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Spermophilus tereticaudus.

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Spermophilus tereticaudus Baird, 1858

Round-tailed Ground Squirrel

Spermophilus tereticaudus Baird, 1858:315, 709. Type locality Fort "Yuma, Cal.—at mouth of Gila river. Altitude 355 feet [lat.] 32°32′ [long.] 114°36′," Imperial Co., California.

Spermophilus neglectus Merriam, 1889:17. Type locality "the valley 1 mile west of Dolan's Spring (altitude about 3,000 feet)," Mohave Co., Arizona.

Spermophilus sonoriensis Ward, 1891:158. Type locality Hermosillo, Sonora.

Citellus chlorus Elliot, 1903*b*:242. Type locality Palm Springs, Riverside Co., California.

Citellus eremonomus Elliot, 1903*b*:243. Type locality Furnace Creek, Death Valley, Inyo Co., California.

CONTEXT AND CONTENT. Order Rodentia, Family Sciuridae, Subfamily Sciurinae, Tribe Marmotini, Subtribe Spermophilina, Genus *Spermophilus* (36 recognized species, Honacki et al., 1982). Subgenus *Xerospermophilus* includes *S. tereticaudus* and *S. mohavensis.* There are four recognized subspecies of *S. tereticaudus* (Hall, 1981):

S. t. tereticaudus Baird, 1858:315, see above (*eremonomus* Elliot and *vociferans* Huey are synonyms).

S. t. chlorus (Elliot, 1903*b*:242), see above.

S. t. neglectus Merriam, 1889:17, see above (*arizonae* Grinnell and *sonoriensis* Ward are synonyms).

S. t. apricus (Huey, 1927:85). Type locality "Valle de la Trinidad, Lower California, Mexico, lat. 31°20′ north, long. 115°40′ west."

DIAGNOSIS. Members of the subgenus *Xerospermophilus* can be separated from those of other North American subgenera of *Spermophilus* on the basis of cranial and dental characters (Hall, 1981). Subgenera *Xerospermophilus, Otospermophilus, Callospermophilus,* and *Potiocitellus* have brachydont molars and a rather smooth junction of the parastyle ridge and the protocone on M1 and M2. Molars are hypsodont and the parastyle ridge joins the protocone at a sharp angle in the subgenera *Spermophilus* and *Ictidomys.* P1 is less than one-fourth the size of P4 in *Otospermophilus, Callospermophilus,* and *Xerospermophilus,* but more than one-quarter as large as P4 in *Potiocitellus.* Upper incisors are thick and recurved in *Otospermophilus*; they are thin and not distinctly recurved in *Callospermophilus* and *Xerospermophilus.* The postorbital process is relatively short and broad in *Xerospermophilus,* and relatively long and narrow in *Callospermophilus.* The skull of *S. tereticaudus* (greatest length 34.3 to 39.3 mm) usually is smaller than that of *S. mohavensis* (greatest length 38.1 to 40.0 mm).

Of the spermophiles, only *S. armatus, S. beldingi, S. elegans, S. franklinii, S. mohavensis, S. perotensis, S. richardsonii, S. tereticaudus,* and *S. townsendii* have dorsal and lateral pelage lacking spots and stripes. The ventral pelage is white in *S. mohavensis, S. tereticaudus,* and *S. townsendii*; and buff, cinnamon, or gray in the other five species. The underside of the tail is white in *S. mohavensis,* red in *S. townsendii,* and buff, drab, or cinnamon in *S. tereticaudus.* The tail is flat in *S. mohavensis* and round in *S. tereticaudus.*

Spermophilus tereticaudus can be distinguished from *S. beecheyi, S. beldingi,* and *S. lateralis* on the basis of serum transferrin mobility in starch gel electrophoresis (Marsh et al., 1969).

Hafner and Yates (1983) showed that *S. tereticaudus* and *S. mohavensis* differ both karyotypically and electrophoretically, although hybridization may occur between the two taxa at one site (Helendale) in southern California. Indications are that these may represent semispecies with incomplete reproductive isolation; nevertheless, retention of specific status for each is recommended at present (Hafner and Yates, 1983).

GENERAL CHARACTERS. *Spermophilus tereticaudus* is a fairly small ground squirrel with a long round tail. The head is small and rounded, pinnae are reduced, and the eyes are large and dark. The feet, especially the hind feet, are large and broad; soles are amply covered with long stiff hairs, except near the tubercles

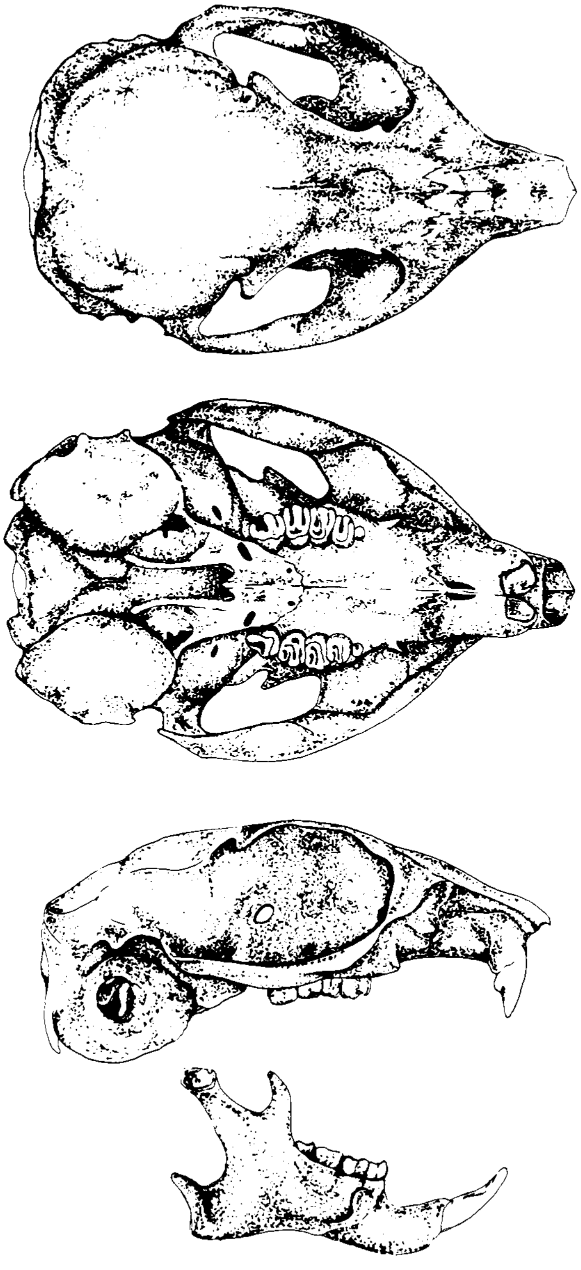

FIG. 1. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of *S. tereticaudus.* Specimen from Maricopa Co., Arizona (OU 7755); female adult, occipitonasal length 36.9 mm. Illustration by Zenith Marsh.

