 1-h exposure to 25° and 30°C. By 29 to 32 days of age, young can maintain a body temperature of 38°C during a 2-h exposure to 25°C (Dolman, 1980).

Richardson's ground squirrels are reproductively mature at emergence from their first hibernation when 11 months old (Michener, 1983a). Peak testis length is attained about 12 days after emergence. Testes regress and assume an abdominal position about 8 weeks after emergence (Michener, 1983a). Within 2 to 4 days of emergence, females exhibit a swollen, bright pink vulva, accompanied by sloughing of cornified epithelium from the vaginal wall (Michener, 1980a). No data are available to establish whether *S. richardsonii* is an induced or spontaneous ovulator. A copulatory plug (average dimensions: 19.8 by 6.9 by 5.8 mm) forms, probably within 1 h of insemination, and is lost within 15 to 17 h (Michener, 1984c).

Females live longer than males. In a population of known-aged adults in southern Saskatchewan, 56% of females ( $n = 95$ ) and 18% of males ( $n = 28$ ) were 2 years old or older (Michener and Michener, 1977). Furthermore, 24% of the females, but only 4% of the males, were at least 3 years old. In a 6-year study in southern Alberta, one of us (GRM) found 5- and 6-year-old females but only one male survived to 4 years of age.

**ECOLOGY.** Predators of *S. richardsonii* (Dorrance, 1974; Goulden, 1975; Lutich et al., 1970; McInville and Keith, 1974; McLean, pers. comm.; Michener, 1979a; Quanstrom, 1968; J. Schmutz et al., 1980; S. Schmutz et al., 1979; Schwab, 1978; Sheppard and Swanson, 1976) include canids (*Canis latrans*; *Vulpes vulpes*), mustelids (*Taxidea taxus*; *Mustela frenata*; *M. vison*; *Mephitis mephitis*), buteos (*Buteo jamaicensis*; *B. regalis*; *B. swainsoni*), harriers (*Circus cyaneus*), falcons (*Falco mexicanus*), eagles (*Haliaeetus leucocephalus*), owls (*Nyctea scandiaca*; *Bubo virginianus*), and black-billed magpies (*Pica pica*). Domestic cats and dogs also hunt ground squirrels. Long-tailed weasels, badgers, and buteos seem to have the greatest impact on ground squirrel populations. Predation by long-tailed weasels on unweaned young in the burrow can reduce the number of juveniles entering the population by >50% (Michener, 1979a). Although long-tailed weasels can kill adult squirrels (Byrne et al., 1978), adults sometimes attack and chase weasels when above ground (Davis, 1985; Dorrance, 1974). Badgers occasionally kill Richardson's ground squirrels by ambushing them above ground (Schwab, 1978), but more commonly dig them out of burrows (Dorrance, 1974; Michener, 1979a). Squirrels are probably most vulnerable to predation by badgers in autumn when they are torpid in their hibernacula but before the ground has frozen (Michener, 1979a). During the nesting period for buteos in southern Alberta, *S. richardsonii* averaged ( $n = 2$  years) 90% of the prey biomass for ferruginous hawks, 76% for red-tailed hawks, and 75% for Swainson's hawks (Schmutz et al., 1980). These buteos were estimated to have killed 15% of the squirrel population in one year and 6% in the other year. *S. rich-*

*ardsonii* males seem more susceptible than females to predation by buteos (Luttich et al., 1970; Schmutz et al., 1979).

The tick *Dermacentor andersoni*, a vector of Rocky Mountain spotted fever and tularemia, and the fleas *Opisocrostitis labis* and *Oropsylla rufestris*, vectors of plague, occur on ground squirrels in Alberta (Brown and Roy, 1943; Hilton and Mahrt, 1971a). Immediately after emergence from hibernation, squirrels are heavily infested with fleas (commonly 20 to 30 per squirrel), but by June–August infestations decline to one or two per squirrel. The effects of flea-transmitted diseases on ground squirrel populations are not known. Moribund squirrels infested with the flesh-eating larvae of *Sarcophaga citellivora* were found in the foothills of southern Alberta (Michener, 1979a), but this fly probably has a minor effect on population mortality rates. Mites and lice also are common ectoparasites of *S. richardsonii* in Alberta (Hilton and Mahrt, 1971a). Endoparasites include coccidians, trypanosomes, cestodes, trematodes, nematodes, and acanthocephalans (Hilton and Mahrt, 1971b, 1972; McGee, 1980; McLeod, 1933). The most common helminth, *Citellinema bifurcatus*, was found in 32% of squirrels in Saskatchewan, including newly emerged juveniles. Males and older squirrels were infested more commonly with helminths than females and younger squirrels (McGee, 1980).

