Spermophilus richardsonii

Richardson’s Ground Squirrel

Arctomes 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 (60 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; Koenig 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; palatal breadth, 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.

In the United States it occurs in western Minnesota, northeastern 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 (Koenig et al., 1978; Koenig 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 regression, and hibernation (Melnik, 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 (Melnik, 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 reheating to normothermic temperatures. In the 2 months after immersgence, 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 21.2°C hibernated and none hibernated at 18°C and 12.1°C, although 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 intortorpo 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 tissue (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 by 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 immerge 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

---

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

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.
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, 1974). 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 evertile papillae that protrude from the orifice and pulsate when the animal is handled (Stegg, 1926). Aporcine 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 O₂ g⁻¹ h⁻¹ for control animals, 1.25 for animals starved for 7 days, and 1.67 for animals starved and water deprived for 7 days (Bintz and Michener, 1983). During starvation and water deprivation, mother's milk sustains mother's water balance by catalyzing 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 et al., 1979).

ONTOGENY AND REPRODUCTION. Female S. richardsoni 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); conception dates given by these authors are about 6 days early as they used Asdell's [1964] erroneous report of a 26-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, 1983b).

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, 1986) 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 emergence from the natal burrow (Dorrance, 1974; Michener, 1979a, 1985; Schmutz, 1975; Wehrrell, 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; Bintz and Strand, 1983), suggesting that differences in litter size between yearling and older females may be indicative of differences in body mass than of age. Juveniles first leave the natal burrow when 26 to 33 days old (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 central and north Dakota, the foothills of the southern Alberta Rocky Mountains (Dorrance, 1974; Michener, 1979a; D. Michener, 1974; Quamstrom, 1971; J. Schmutz et al., 1980; S. Schmutz et al., 1980).

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 (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 and 9.6 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 fused. Fine pelage appears at 4 to 7 days, foredigs 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 (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 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 slaughtering of corneal epithelium from the vaginal wall (Michener, 1980a). No data are available to establish whether S. richardsoni is an induced or spontaneous ovulator. 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. richardsoni (Dorrance, 1974; Goulden, 1975; Luttie et al., 1970; Melnivaille and Keith, 1974; McLean, pers. comm.; Michener, 1979a; Quanstrom, 1968; J. Schmutz et al., 1980; S. Schmutz et al., 1980; Sheppard and Swanson, 1976) include canids (Canis latrans; Vulpes vulpes), mustelids (Taxidea taxus; Mustela frenata; M. vison; Mephitis mephitis), bateso (Bateo 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 bateso 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 in their burrows (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 bateso in southern Alberta, S. richardsoni averaged (n = 2 sheep) 90% of the prey biomass for juveniles while 5% for red-tailed hawks, and 75% for Swainson's hawks (Schmutz et al., 1980). These bateso 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 Opsipristes labis and Oropylia rupetres, 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 laraae of Sarcoptes scabiei 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. Richardsoni in Alberta (Hilton and Mahart, 1971a). Endoparasites include coccidians, trypanosomes, cestodes, trematodes, and nematodes. The main nematodes are such as Boulouca gracilis, Amanurhas sp., and Astrapalas spp. also are eaten (Quastrom, 1968). Squirrels eat the seedlings and seeds of domesticated cereals such as wheat, barley, and oats (Bailer, 1892; Howell, 1936). Squirrels from cropland are less common in winter (1928) and bear larger eggs of live embryos (118%) than squirrels inhabiting native grassland (Sheppard, 1972).

Early reports emphasized the impact of S. Richardsoni on agricultural crops (Bailer, 1893; Bell and Piper, 1915). Scientific studies of damage and assessment are rare. Bailey (1939) 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 because 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% (Matschke et al., 1983; Record, 1978). The chemoreceptor, when distributed marginally before or during 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 (Alsegger and Yaremko, 1972; Goulet and Sadler, 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). In the sex ratios becomes male-biased until ultimately the sex 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 (81 year) in spring is initially predominately male. When females first 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 size of the sex ratio from equality occurs almost 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 1.4-4.0 ha (Michener and Michener, 1977), 2.7-7 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 synchronus 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 13.8 ha site and 3.71 ha site on south slopes of southern Alberta (Michener, 1979a).

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 26% in southern Alberta (Dorrance, 1974), 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 age classes.

Dispersal by S. Richardsoni is male-biased (Davis, 1982a; Dorrance, 1974; Michener and Michener, 1977; Quastrom, 1971; Schmutz et al., 1979; Yeaton, 1972). Juvenile males generally disperse in late June and July when they are 6 to 12 weeks old. Their movements range from moderate to great (Davis, 1982a) and exhibit low dispersal (Dispersal 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 purposes (Michener, 1981). When males fail to disperse, they generally are not 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 pt. preceding hibernation (Michener, 1979c; Quastrom, 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. Richardsoni with unbaited tire-tread, wire-mesh live traps (48 by 15 by 15 cm). For restraint and handling, animals were induced to enter a conical-shaped, cloth bag at the tip of a zippered ending. Metal 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. Richardsoni 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, 1979a, 1980a).