Fig. 2. Adult male *S. tereticaudus* in winter pelage, with creosote bush (*Larrea*) in background. Photo by Carolyn Engel-Wilson.

(Baird, 1858). Claws of the forefeet are heavy, recurved, and longer than those of the hind feet. The pollex is reduced. The dental formula is I 1/1, C 0/0, P 2/1, M 3/3, total 22.

The skull (Fig. 1) is moderately built and rounded in profile. The rostrum is short. The postorbital processes are pronounced and make the postorbital constriction well marked. The nasals are expanded and somewhat inflated anteriorly. The supraorbital shelf is broad but lightly ossified. Parietal ridges are not well marked, although the superior nuchal line is pronounced. The occipital region is at a right angle to the horizontal plane of the skull. The shelf formed in the orbit by the dorsal part of the maxilla and the zygomatic plate is broad and deep. The zygomatic arch is compressed, with the broad face of the arch forming about a 30° angle with the horizontal plane of the skull. Parietals are slightly inflated. Tympanic bullae are greatly inflated. Maxillary toothrows are slightly divergent anteriorly. The incisors are orthodont. The palatine foramina are small.

Ranges of standard external measurements (in mm; Allen, 1895; Elliot, 1901, 1903*b*; Grinnell and Dixon, 1918, Howell, 1938; Ward, 1891) are: total length, 204 to 278; length of tail, 60 to 112; length of hind foot, 32 to 40; length of ear, 5.0 to 8.5. Ranges of cranial (Fig. 1) measurements (in mm) are: greatest length of skull, 34.3 to 39.3; interorbital breadth, 7.8 to 10.3; zygomatic breadth, 21.3 to 24.6; postorbital constriction, 11.7 to 13.6; length of nasals, 8.0 to 13.7; palatal length, 16.0 to 18.3; length of maxillary toothrow, 6.7 to 8.5. Body mass varies considerably from season to season (Neal, 1965*c*), but generally ranges between 110 and 170 g. Hudson (1964*b*) stated that the average mass is 125 g.

Round-tailed ground squirrels (Fig. 2) are pale rodents that blend with the sandy soil of the deserts they inhabit (Allen, 1895). Older hairs become faded from the intense sunlight (Johnson et al., 1948). There are two general color phases (in both summer and winter pelages): drab and cinnamon. The summer pelage is brighter and coarser than the winter coat (Hall, 1981). Pelage color is fairly uniform, without spots or flecks. The dorsal surface of the body is pinkish cinnamon, vinaceous cinnamon, light drab, cinnamon drab, or ecru drab (Howell, 1938). Lateral surfaces are more buffy. The ventral surface of the body is white. The sides of the head are dull white. Whiskers are black. The dorsal surface of the tail matches the dorsal body surface, but the distal half has more black hairs. The ventral surface of the tail is cinnamon, buff, or drab.

DISTRIBUTION. Round-tailed ground squirrels inhabit desert areas of the southwestern United States and northwestern Mexico (Fig. 3). Their range includes portions of the Mojave, Yuma, and Colorado deserts. They occur in southeastern California, southern Nevada, western Arizona, northeastern Baja California, and Sonora. The elevational distribution is from 70 m below sea level to 1,190 m above sea level (Cockrum, 1960; Grinnell and Dixon, 1918).

Although *Spermophilus* fossils are common in late Tertiary strata (Black, 1963; Mead et al., 1983), the only fossil record of *S. tereticaudus* is from a packrat (*Neotoma*) midden in Yuma County, Arizona. The specimen was estimated to be 8,150 ± 260 years old (Mead et al., 1983).

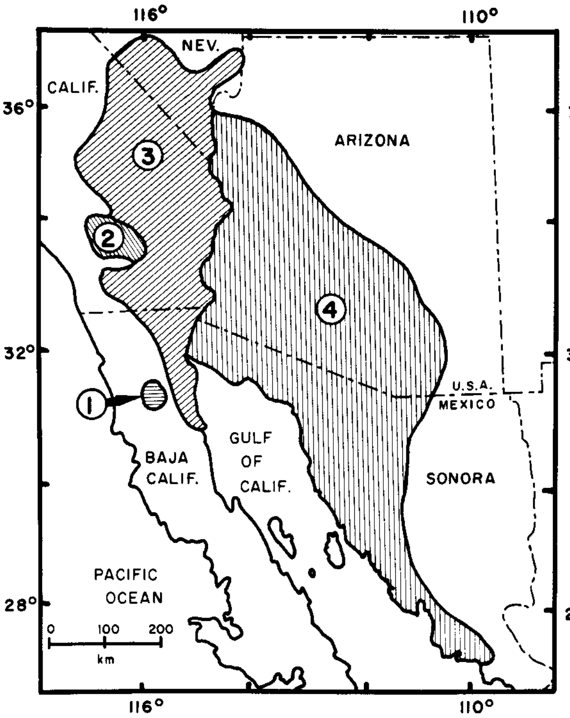

Fig. 3. Distribution of the subspecies of *Spermophilus tereticaudus*: 1, *S. t. apricus*; 2, *S. t. chlorus*; 3, *S. t. tereticaudus*; 4, *S. t. neglectus* (redrawn from Hall, 1981).

FORM. Dice and Blossom (1937) found that dorsal hairs of *S. t. neglectus* gave an average reading of 19.0% for reflected red as measured with a tint photometer. *S. tereticaudus* and *Ammospermophilus leucurus* have a thicker Malpighian layer, greater melanization, "more prominent scale-like folds," a weaker reaction with dihydroxy-dinapthyl-disulfide, and probably more superficial keratinization in the epidermis than other desert rodents and some nondesert species (Quay, 1964:61). The dermis often has more cells (mainly fibroblasts and macrophages) and fewer connective-tissue fibers in desert ground squirrels. *A. leucurus*, *S. tereticaudus*, and *S. lateralis* have dorsal sweat glands. The secretory cells have large nuclei and granular cytoplasm (Quay, 1964). There are 8–12 mammae (Burt and Grossenheider, 1976; Mearns, 1907).