Richardson's ground squirrels are predominantly herbivores, consuming primarily leaves, flowers, and seeds (Richardson, 1829). In a late-summer sample of 18 stomachs, vegetation formed 90% of the contents, with insects accounting for most of the remainder (Bailey, 1893). Squirrels also feed on road-killed conspecifics. Most dietary information for *S. richardsonii* is for areas where vegetation has been altered by agricultural practices. Forage grasses and legumes such as *Bromus inermis*, *Agropyron cristatum*, *Trifolium pratense*, *T. repens*, and *Melilotus alba* are major food items on overgrazed pastures in eastern North Dakota. However, prairie natives such as *Bouteloua gracilis*, *Amaranthus* sp., and *Astragalus* spp. also are eaten (Quanstrom, 1968). Squirrels eat the seedlings and seeds of domesticated cereals such as wheat, barley, and oats (Bailey, 1893; Howell, 1938). Squirrels from cropland are larger in size (103%) and bear larger numbers of live embryos (118%) than squirrels inhabiting native grassland (Sheppard, 1972).

Early reports emphasized the impact of *S. richardsonii* on agricultural crops (Bailey, 1893; Bell and Piper, 1915). Scientific studies of damage assessment are rare. Bailey (1893) and Brown and Roy (1943) noted that populations in cultivated areas seem large because squirrels are concentrated along margins of fields. However, cultivated fields, especially under irrigation, support few squirrels because burrows are destroyed by plowing and flooding and because the squirrels rarely inhabit sites where tall vegetation restricts their visual field.

Chemical toxicants such as strychnine and zinc phosphide, distributed on wheat or rolled oats, can result in an immediate mortality of >70% (Matschke et al., 1983; Record, 1978). The chemosterilant mestranol, when distributed shortly before or in early pregnancy, suppresses reproduction for one season (Goulet and Sadleir, 1974). Post-treatment reinvasion by squirrels from surrounding areas generally rapidly returns populations to pre-treatment levels (Alsager and Yaremko, 1972; Goulet and Sadleir, 1974).

Sex ratios among neonates and juveniles approximate 1:1 (Dorrance, 1974; D. Michener and Michener, 1971; G. Michener and Michener, 1977; Nellis, 1969; Sheppard, 1972; Schmutz et al., 1979), though Michener (1979a, 1980b) recorded male-biased litters at birth and at emergence in 1 of 3 years in the Alberta foothills. Cumulative numbers of juveniles captured during the summer include more males than females because males are more likely to disperse and disperse greater distances than females. However, the sex ratio among resident juveniles remains approximately 1:1 until females enter hibernation (Schmutz et al., 1979). Thereafter, the sex ratio becomes male-biased until ultimately the above-ground population consists only of juvenile males (Dorrance, 1974; D. Michener, 1974; Michener, 1979a). Males emerge from hibernation before females (Michener, 1983a), so the population of adults ( $\geq 1$  year) in spring is initially predominantly male. When females emerge from hibernation the population becomes predominantly female, typically with 2 to 10 females per male (Dorrance, 1974; Michener, 1979a, 1983a; D. Michener and Michener, 1971; G. Michener and Michener, 1977; Nellis, 1969; Schmutz et al., 1979; Sheppard, 1972). The change in the sex ratio from equality occurs between the juvenile and yearling year (Michener and Michener, 1977).

Average annual densities of adult squirrels based on 3- or

4-year studies at large (>10 ha) sites were 1.4/ha (Michener and Michener, 1977), 2.7/ha (Dorrance, 1974), and 5.2/ha (Michener, 1983a). Squirrels usually are not distributed homogeneously; G. Michener (1972) recorded a density of 5.3 adults/ha on a 1.5-ha portion of a 108-ha site that had an overall density of 1.2 adults/ha (Michener and Michener, 1977). Average densities of greater than 10 adults/ha were noted on several small (<2 ha) study sites: 12.0/ha (Dorrance, 1974), 19.1/ha (Michener, 1979a), and 27/ha (Davis, 1984a). Density increases dramatically with the synchronous emergence of litters from natal burrows. In a 4-year study, Dorrance (1974) noted an average density in June of 9.6 juveniles/ha on a 13-ha site and 56.3 juveniles/ha on a 2-ha site.

