Spermophilus richardsonii (Sabine, 1822)  
Richardson's Ground Squirrel

Arctomys richardsonii Sabine, 1822:589. Type locality Carlton House, Saskatchewan.
Spermophilus richardsonii Cuvier, 1831:323.


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 mm 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; Koeppel et al., 1978). S. richardsonii differs from S. elegans by having a body length greater than 275 mm, hindfoot 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 fringes 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; palatal 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 1.1/1, 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 Mani- toba. 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 sympatric with the sibling species S. elegans (Koeppel et al., 1978; Koeppel 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 Illinoisan Sandhills and Doby Springs faunas and Rancholabrean sites in Alberta, South Dakota, Colorado, Idaho, Kansas, New Mexico, and Wyoming (Kurten 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 rewar ming 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). Inter torpor 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 21°C hibernated and none hibernated at 18°C and 21°C, though about 5% exhibited infrequent, brief bouts of torpor (Demenex and Henderson, 1978). Captive squirrels invariably urinate, occasionally defecate, but rarely eat or drink during the intertorpor arousal (Demenex 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 (Demenex and Henderson, 1978; Winston and Henderson, 1981).
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 rewarming 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 scrotal arch probably contribute to efficient rewarming 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 (Herding 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 emerge 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, 1974a) and from late May to early June in northwestern Saskatchewan, and from late May to early June in southern Alberta and the foothills of the southern Alberta Rocky Mountains (Dorrance, 1974a; Michener, 1975a; 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 neotes 18-24 h old are 55.7 mm, 9.3 mm, and 7.8 mm, respectively (Koeppl, 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 g (Dolman, 1980; Harper et al., in litt.; Koeppl, 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 folded. Fine pelage appears at 4 to 7 days, forelegs 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 (T = 23.1 days), and adult pelage develops at 22 to 28 days (Harper et al., in litt.). Fetuses 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 after 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 a monogamous or polygamous species. A copulatory plug (average dimensions: 19.8 by 6.9 by 5.6 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; Goulsen, 1975; Tuttle et al., 1970; Melinville and Keith, 1974; McLean, pers. comm.; Michener, 1975a; Quanstrom, 1968; J. Schmutz et al., 1980; S. Schmutz et al., 1979; Schwal, 1976; Sheppard and Swanson, 1976) include canids (Canis latrans; Vulpes vulpes), mustelids (Taxidea taxus; Mustela frenata; M. vison; Mephitis mephitis), bunoidea (Buteo jamaicensis; B. regalis; B. swainsoni), harrriers (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 bunoidea 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 at their burrow entrances. Swainson’s hawks (Buteo swainsoni) 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 buns and bunos to early June, S. richardsonii oviparous (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 bunoidea were estimated to have killed 15% of the squirrel population in one year and 6.5% in the other year. S. rich-
ardsonii males seem more susceptible than females to predation by buteos (Luttwich et al., 1970; Schmutz et al., 1979).

The tick Dermacentor andersoni, a vector of Rocky Mountain spotted fever and tularemia, and the fleas Oropsylla labis and Oropsylla rueperti, 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 louse of Spermophilus richardsoni were found in the snow in 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, 1971). Endoparasites include cockroaches, trypanosomes, cestodes, trematodes, and blood-sucking lice. Ticks also are common ectoparasites of S. richardsonii in Alberta (Hilton and Mahrt, 1971). The most common helminth, Citellus bifurcatus, was found in 32% of squirrels in Saskatchewan, including newly emerging juveniles. Males and older squirrels were infested more commonly with helminths than females and younger squirrels of the same age class.

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 (Brown and Roy, 1943). Squirrels also feed on scattered crops, particularly corn and sunflower seeds. 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 various winter ranges in eastern North Dakota (Brown and Roy, 1943; Battelle gracilis, Amanthus sp., and Astrapalus sp. are eaten (Quanstrom, 1968). Squirrels eat the seedlings and seeds of domesticated cereals such as wheat, barley, and oats (Bailey, 1892; Howell, 1938). Squirrels from crowder are larger in size (1938) and bear larger teeth 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 (1895) 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 phosphate, distributed on wheat or rolled oats, can result in an immediate mortality of >70% (Matsche et al., 1983; Record, 1978). The chemical control, when distributed shortly before or in early pregnancy, suppresses reproduction for one season (Goulet and Sadler, 1974). Post-treatment reinvasion by squirrels from surrounding areas generally rapidly returns populations to pre-treatment levels (Alsager and Yarmen, 1972; Goulet and Sadler, 1974).

Sex ratios among neotenes 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) reported 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). The sex ratio becomes male-biased until ultimately 40% of the above-ground population consists only of juvenile males (Dorrance, 1974; D. Michener, 1974; Michener, 1979a). Male emerge from hibernation before females (Michener, 1983a), so the population of adults (2+ year) in spring is initially predominantly male. When female 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 1.4-2.7 ha (Michener and Michener, 1977), 2.7-5.4 ha (Dorrance, 1974), and 5.2-7.4 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: 12-0.0 ha (Dorrance, 1974a, 1974b; Nellis, 1979), and 27-0.7 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 of June in 9.6 juveniles/ ha on a 13-ha site and 0.7 influencers 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 sex classes.