Spermophilus tereticaudus normally has 12 thoracic vertebrae, but Bryant (1945) reported one individual with 13. The proximal end of the baculum is broad, the shaft narrower, and the distal end spoon-like and toothed (Burt, 1960). Three bacula averaged 2.7 mm long and 1.0 mm wide distally. The os clitoridis is 1.4 mm long (Burt, 1960; Layne, 1954), with a toothed disc at the distal end and a shaft enlarged proximally (Layne, 1954).

Mean mass (mg) and percent of body mass of organs of control animals kept at 25°C were (Balcer et al., 1976): heart, 0.41, 0.4% ($n = 16$); liver, 4.61, 4.5% ($n = 16$); kidney, 0.85, 0.8% ($n = 16$); brown adipose tissue (BAT), 0.83, 0.7% ($n = 15$). Fat content in animals with an average body mass of 107 g was 7.8 ± 4.2% (Scott et al., 1972). Brain mass (2.4 g) calculated from braincase volume (Mace et al., 1981) and encephalization quotient (0.80; Meier, 1983) were the lowest among congeners measured.

FUNCTION. There are two annual molts in *S. tereticaudus* (Howell, 1938), one in March, April, or May, the other in August or September depending on locality. Seemingly, the head and throat are first to molt, the rump and belly next (Burt, 1934; Howell, 1938), and the tail last (Howell, 1938; Mearns, 1907). Juveniles molt to adultlike pelage in late June in southern Arizona (Dunford, 1975).

The average heart rate of 19 *S. tereticaudus* kept in the laboratory at 23°–25°C was 255 (±47) beats/min (Hudson, 1971). When Hudson (1971) isolated hearts from animals, perfused them with Krebs-Henseleit medium, and decreased the temperature of the medium by 0.5°C/3 min, the heart rate decreased from 77.6 bpm at 20°C to 2.1 bpm at 5.7°C. Hudson (1971) found that *S.*

tereticaudus has a smaller heart and slower heart rate than *S. tridecemlineatus*; it also has a lower basal metabolic rate (BMR). Hypothyroidism of *S. tereticaudus* may contribute to its lower heart rate (Hudson, 1971).

Serotonin in whole brain homogenates of males ($n = 2$) sacrificed in the morning (0800–0900 h) was 0.385 μg/g, whereas that of females ($n = 3$) was 0.434 μg/g (Spafford and Pengelley, 1971). Males ($n = 3$) sacrificed in the evening (1900–2000 h) had 0.400 μg/g, and females ($n = 2$) had 0.428 μg/g. The difference in serotonin concentrations between males and females was significant ($P < 0.05$). Serotonin concentrations were higher in hibernators *S. tereticaudus* and *S. lateralis* than in the nonhibernator *S. leucurus* (Spafford and Pengelley, 1971).

Awake, *S. tereticaudus* had electroencephalogram waves of 8 to 12 Hz and less than 50 uV, and had elevated electromyograms (EMGs). Animals in slow wave sleep (SWS) had EEGs of 0 to 2 Hz and 75 to 125 uV with spindles of 3 to 6 Hz and 50 to 100uV, lower EMGs, and slower heart rates. Torpor was characterized by greater total amounts of sleep, greater percentage of SWS, and less percent time in rapid eye movement (REM) sleep than during euthermic periods (Walker et al., 1979).

Yousef and Johnson (1975) measured VO_2 at 0.66 ml O_2 g^{-1} h^{-1} ($n = 11$). This was 60% of the VO_2 predicted from body mass. Scott et al. (1972) obtained similar results: $VO_2 = 0.61$ ml O_2 g^{-1} h^{-1}, 59% of expected. They concluded that oxygen consumption of rodents was influenced by their ecological distribution: desert rodents had lower VO_2 than expected. Similarly, Yousef and Johnson (1975) determined in a study of 12 rodent species that species from low-elevation deserts (including *S. tereticaudus*) had lower O_2 consumption than species from arid woodlands and montane forests. Oxygen consumption was considerably lower in torpid than in active *S. tereticaudus* (Scott, 1976).

The rate of increase in O_2 consumption in *S. tereticaudus* decreased with increased running velocity; this species is a more efficient runner than *Dipodomys spectabilis* or *Rattus norvegicus* (Taylor and Schmidt-Nielsen, 1969). The latter authors formulated a linear equation relating O_2 consumption (M, in ml O_2/g·h) to running speed (V, in km/h) as $M = 0.63V + 1.40$ in *S. tereticaudus*.

The composition of bile acids in three *S. tereticaudus* was 59% cholic acid, 22% chenodeoxycholic acid, 15% deoxycholic acid, 2% lithocholic acid, and a trace of $3\beta,12\alpha$-dihydroxycholanic acid (Yousef et al., 1973*b*). *S. tereticaudus* does not become postabsorptive until at least 24 h after food intake (Hudson, 1967), in contrast to postabsorptive times of 2 to 4 h in many small birds and mammals. Round-tailed ground squirrels will not enter torpor before they become postabsorptive (Hudson, 1967).

Spermophilus tereticaudus cannot survive on a diet of dry grain without water (Schmidt-Nielsen and Schmidt-Nielsen, 1952). Physiological water requirements in nature generally are met by the consumption of succulent foods. Fraction of turnover of body water is 17.1%/day (Yousef et al., 1974). Daily turnover of body water was 14.1 ml (Yousef et al., 1973*a*). Total body water was 82.1 ml (70.2 g/100 g body mass, $n = 21$). Hudson (1964*b*) found that animals maintained at temperatures between 35° and 40°C lost an average of 6.3% body mass per day. Animals required less than 2% of their body mass in free water to maintain a stable body mass.

Hudson and Wang (1969) found that the thyroid gland of *S. tereticaudus* has reduced activity during most of the year, and was completely inactive in 13 of 16 individuals during summer. Reduced thyroid activity in the late spring, summer, and early fall probably is associated with thermoregulation rather than with torpidity (Hudson and Wang, 1969). Hudson (1968) found that daily injections of less than 24 μg of 1-thyroxine pentahydrate for 5–17 days increased the metabolic rate of *S. tereticaudus* almost two-fold, but did not prevent torpor.