The following interyear recovery rates of adult females, adult males, juvenile females, and juvenile males have been obtained in studies encompassing at least two winters: 37%, 21%, 21%, and 3% in central Alberta (Dorrance, 1974), 47%, 29%, 25%, and 10% in southern Saskatchewan (Michener and Michener, 1971), 54%, 38%, 27%, and 11% in the foothills of southern Alberta (Michener, 1979a), and 45%, 29%, 21%, and 7% in southern Alberta (Schmutz et al., 1979). A combination of dispersal, predation, and overwinter mortality accounts for total losses and for the differential losses between sexes in each age class.

Dispersal by *S. richardsonii* is male-biased (Davis, 1982a; Dorrance, 1974; Michener and Michener, 1977; Quanstrom, 1971; Schmutz et al., 1979; Yeaton, 1972). Juvenile males generally disperse in late June and July when they are 8 to 12 weeks old. The distances moved and the fates of most emigrants are not known, though movements of 3 to 10 km have been recorded for marked individuals (Dorrance, 1974; Quanstrom, 1971). Although most studies report more emigration and immigration by males than females, Michener (1979a) found that no locally born juveniles (seven males, eight females) emigrated from a 0.72-ha site in one year and loss (dispersal plus mortality) of juvenile females exceeded that of juvenile males in another year. Emigration by juveniles, particularly females, may be related to an individual's inability to appropriate a portion of the mother's range for its own use (Michener, 1981). When males fail to disperse as juveniles they are likely to do so as yearlings (Michener, 1981; Michener and Michener, 1977).

Squirrels exhibit seasonal variation in the sizes of their ranges. Females occupy larger areas following emergence of the litter than they do during gestation and lactation or during the 4 weeks preceding hibernation (Michener, 1979c; Quanstrom, 1968; Wehrell, 1973). However, Davis (1982a) reported that ranges were largest during gestation and lactation. Ranges of males decrease in size after the breeding season, increase in midsummer, then decrease again before hibernation (Michener, 1979c).

Michener (1983a, 1984a) reported a 96% success rate during spring in capturing *S. richardsonii* with unbaited treadle-type, wire-mesh live traps (48 by 15 by 15 cm). For restraint and handling, animals were induced to enter a conical-shaped, cloth bag with a zippered opening in the narrow end. Metal ear tags provide permanent identification (Fig. 1), and commercial hair dye temporarily marks the pelage, permitting identification of individuals from a distance. Davis and Murie (1985) attached radiocollars to adult males to track their movements in the mating season. Vaginal lavages can be made at least daily in the field and stained to determine vaginal estrus (Michener, 1980a, 1984c). *S. richardsonii* rarely breeds in captivity. Field-impregnated females successfully bear and rear litters in standard plastic cages (47 by 37 by 20 cm; Davis, 1982b; Michener, 1977a, 1980a).

Sheppard (1972) used lens weight less than 10.5 mg, epiphyseal line apparent or open, and molar teeth little worn to distinguish yearlings from older adults. Yearling females emerge from hibernation at significantly lower masses than older females, but body mass is not a reliable criterion for distinguishing age classes after females have been above ground for several weeks (D. Michener, 1974; Michener, 1984a).

**BEHAVIOR.** Time of emergence from hibernation is correlated with soil and air temperatures (Michener, 1973a, 1977a, 1979b). Squirrels generally emerge in late February and March in southern Alberta (Michener, 1983a, 1985; Schmutz et al., 1979) and in late March and April in central Alberta, the foothills of southern Alberta, southern Saskatchewan, southern Manitoba, and eastern North Dakota (Davis, 1982a; Dorrance, 1974; D. Michener, 1974; Michener, 1979b; Quanstrom, 1968; SOWLS, 1948). Females emerge about 1 to 2 weeks after males, yearlings emerge at the same time as older squirrels of the same sex, and emergence

tends to be synchronous such that 75% of squirrels within each cohort emerge in a 1- to 2-week period (Dorrance, 1974; Michener, 1983a). Litters emerge from natal burrows about 56 days after females emerge from hibernation (Michener, 1985).

Although the active season lasts approximately 7 months, typically March through September in central Alberta, the foothills of southern Alberta, and southern Saskatchewan, individuals are above ground for only 3 to 3.5 months each year (Dorrance, 1974; D. Michener, 1974; Michener, 1979a, 1979b). The sequence of entry of cohorts into hibernation (Michener, 1984b) is: adult males (June and early July), adult females (July and early August), juvenile females (late August and early September), and juvenile males (September and early October). Immergence occurs several weeks earlier in southern Alberta (Michener, 1984b). The immergence schedule reflects the chronological sequence in which adult males, adult females, and juveniles commence fat deposition following the energetic demands of mating, gestation and lactation, and growth, respectively (Bintz and Strand, 1983; Michener, 1984b). The pattern of immergence results in a period of approximately 2 months when only juveniles are above ground.