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 6 to 12 weeks old. These movements are frequent and of most individuals by early August, 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 none locally born juveniles (seven males, eight females) emigrated from a 0.7-ha study area; however, most juveniles 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 during the juvenile age 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 do during gestation and lactation or during the 4 weeks preceeding hibernation (Michener, 1979c; Quanstrom, 1968; Wehrell, 1975). 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, 1979e).

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 5 cm). For restraint and handling, animals were induced to enter a conical-shaped cloth bag that was then pulled over the animal's head. Alternative methods provide permanent identification (Fig. 1), and commercial hair dye temporarily marks the pelage, permitting identification of individuals from a distance. Davis and Murie (1983) attached radiocollars to adult males to track their movements in the mating season. Vaginal lances 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 a weight loss 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 adults (Michener, 1979e). Yearling females have been above ground for up to 1 year (Michener, 1974, 1978b; 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). 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 and females (September and early October). Immersgence occurs several weeks earlier in southern Alberta (Michener, 1984b). The immersgence schedule reflects the chronological sequence in which adult males, adult females, and juveniles commence fat deposition following the emergence. Littering, copulating, 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; Quaistan, 1968).

Richardson's ground squirrels are active diurnally. In spring and autumn, they exhibit a unimodal activity pattern, with no morning 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 9 a.m., 100 min after sunrise, but delay emergence if the weather is cool or inclement (Michener, 1968).

Davis (1984a), G. Michener (1972), Michener and Sheppard (1972), Quaistan (1971), Sheppard and Yoshiada (1971), Wehrell (1973), and Yeaton (1969) described over 35 postures and behaviors associated with feeding, moving, alert, and interacting with conspecifics. These are 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 postparturition 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 to predators (Davis, 1982a, 1984a; 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 they are seen below ground interacting 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, the male mounts from behind, the pair rolls to one side, and copulation 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, 1984a), D. Michener (1972), Michener and Sheppard (1972), Michener and Sheppard (1972a, 1979c, 1980c, 1981), Michener and Michener (1973), Quaistan (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). 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 and provisions and defends her burrow from 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 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 interact with those of 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. richardsoni 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 social interactions and kin tenuates and between maternal and offspring 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 matrilocal (Davis, 1982e, 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 breading females than lactating 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 do not associate with the home cage on the day of parturition are not provisioned by mothers (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, captive pairs respond differently to kin and unrelated squirrels (Davis, 1982a; G. Michener, 1974; Michener and Michener, 1973; Michener and Sheppard, 1972; Sheppard and Yoshiada, 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. richardsoni consists of chirps, chirrs, whistles, squeals, and teeth clatters (Koeppl et al., 1978). Davis (1985) identified two major types of alarm calls: a retreat chirp generally given in response to the presence of a long whisk 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 submeta- centric 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. richardsoni (2n = 36) is syntopic with S. elegans (2n = 34), hybrids with a karyotype intermediate between those of the parental types (2n = 35) are common (Koeppl et al., 1978; Nadler et al., 1971). Hybrid males may have the small Y-chromosome of S. richardsoni 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 phosphoglucosmutase 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. richardsoni and S. elegans as Citellus richardsoni, but differences in bacular morphology (Bart, 1960), skeletal morphology (Fagerstone, 1982; Neuner, 1975; Robinson and Hoffmann, 1975), alarm calls (Fagerstone, 1982; Koeppl 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 Howells's (1938) revision, S. elegans was referred to as Richard- son's ground squirrel, Spermophilus (or Citellus) richardsonii elegans, in published reports. In preparing this account, we excluded such accounts and cited only studies involving S. (richardsonii) richardsonii. Vernacular names for S. richardsonii include gopher and flickertail.

We thank L. S. Davis, T. M. Dolman, S. H. Jenkins, and J. O. Murie for comments on the manuscript. J. K. Godwin and K. R. VandeLigt for assistance with preparation of the Literature Cited and Fig. 3, and J. O. Murie and the Museum of Zoology, University of Alberta, for providing the specimen for Fig. 2.

LITERATURE CITED


CUVIER, G. 1831. Supplement à l'histoire naturelle générale et particulière de Buffon, offrent la description des mammiferes et des oiseaux les plus remarquables découverts jusqu'à ce jour. 1:1–470.


—. 1977b. Gestation period and juvenile age at emergence in Richardson’s ground squirrel. Canadian Field-Nat., 91:410–413.


—. 1979b. The circannual cycle of Richardson’s ground squirrels in southern Alberta. J. Mamm., 60:760–768.


RICHARDSON, J. 1829. Fauna Boreali-Americana; or the zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the late northern land expeditions, under command of Captain Sir John Franklin, R. N. Part first, containing the quadrupeds. John Murray, London, 300 pp.


SOWLS, L. K. 1948. The Franklin ground squirrel, Citellus franklinii (Sabine), and its relationship to nesting ducks. J. Mamm., 29:113–137.


Editors of this account were B. J. VERTS and J. K. JONES, JR. Managing Editor was TIMOTHY E. LAWLOR.