Plasma thyroxine (T_4) concentrations averaged 42.0 ng/ml in 45 *S. tereticaudus* (Scott et al., 1976), with no significant difference between sexes. Plasma T_4 concentrations decreased considerably during summer months, and increased again with exposure to cold during the breeding season (Scott, 1976).

The maximum uptake of labelled iodine (I^{131}) in *S. tereticaudus* is 7.5%, the neck/thigh ratio of I^{131} activity is 5.8, and the TSR (minimum dose of exogenous T_4 that inhibits I^{131} release) is 0.74 μg/100 g body mass (Yousef and Johnson, 1975). Rodents from low deserts (for example, *S. tereticaudus*) have lower TSR values than rodents from arid woodlands or montane forests; this may be related to metabolic differences that allow lowland species to tolerate higher ambient temperatures (Yousef and Johnson, 1975).

Adrenal glands of adults are heaviest in March for males and April for females and lightest in September for males and August for females (Neal, 1965*c*). Plasma concentrations of corticosterone were 74 ng/ml ($n = 11$), and showed no significant relation to sex (Vanjonack et al., 1975); these tend to be lower in rodents such as *S. tereticaudus* that inhabit deserts of low elevation, and may serve to increase tolerance to heat and aridity. Kilduff et al. (1980) found that melatonin implants caused more frequent daily torpor periods, decreased activity, and increased total sleep time (concurrent with depressed body temperatures).

Spermophilus tereticaudus shows a circannian cycle of body mass in the laboratory at 12°C with a 12L:12D photoperiod and food available ad libitum. This cycle does not correspond to the circannian rhythm of hibernation (Pengelley and Kelly, 1966). Increases in body mass during the cycle are coincident with increases in body fat content (Neal, 1965*c*). Males tend to accumulate fat earlier in the spring (March–May) than females (June–July), possibly because of the role of the female in caring for young (Neal, 1965*c*). Fat reserves are expended in both sexes during the first few months after emergence from hibernation. Dunford (1975) noted a decrease in body mass of males during the copulatory period (March).

Acclimation to heat by *S. tereticaudus* caused a significant increase in body mass (Balcer, 1977). Both heat-acclimated (kept at 35°C for 6 weeks) and cold-acclimated animals (kept at 5°C for 6 weeks) had absolute BAT mass significantly greater than that of control animals (kept at 24°C for 3 weeks or more), although only heat-acclimated animals had greater ratios of BAT mass/body mass than controls (Balcer and Chaffee, 1981). Cold-acclimated animals had significantly greater BAT, liver, heart, and kidney mass (as percent of body mass) than heat-acclimated animals (Balcer, 1977). At 40°C, *S. tereticaudus* lost about 3.2 g (2.1% of body mass) in 2 h. Loss of mass at 46°C was 7.8 g (5.7%) in 2 h. *S. leucurus* lost 5.5% of its body mass at 43°C in 2 h (Balcer, 1977).

Enzymatic oxidative potential is significantly lower in *S. tereticaudus* than in *S. lateralis* (Balcer et al., 1976). Succinoxidase specific activity was 39.90 μl O_2 mg protein^{-1} h^{-1} in BAT, 20.83 μl in liver, 35.94 μl in heart, 10.19 μl in muscle, and 34.34 μl in kidney of *S. tereticaudus*. The specific activity of glutamic acid oxidase was 15.30 μl O_2 mg protein^{-1} h^{-1} in BAT, 7.39 μl in liver, 21.02 μl in heart, 1.88 μl in muscle, and 17.95 μl in kidney. Alpha-glycerophospate dehydrogenase specific activity was 35.75 μg O_2 mg^{-1} h^{-1} in BAT, whereas that of cytochrome oxidase in BAT was 0.015 μg (Balcer et al., 1976). Cold-acclimated *S. tereticaudus* had greater succinoxidase and alpha-glycerophosphate activities in BAT than heat-acclimated individuals (Balcer and Chaffee, 1981). Balcer et al. (1976) suggested that the low enzymatic potential in this species may be directly related to its tolerance of high ambient temperatures.

Body temperature (T_b) of *S. tereticaudus* is 36°C at an ambient temperature (T_a) of 30°C (Hudson et al., 1972). Ambient temperatures of up to 46°C can be tolerated for 2 h, but body temperature rises to 41.4°C (Hudson and Wang, 1969). Toleration of high T_a is not associated with torpor (Hudson and Deavers, 1972, 1973). T_b is independent of T_a from T_a of 10°C (or lower) to 31°C (Hudson, 1964*a*). In summer, the lower critical temperature increases by 3°C. Body temperature at night is 3–6°C below daytime body temperature (Hudson, 1964*a*). A seasonal change in body temperature occurs in *S. tereticaudus*: T_b is lower in summer and fall than in winter and spring. The drop in T_b is accompanied by a decrease in thermoneutral metabolism. This cycle of body temperature is opposite that of the arctic ground squirrel, *S. parryii* (Hudson, 1964*a*). During arousal from torpor, the maximum rate of increase in T_b (at $T_a = 24$°C) is 0.2°C g^{-1} min^{-1} (Hudson and Bartholomew, 1964).

Basal metabolic rate at 30°C during the day is 1.0 ml O_2 g^{-1} h^{-1}, whereas nighttime BMR is 0.60 ml O_2 g^{-1} h^{-1} (Hudson, 1964*a*). Lower ambient temperatures result in greater daily variation of BMR. BMR remains fairly constant at T_a between 29° and 38°C. The lower BMR of this species, compared to *S. lateralis* and *A. leucurus*, is adaptive to its desert existence because heat production (Hudson, 1964*a*) and food and water requirements (Yousef and Johnson, 1975) are lower.

ONTOGENY AND REPRODUCTION. Estimates of gestation range from at least 25 days (Neal, 1965*b*) to about 27 days (Reynolds and Turkowski, 1972), to probably 28 to 35 days (Neal, 1965*b*). Number of young in 222 litters averaged 6.5 and ranged from 1 to 12 (Reynolds and Turkowski, 1972). Reynolds and Turkowski (1972) found that 75 to 80% of the variability in litter size is accounted for by variability in the extent of rainfall between October and February. They estimated that each 2.5 cm of rain during this period increased the mean litter size by one.