Richardson's ground squirrels use burrows for hibernation, sleeping, refuge from predators and inclement weather, copulation, and rearing litters. Burrows can extend for 4 to 15 m from the opening, descend to depths of 1 to 2 m, and include chambers 15 to 23 cm in diameter (Howell, 1938; Quanstrom, 1968).

Richardson's ground squirrels are active diurnally. In spring and autumn, animals exhibit a unimodal distribution of above-ground activity from about 0800 to 1800 h, whereas, in midsummer, activity is bimodal with peaks at 0600 to 1000 h and at 1400 to 1900 h (Michener, 1968; Yeaton, 1969). Squirrels typically emerge about 95 to 130 min after sunrise, but delay emergence if the weather is cool or inclement (Michener, 1968).

Davis (1984a), G. Michener (1972), Michener and Sheppard (1972), Quanstrom (1971), Sheppard and Yoshida (1971), Wehrell (1973), and Yeaton (1969) described over 35 postures and behaviors, of which feeding, moving, alert, and interacting with conspecifics were the most common activities of squirrels when above ground. Males spent less time feeding and more time moving and interacting during the mating period than during the remainder of the active season. Proportion of time spent feeding by males increases postbreeding to 50 to 65% of above-ground time (Davis, 1982a; McLean, pers. comm.; Michener, 1979c; Yeaton, 1969), and may ultimately occupy 80 to 90% of above-ground time in the 6 weeks preceding entry into hibernation (Michener, 1979c). Adult females feed 50 to 70% of the time above ground from emergence in spring until midsummer (Davis, 1982a, 1984b; Michener, 1979c; Wehrell, 1973; Yeaton, 1969), and up to 80% of the time in the 4 weeks before entry into hibernation (Michener, 1979c; Wehrell, 1973). Juveniles feed 40 to 80% of the time above ground (Davis, 1982a; Michener, 1981; Yeaton, 1969). About 5 to 15% of the time adult females spend above ground they interact with conspecifics; interactions are most common shortly after juveniles first leave the natal burrow (Davis, 1982a; Michener, 1979c, 1980c).

For adult males, social interactions are most frequent during the mating season when they initiate aggressive interactions with other males and sexual interactions with females. Adult males attempt to establish territories in areas occupied by newly emerged females; if asynchronous emergence of females results in a sparse and unpredictable distribution of females, males are not territorial in the mating period (Davis and Murie, 1985; Michener, 1983a). Most copulations occur below ground. When above ground, the male mounts from behind, the pair rolls to one side, and coition occurs with the male lying on his side and the female lying partially on her side with head and shoulders raised (Davis, 1982c). The copulatory mount typically lasts 3 to 4 min, after which the male usually grooms his genital area. Some females copulate with more than one male. Males sustain injuries, predominantly inflicted by other males, during the mating season, and they lose weight during the 1.5 to 2 weeks of most intense mating activity. In contrast, females rarely are injured during the mating period and they gain weight from emergence to parturition with the exception of a 1-day interruption in weight gain on the day of insemination (Michener, 1983a, 1984a).

Based on descriptions of spacing patterns and social organization by Davis (1982a, 1984b), D. Michener (1972), Michener (1973b, 1979c, 1980c, 1981), Michener and Michener (1973), Quanstrom (1968, 1971), Wehrell (1973), and Yeaton (1969, 1972), three major phases can be identified in the spatial and social

patterns of squirrels following the mating period (Michener, 1983b). (1) The 7-week pregnancy-lactation phase is characterized by even dispersion of females, each of which has a core area that overlaps only slightly with those of neighbors. Females exhibit site-dependent dominance and are aggressive toward conspecifics, particularly males and unrelated females. Each female rears her litter in isolation in a burrow which she excavates and provisions with nest material by herself. (2) In the 4-week juvenile emergence phase, newly emerged juveniles gradually range further away from the natal burrow and, about 2 weeks after emergence (when 6 weeks old), they begin to interact with neighboring adults and juveniles from other litters. Social interactions among littermates and between mother and offspring are predominantly amicable, whereas those between distantly related squirrels are predominantly agonistic. (3) During the pre-hibernation phase, squirrels spend less time above ground and use progressively smaller ranges until each enters hibernation. Juveniles no longer share burrows with littermates and the mother, and each establishes a core area that is distinct from, though in proximity to, those of family members. Those juveniles that disperse do so early in the pre-hibernation phase. Kin continue to interact amicably and others agonistically, but interactions become infrequent among all conspecifics.