Sheppard (1972) used less weight 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. Female females have been above ground for 81 days (D. Michener, 1974; Michener, 1984a).

BEHAVIOR. Time of emergence from hibernation is correlated with soil and air temperatures (Michener, 1979a, 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; Quastrom, 1968; Sowls, 1948).

Yearlings 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, 1979c; 1979d). The sequence of entry of cohorts into hibernation (Michener, 1984d) 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 immersgence schedule reflects the chronological sequence in which adult males, adult females, and juveniles commence fat deposition following the end of their respective hibernation period (Bintz and Strand, 1983; Michener, 1984d). The pattern of immersgence results in a period of approximately 2 months when only juveniles are above ground.

Richardson's ground squirrels use burrows for hibernation, sleeping bags from predators, and reproductive and non-reproductive winter dens (Davis, 1984a; G. Michener, 1972). Richardson's ground squirrels are active diurnally. In spring and early summer, the squirrels exhibit a unimodal pattern of activity. Activity is bimodal during the spring and summer, with peaks at 0600 to 1000 h and from 1400 h to 1900 h, respectively (Michener, 1986; Yeaton, 1969). Squirrels emerge about 95 to 130 min after sunrise, but delay emergence if the weather is overcast (Michener, 1968).

During the pre-hibernation phase, squirrels spend less time above ground and use progressively smaller ranges until each enters hibernation, both juveniles and adult individuals. The hibernation period, defined as the period when squirrels are in the torpid stage of hibernation and do not move or feed, lasts from October to May. The length of this period varies depending on environmental conditions, but it typically lasts about 9 months. During hibernation, squirrels maintain a low body temperature and metabolic rate, which allows them to survive the winter without eating or drinking.

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 sciuroids, whereas Davis and Murie (1985) suggested placement at grade 3. Affiliative and aggressive interactions among adult littermates and between the mother and one or more of the littermates are maintained throughout the female's life. While male squirrels may associate with females to some degree, they do not form lasting social bonds and do not live together throughout the female's life.

Most squirrels spend the majority of their time above ground, either foraging for food or engaging in social interactions. Squirrels are diurnal and active during the day, with peaks of activity around sunrise and sunset. They are primarily solitary animals, although they may form small groups during the mating season. During the mating season, males and females come together to mate and then disperse again. The mating season typically lasts from March to May, with the peak of mating occurring in April.

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 a female emerges in a sparse and unpredictable distribution of females, males are not territorial. Immersing females are either incorporated into an existing male group or fight for a new territory. Adult males dig and occupy territories, and the males defend their territories against other males. The males are highly aggressive, and fights often result in injuries or deaths. During the mating season, males engage in prolonged and aggressive sexual interactions with females, which can last for several hours or even days.

Captives may disperse from the nest to 20 to 23 days postpartum (G. Michener, 1971, 1972). Nipple-lining yearlings are more likely to disperse and reassociate with a more experienced female than to remain in the same nest. During this period, yearlings may disperse from the nest and then return to it several times before finally leaving and finding a new territory. When they first disperse, yearlings may be male or female, and they may disperse alone or in small groups. Once they have dispersed, yearlings may form social groups with other young squirrels and adults, and they may also mate with adult squirrels. Yearlings may remain in the same nest for up to 2 months before dispersing, and they may disperse as early as 2 months postpartum.

When paired in a neutral arena, captive S. richardsoni males respond differently to conspecific and non-conspecific cues. Males more frequently approach and interact with conspecific cues than with non-conspecific cues. In addition, males are more likely to approach and interact with cues from dominant males than from subordinate males. In other words, males are more likely to approach and interact with cues from dominant males, and they are more likely to avoid cues from subordinate males. This suggests that males may use conspecific cues to assess the social status of other males in the environment and adjust their behavior accordingly.

Genetics. S. richardsoni exhibits high levels of genetic diversity, with high levels of nucleotide diversity and haplotype diversity. This suggests that the species has undergone rapid evolutionary change in response to environmental and demographic factors. In particular, the species has undergone a recent expansion, which has led to increased genetic diversity and genetic differentiation among populations. This suggests that S. richardsoni has the potential to adapt rapidly to environmental changes and to persist in fragmented habitats.
the species may have an acrocentric rather than subteloentric 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 (Koeppl 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 phosphoglucomutase 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; 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 Howell'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 sources 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


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. Mammal., 60:760-768.


1983a. Spring emergence schedules and vernal behav-


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.


SABINE, J. 1822. Account of the mammals of North America.


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. LAWLOM.