The reproductive season may start as early as midJanuary, when testes begin to enlarge (Ryan, 1968). Males with scrotal testes have been observed from midFebruary to late April. Motile spermatozoa are present in at least some males between early January and midApril (Neal, 1965*b*). Reynolds and Turkowski (1972) found a high correlation between earliest dates at which males had scrotal testes and the amount of rain that fell during the preceding December and January. The breeding season begins about 9 days earlier for each additional 1.27 cm of rainfall in December and January. A similar correlation between the amount of winter rainfall and the timing of reproductive phases was found by Dunford (1975). At the beginning of the breeding season, estrogens cause the labia to swell to 10 times their nonbreeding size, separate, and uncover the vaginal opening (Neal, 1965*b*). Neal (1965*b*) observed the earliest breeding in his study in southern Arizona during the last week of February. Dunford (1975) stated that copulation occurred in early March near Tucson, Arizona.

Pregnant females are observed from midMarch to late April in Arizona (Neal, 1965*b*; Reynolds and Turkowski, 1972). Ryan (1968) reported a pregnant female as late as 1 May in southern California. Dunford (1975) observed most litters on his Arizona study site in May and June. Some authors (Cockrum, 1982; Jaeger, 1961; Neal, 1965*b*) believe that a second litter may be born during the summer (July), but there is no evidence for this (Reynolds and Turkowski, 1972).

Testes regress in midApril, and no motile spermatozoa are found after midMay (Neal, 1965*b*). After the period of lactation from April to June (Neal, 1965*c*), the teats of adult females become inactive (Neal, 1965*a*). The labia return to nonbreeding size and the vaginal opening closes.

Observations of newborn *S. tereticaudus* are based on captive animals, as young in the wild remain in their natal burrows for the first month of life (Neal, 1965*c*). Neonates are unpigmented and hairless, except for vibrissae, and eyes and ears are closed. Average mass at birth is 3.7 g ($n = 26$), and ranges from 2.7 to 4.7 g (Neal, 1965*a*). The front legs are better developed than the hind legs, and are used in crawling. Although coordination is poor, neonates can turn themselves when placed on their backs. They are able to vocalize, and emit high-pitched squeaks during suckling (Pengelley, 1966). Ultrasound has not been demonstrated in this species.

By the fourth day of life, young have fine hairs on the head. By the seventh day, crawling is improved but not yet well-coordinated. The front legs are still better developed than the hind legs. The pigmentation of the back is beginning to increase. Lower incisors have erupted. After 2 weeks, the back of the head is covered with hair, and the dorsum has fine hairs. After 3 weeks, the young are covered completely with hair, and the ears are open. Many vocalizations are uttered. The upper incisors erupt between the third and fourth weeks. At 25 to 27 days, the eyes open and young are capable of coordinated running.

Neal (1965*a*) measured growth rates of captive young from four litters. Body mass increased in four stages. The rate of mass gain was 11%/day during the first 2 weeks, 4.5%/day during weeks 2–6, 1.7%/day between 6 and 12 weeks, and 0.53%/day between 12 and 17 weeks. Number of days (from birth) required to achieve 90% of adult dimensions was: body mass, 79; hindfoot length, 66; body length, 70; and tail length, 210 (Neal, 1965*a*). The growth rate constant ($\mathrm{k} = [\ln \mathrm{M}_2 - \ln \mathrm{M}_1]/[\mathrm{t}_2 - \mathrm{t}_1]$) is 0.65 (Levensen, 1979). Zullinger et al. (1984) calculated $\mathrm{k} = 0.0214$ from the Gompertz equation ($\mathrm{M(t)} = \mathrm{A}\ \mathrm{e}^{-\exp(-K[t-1])}$). They noted that growth in *Spermophilus* species differed from that predicted by the Gompertz equation: increase in mass was slow until weaning. Captive young probably grow more rapidly than wild young (Neal, 1965*a*). Growth in *S. tereticaudus* is more rapid than in *Ammospermophilus harrisii* (Neal, 1965*a*).

Young are weaned when about 5 weeks old. At this time, fecal pellets become dark (Neal, 1965*a*). Young of both sexes do not become sexually mature until they are 10 to 11 months old.

ECOLOGY. *Spermophilus tereticaudus* inhabits sandy arid regions of the Lower Sonoran Life Zone (Grinnell, 1913). It is more common in low, flat areas (Grinnell and Dixon, 1918; Neal, 1964) with desert shrubs. It often occupies sand dunes (Bradley and Deacon, 1971). Johnson et al. (1948) found burrows in fine sand accumulated along banks and among shrubs; Ryan (1968) noted higher densities in areas with more coarse, hard-packed sand and gravel.

Common woody vegetation in *S. tereticaudus* habitat includes (Drabek, 1973; Grinnell, 1914; Huey, 1927; Mares et al., 1977; Reynolds and Turkowski, 1972; Ryan, 1968) creosote bush (*Larrea tridentata*), mesquite (*Prosopis juliflora* and *P. glandulosa*), salt bush (*Atriplex*), and palo verde (*Cercidium microphyllum* and *C. floridum*). Common annuals include (Reynolds and Turkowski, 1972) needle grama (*Bouteloua aristoides*), sixweeks three-awn (*Aristida adscensionis*), and Mediterranean grass (*Schismus barbatus*). Dice and Blossom (1937) captured *S. t. neglectus* in grass-mesquite, *Isocoma*, cottonwood-willow, cholla-mesquite-hackberry, creosote bush, and upper bajada associations.

The habitat of *Spermophilus tereticaudus* is characterized by extreme temperatures and relatively low humidity. During a 1-week period, air temperatures ranged from −5° to +39°C, soil temperatures from 11° to 74°C at the surface, and relative humidities from 24 to 90%. Temperatures in the deepest part of the burrow (about 1-m deep) ranged from 22° to 25°C (Vorhies, 1945).

Spermophilus tereticaudus, like most sciurids, is omnivorous. Green vegetation and seeds constitute the major part of the diet. During spring, green vegetation constitutes approximately 80%, seeds approximately 15%, and insects about 5% of the volume of the stomach contents (Bradley and Deacon, 1971). During summer, 100% of the diet is green vegetation. In fall, 75% is green vegetation and 25% is seeds, and in winter 65% is green vegetation and 35% is seeds. Summer diet, based on behavioral observations (Drabek, 1970), included *Prosopis juliflora* (41% of observations) leaves, flowers, bark, and bean pods; *Larrea tridentata* fruits (22%), and *Pectis papposa* (10%). Insects were not eaten during June, but accounted for 19% of the diet in August. Insects consumed were mainly ants (Hymenoptera), termites (Isoptera), and grasshoppers (Orthoptera; Drabek, 1970). Food consumed generally has about 80% water content (Bodenheimer, 1957). Green vegetation includes leaves and stems of grasses and annuals, leaf buds (Chew, 1965), herbs (Jaeger, 1961), and leaves of mesquite (Grinnell and Dixon, 1918; Vorhies, 1945). Seeds eaten are those of mesquite (Allen, 1895) and annuals (Ryan, 1968).