Armitage (1981) and Michener (1983b) placed *S. richardsonii* at the second grade (viz., single-family kin clusters) of a 5-grade scale of increasing sociality for ground-dwelling sciurids, whereas Davis and Murie (1985) suggested placement at grade 3. Affiliative bonds established between mothers and daughters and between littermate sisters are retained throughout life. Females tend to remain in or near their natal area in adulthood, so female kin are likely to share space as adults. Males typically disperse individually as juveniles or yearlings, so they do not associate with family members in adulthood. Retention of social bonds between female kin, female philopatry, and male dispersal result in a social system that is matrilineal and matrifocal (Davis, 1982a, 1984b; Michener, 1983b). Davis (1985) suggested that some adult males play an indirect role in parental care via alarm calling and chasing nest predators such as weasels.

Captive mothers retrieve pups that are displaced from the nest until 20 to 25 days postpartum (G. Michener, 1971, 1972). Nulliparous yearlings are less likely to retrieve and more likely to attack neonates placed in their cages than are older females that reared pups in previous years (Michener, 1973c). Some yearling males retrieve pups placed in the home cage, but their response is slower and more erratic than that of mothers; other yearling males attack neonates (G. Michener, 1972). Males and non-lactating females that retrieve young also lick pups, rearrange nest paper around pups, and assume a nursing posture over pups (G. Michener, 1972, 1973c). When mothers are presented with one of their 20- to 29-day old pups in an arena with no nest, they pick up the pup and carry it in the mouth (G. Michener, 1974). Lactating females in the field retrieve pups placed beside the entrance to the nest burrow (G. Michener, 1972), and mothers carry pups when changing nest sites (Wehrell, 1973). When young are too large to carry, the mother induces them to follow her to the new nest site.

When paired in a neutral arena, captives respond differently to kin and unrelated squirrels (Davis, 1982b; G. Michener, 1974; Michener and Michener, 1973; Michener and Sheppard, 1972; Sheppard and Yoshida, 1971). Kin discrimination is exhibited by young before the eyes open. Initial interactions between captives usually involve nasal contacts, suggesting that discrimination is, at least in part, based on olfactory cues. Kin differential behavior also is exhibited in the field (Davis, 1984a; Michener, 1973b, 1981; Yeaton, 1972). Long-distance recognition can occur in the field, apparently based on the hesitant behavior of trespassing conspecifics and their tendency to flee when approached by a resident (Michener, 1973b).

The basic acoustical repertoire of *S. richardsonii* consists of chirps, churrs, whistles, squeals, and teeth clatters (Koepl et al., 1978). Davis (1985) identified two major types of alarm calls: a short chirp generally given in response to aerial predators and a long whistle usually given in response to terrestrial predators. Conspecifics typically react to a chirp by running to a burrow and to a whistle by standing upright.

**GENETICS.** The karyotype contains 30 biarmed (metacentric and submetacentric) and 4 acrocentric autosomes, a submetacentric X-, and a subtelocentric Y-chromosome equal in size to the smallest autosomes (Nadler et al., 1971). In north central Montana,

the species may have an acrocentric rather than subtelocentric Y (Nadler, 1964). Where *S. richardsonii* ( $2n = 36$ ) is syntopic with *S. elegans* ( $2n = 34$ ), hybrids with a karyotype intermediate between those of the parental types ( $2n = 35$ ) are common (Koepl et al., 1978; Nadler et al., 1971). Hybrid males may have the small Y-chromosome of *S. richardsonii* or the large acrocentric Y of *S. elegans*. Hybrid females possess X-chromosomes of unequal size, each resembling one of the parental types (Nadler et al., 1971).

Polymorphisms are known for the transferrin, malate dehydrogenase, and phosphoglucumutase loci (Nadler et al., 1982).

**REMARKS.** The Law of Priority indicates that the generic name *Spermophilus* should be used in preference to *Citellus*. Howell (1938) combined *S. richardsonii* and *S. elegans* as *Citellus richardsonii*, but differences in bacular morphology (Burt, 1960), skeletal morphology (Fagerstone, 1982; Neuner, 1975; Robinson and Hoffmann, 1975), alarm calls (Fagerstone, 1982; Koepl et al., 1978), biochemistry (Nadler et al., 1974, 1982), and diploid number (Nadler et al., 1971) indicate that the two should be considered separate, though sibling, species. For approximately 30 years after Howell's (1938) revision, *S. elegans* was referred to as Richardson's ground squirrel, *Spermophilus* (or *Citellus*) *richardsonii elegans*, in published reports. In preparing this account, we excluded such sources and cited only studies involving *S. (richardsonii) richardsonii*. Vernacular names for *S. richardsonii* include gopher and flickertail.

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