Squirrels living near cultivated fields may eat alfalfa and dates (Grinnell and Dixon, 1918). Other foods consumed include bulbous roots (Bailey, 1923), insects (Bailey, 1923; Bradley and Deacon, 1971; Drabek, 1970; Dunford, 1975), fruits of creosote bush (*Larrea*) and cacti (Chew, 1965; Cockrum, 1982; Drabek, 1970; Vorhies, 1945), mesquite (*Prosopis*) bark (Dunford, 1975) and carrion (Drabek, 1970), including that of conspecifics (Jaeger, 1961). One squirrel was observed by Dunford (1975) to feed on a newly dead lizard (*Cnemidophorus*). Predation on vertebrates has been observed: Bradley (1968*a*) reported two instances of round-tailed ground squirrels killing and eating English sparrows (*Passer domesticus*).

Predators of round-tailed ground squirrels include (Drabek, 1970; Dunford, 1975, 1977*a*; Jaeger, 1961) coyotes (*Canis latrans*), badgers (*Taxidea taxus*), ravens, hawks, falcons (for example, *Falco mexicanus*), and snakes (*Pituophis melanoleucus*, *Masticophis flagellum*, *Crotalus scutulatus*). Domestic cats also prey on ground squirrels. Dissection of a Gila monster (*Heloderma suspectum*) that emerged from an *S. tereticaudus* burrow in southern Arizona revealed that it had eaten a round-tailed ground squirrel (Swarth, 1929). Other potential predators, based on behavioral responses of the ground squirrels (Drabek, 1970), include the roadrunner (*Geococcyx californicus*) and Bendire's thrasher (*Toxostoma bendirei*). *S. tereticaudus* occurred in 2% of 51 stomachs of *Ammospermophilus leucurus* examined (Bradley, 1968*a*). American Indians ate round-tailed ground squirrels in the early 1900's (Elliot, 1904). Potentially dangerous invertebrates are few, but median lethal dose of scorpion (*Centruroides sculpturatus*) venom to *S. tereticaudus* was 1.9 g/100 g body mass, about 10 times the dose of a natural sting (Turkowski, 1969).

Nematode parasites of *S. tereticaudus* include *Subulara nevadense* and *Citellina trivadiata* in the caecum, and *Syphacia citelli* in the caecum and large intestine (Babero, 1973). External parasites found on *S. t. neglectus* (Lang, 1972*a*) were: lice, *Enderleinellus osborni* ($\bar{X} = 20$/host) and *Neohaematopinus citelli*-

nus ($\bar{X}$ = 8–10/host); fleas, *Echidnophaga gallinacea* ($\bar{X}$ = 4/host) and *Thrassis arizonensis* ($\bar{X}$ = 20 to 30/host); mites, *Haemolaelaps glasgowi* ($\bar{X}$ = 10/host; Lang, 1972*b*) and *Trombicula arenicola* ($\bar{X}$ = 30/host); ticks, *Dermacentor parumpertus* and *Ornithodoros* (possibly *talaje*). Lang (1974) also examined nests for the presence of external parasites. These included: mites, *Haemolaelaps glasgowi* ($\bar{X}$ = 80/nest); ticks, *Ornithodoros* (possibly *talaje*) and *Brevisterna utahensis*; predaceous mites, *Trombicula arenicola* ($\bar{X}$ = 8/nest), *Ameroseius* sp. ($\bar{X}$ = 9/nest), and a species of Cunaxidae; other parasites, *Hypoaspis* sp., species of Microzetidae, Lohmannidae, and Lordalychidae; springtails (Collembola); beetles of Tenebrionidae, Carabidae, Histeridae, Staphylinidae, Nitidulidae, and Curculionidae; acrolophid webworms (Lepidoptera); therevid fly larvae (Diptera); fleas, *Thrassis arizonensis*; formicid ant species; oniscid sowbugs (Isopoda); and pseudoscorpions, *Chelanops arizonensis*. In all, more than 2,200 mites from 11 species in 10 families were found in 21 nests.

Drabek (1970) estimated density of a resident summer population at 5.3/ha (on a 63-ha site) in southcentral Arizona. Dunford (1977*a*) studied a crowded population in Arizona for 2 years and found an average late January density of 40/ha. Density increased between January and early March as females emerged from hibernation, then remained relatively stable until early May, when young emerged. Average density in early May was 210/ha. By late July, the density had declined to 136/ha because of death or dispersal of many juveniles.

At Dunford's (1977*a*) study site, immigration by males occurred mostly in January and February. Emigration of 29–45% of the juveniles (mainly males) occurred in June. Females tended to remain in their natal areas. Drabek (1970) also noted that juvenile males, not females, generally are the dispersers. Juvenile dispersal was not significantly related to size of litter, age of mother, size of mother's home range, food availability, intralitter aggression, or local population density (Dunford, 1975, 1977*a*).

Average sex ratio (females/male) over 4 years in a natural population in April was 2.7:1 (Dunford, 1977*a*). The sex ratio at birth of 10 litters born in captivity was 0.8:1 (Pengelley, 1966). Sex ratios of juveniles at emergence from the burrow were 1.2:1 (n = 58) and 1.1:1 (n = 63) two consecutive years in one population (Dunford, 1975).

Estimates of home range size by the minimum-area method in southcentral Arizona were 0.30 ha for adults, and 0.31 ha for juveniles (Drabek, 1973). The home ranges of adult males were not significantly different than those of adult females (Drabek, 1973). The spatial distribution of home ranges, based on number of occupied squares, appears to differ from year to year; it may be clumped, random, or regular (Dunford, 1977*c*). Home ranges of females may overlap by as much as 81%. Between February and July, the least overlap (30–40%) occurred in April and the greatest (81–97%) in February (Dunford, 1977*c*). Forty-eight percent of females that survived between years remained in the same home range, and all surviving females remained in the "immediate vicinity" of their previous range (Dunford, 1975).

In the early part of this century, reclamation of desert areas for farmland forced movement of round-tailed ground squirrels to peripheral habitats. Some damage to grain fields and irrigation ditches by these squirrels resulted in control efforts. The most common form of control was baiting with strychnine-coated barley (Dixon, 1922; Grinnell and Dixon, 1918).

These ground squirrels may be caught in live traps, rat traps, or dead-fall traps. Appropriate baits include raw peanuts, sunflower seeds, and mixtures of oatmeal and peanut butter. Individuals have been marked by toe-clipping and dyeing the fur. Nyanzol A or D dye applied to the limbs facilitates recognition of individuals (Drabek, 1970; Dunford, 1975).

Animals have been kept in captivity successfully under variable environmental conditions. Free water is essential if animals are fed dry foods. Animals in captivity have eaten grains (rolled oats), seeds (sunflower, mesquite), fruit (raisins, apples), green vegetation (leaves, lettuce), carrots, and commercial laboratory chow (Balcer and Chaffee, 1981; Hudson, 1964*a*; Neal, 1965*a*; Turkowski, 1969; Yousef et al., 1974).

BEHAVIOR. *Spermophilus tereticaudus* emerge from their burrows in January and February during the precopulatory phase. The pregnancy phase occurs after breeding in early March until the young are born in April and May; lactation extends through June. Juvenile dispersal occurs during June and July. The inactive phase begins in August or September and continues until January (Dunford 1975).

During the inactive phase, squirrels remain in their burrows most of the time. Some aboveground activity has been observed in fall and winter (Bradley and Deacon, 1971; Hall, 1946), although these probably are short periods of activity. Hudson (1964*a*) suggested that this species does not hibernate, but exhibits periods of torpor (inactivity). Hall (1946) also mentioned that, although squirrels remain in their burrows during winter, they may not hibernate.

Captive *S. tereticaudus* entered shallow torpor (T_b 23–28°C) each night from October to January when T_a was 20–25°C. Lower T_a (11°C) caused animals to enter deep torpor (T_b 11°C) in 2 to 3 days (Bickler, 1984). High ambient temperatures (40°C) in the laboratory (similar to temperatures in the squirrels' natural habitat) during August and September caused squirrels to enter torpor (Hudson, 1964*a*). Food deprivation during these months also can promote torpor (Walker et al., 1979). Hudson (1964*a*) observed that food deprivation in summer and fall induced torpor within 3 days in three of seven *S. t. chlorus*, but did not induce torpor in nine *S. t. tereticaudus*. *S. t. chlorus* could not be induced to enter torpor during spring or winter even when deprived of food or exposed to low ambient temperatures. When torpor is induced by food deprivation, squirrels exhibit a relatively continuous sleep state. The amount of REM sleep is less during torpor sleep than during euthermic sleep (Walker et al., 1979).

Pengelley and Kelly (1966) observed that *S. tereticaudus* is a "poor hibernator" compared to *S. lateralis*, *S. mohavensis*, *S. beecheyi*, and *S. variegatus*; *S. tereticaudus* exhibits shorter periods of uninterrupted inactivity. Cade (1964) believed that ancestral species of the tribe Marmotini were hibernators that evolved to "deep hibernators," and subsequently to species (such as *S. tereticaudus*) not dependent on hibernation or torpor. Pengelley and Kelly (1966), in a discussion of the evolution of hibernation patterns in the genus *Spermophilus*, suggested that *S. tereticaudus* evolved toward more freedom from "obligatory" hibernation and endogenous circannian rhythm of hibernation characteristic of ancestral *Spermophilus* species.

Bimodal peaks of activity during morning and late afternoon in round-tailed ground squirrels have been observed by Bodenheimer (1957), Drabek (1970), Huey (1927), Johnson et al. (1948), and Vorhies (1945). Grinnell and Dixon (1918) and Hudson (1964*b*), however, noted increasing activity as air temperatures rose. Drabek (1973) observed a bimodal activity pattern during summer, and a single activity period during spring and fall. Ambient temperature influences the number of squirrels above ground and their level of activity. Longer periods of aboveground activity are noted on overcast afternoons. Strong winds cause squirrels to emerge later in the morning. Squirrels seek shelter in their burrows during rain (Drabek, 1973).

Torpor induced by high temperatures may represent a behavioral adaptation to heat load by *S. tereticaudus* (Hudson, 1964*a*). Schmidt-Nielsen (1964) also suggested that the bimodal activity pattern may reduce heat load, allowing squirrels to conserve water rather than expend it to thermoregulate. *S. tereticaudus* may avoid or compensate for high temperatures and low humidity by alterations in daily activity patterns, use of shade and climbing into shrubs (to avoid contact with the hot sand), use of burrows, hibernation or estivation in late summer, and selection of succulent vegetation (Vorhies, 1945). Increase of T_b of captive *S. tereticaudus* to more than 40°C resulted in much faster ventilation (Bickler, 1984). In instances of extreme heat, *S. tereticaudus* and other ground squirrels rub saliva over their body surfaces to aid in evaporative cooling (Hudson and Deavers, 1972).

Round-tailed ground squirrels dig their own burrows, usually at bases of shrubs, or use burrows of kangaroo rats and other rodents (Elliot, 1904; Hall, 1946; Jaeger, 1961; Swarth, 1929). Grinnell and Dixon (1918) and Grinnell (1937) found fewer than four burrows near any cluster of mesquite shrubs. Mares (1973) most commonly found burrows under *Larrea* bushes in flat areas. Burrows also may be found in fine sand in "water-cut banks" (Johnson et al., 1948:352).

Burrow construction is accomplished by loosening soil with quick scraping movements of the front feet. The hind feet push the soil back toward the burrow entrance. Mounds usually are not formed around entrances because squirels scatter accumulated soil (Drabek, 1970). Burrows descend at a slant, and continue for 0.5 to 4.0 m (Drabek, 1970). Burrow depth ranges from 25 to about 50 cm (Drabek, 1970). Burrows are narrow, with an average diameter of 5.7 cm ($n = 23$; Drabek, 1970). Active burrows are plugged at about 45 cm. Nests of grass are located in lower sections of the burrows (Lang, 1974). Most burrows have two entrances, some have up to four (Drabek, 1970).

Round-tailed ground squirrels move about by walking, running or galloping, and jumping in and out of shrubs. They are able to climb into shrubs and low trees, and have been seen 5 m above the ground (Huey, 1927; Swarth, 1929). They seemingly are agile along heavy branches, but climbing becomes awkward along smaller branches that bend under their weight (Johnson et al., 1948).

Methods of grooming include dusting, sunning, and washing. Squirrels have dusting areas near their burrow entrances. Animals eat by holding food in their forepaws while resting on their hind legs. The alert posture is an upright, motionless position used in response to potential predators. Movement of the tail from side to side occurs in territorial situations and in response to terrestrial predators. Play, including boxing, wrestling, and chasing, is common among sibling juveniles (Drabek, 1970).

Time budgets of round-tailed ground squirrels in southern Arizona show that they spend approximately 50% of the time foraging (Dunford, 1975). Squirrels climb into mesquite trees to forage on leaves (Jaeger, 1961). Huey (1927) observed these squirrels to climb mesquite trees and to snip branches which held bean pods, let the pods fall, then descend to retrieve and carry the pods to their burrow entrances or to a shady spot before breaking them open. These squirrels may consume so much plant material at one time that their movements become hampered (Stephens, 1906). Seemingly they do not hoard food (Bodenheimer, 1957; Drabek, 1970). Some authors believe that *S. tereticaudus* never drinks free water (Bailey, 1923; Grinnell and Dixon, 1918), whereas Bodenheimer (1957) stated that water is consumed when available.

In a study of homing ability, Bradley (1968*b*) found that 40% of adult *S. tereticaudus* could home from 310 m, but none could home from 620 m. *Ammospermophilus leucurus* homed from 620 m with 92% success. Round-tailed ground squirrels outside familiar areas probably home by searching randomly until they find a familiar area then use learned visual cues to reach their home range (Bradley, 1968*b*).

Early investigators described the vocalization of *S. tereticaudus* as a "mellow whistle" (Elliot, 1903*a*:211), "high-pitched squeak or shrill whistle" or "shrill wiry cry" (Grinnell and Dixon, 1918: 670, 673), "peculiar low hissing whistle, sounding more like the note of some bird" (Stephens, 1906:70), and "explosive, high-pitched rasping note" or "sharp peeps" (Jaeger, 1961:122–123). Dunford (1977*b*:783) described the alarm call as a "nearly pure tone whistle," with an average frequency (at midpoint) of 8.7 kHz and average duration of 142 ms. Squirrels uttering separate whistles are difficult to locate (Grinnell and Dixon, 1918; Stephens, 1906). These whistles serve to warn of potential predators (Dunford, 1977*b*). The alert standing posture associated with alarm calling also may serve to warn of predators (Drabek, 1970). Clustered whistles are shorter and softer than separate whistles, and are uttered during social interactions with conspecifics (Dunford, 1977*b*). Squirrels that heard clustered whistles stopped what they were doing and often stood up on their hind feet. Single whistles caused squirrels to run to their burrow entrances before assuming the alert posture (Dunford, 1977*b*). Burt (1933) noted that young *S. t. neglectus* responded to warning vocalizations of adults by crouching and remaining still.

Females vocalize more frequently than males; they also are more closely related to neighbors than are males. These factors caused Dunford (1977*b*) to conclude that alarm calling probably is selected for through kin selection. Vocalizing squirrels apparently do not increase their susceptibility to predation because they usually call from their burrow entrances, and call only when the predator is still far away.

Effectiveness of warning communication is greatest in dense populations (Dunford, 1977*a*). Dunford (1977*a*) attributed the low predation rate in his study population to the high density of squirrels and good visibility allowed by the low vegetation. Drabek (1970) also believed that high density contributed to effective predator defense. He suggested that the alert upright posture, rather than vocalization, was the main warning signal for potential predators. He rarely heard vocalizations when terrestrial predators approached, and never heard them in response to aerial predators.

Round-tailed ground squirrels exhibit a semicolonial social organization, but maintain individual burrows during much of the year (Drabek, 1970). Burrows are shared from January to early March, from May to June, and probably during some of the months of winter inactivity (Dunford, 1975, 1977*a*). Burrows are not shared while females are pregnant or after young have been weaned. Squirrels can approach burrows of neighbors without being chased only if the neighbors are inactive (Drabek, 1973). Interaction rates within a population of *S. tereticaudus* in Arizona were high before and during the breeding season (Dunford, 1975, 1977*c*). Rates decreased after copulation in March and remained low until parturition. Interaction rates were high between mother and young and among sibs until the young dispersed in June. Rates of interaction among mother-offspring groups were low, but these encounters were more aggressive than intraunit interactions (Dunford, 1975). In general, juvenile females had the same interaction rates as juvenile males (Dunford, 1977*a*).

Patterns of social interactions are different between sexes and age classes (Dunford, 1977*c*). Males initiated more encounters with conspecifics during late winter and early spring than expected (from proportion of active males sighted), whereas females were approached more than expected. During July, young were approached more often than would be expected by chance alone. Differences between sexes were observed in kissing, nose contact with body of conspecific, and mounting in the precopulatory phase. Aggressive behaviors (lunging, kicking, and fighting) were most frequent in March and April. All categories of behavior varied significantly from season to season (Dunford, 1977*c*).

Interactions generally were more frequent among kin (mother-offspring or sibs) than among unrelated animals (Dunford, 1975, 1977*c*). Kin kissed more and fought less than expected during the precopulatory phase. In late summer, kin lunged, drummed their feet, and waved their tails less than expected. When two interacting individuals separated, kin withdrew shorter distances than unrelated individuals during the precopulatory phase, but later in the year no significant differences were observed. Huey (1927) noted that juveniles played in small groups (up to six) for as long as 30 min, but did not note whether these were kin groups.

Males are dominant from January until early March. Females become dominant in March and April. In July of one year neither sex was dominant, but the following July, males were dominant. Adults won all interactions with juveniles in May and June, but juveniles won some (still a minority) of interactions with adults in July. Dominance probably is correlated with body mass in males, but age seems to be a better correlate of dominance in females (Dunford, 1975, 1977*c*).

In *S. tereticaudus*, males do not defend territories or females in the precopulatory phase, though they are dominant over females during the breeding season, similar to the situation in *S. armatus*, *S. beldingi*, *S. richardsonii*, and *S. tridecemlineatus*. In contrast, male *Marmota* and *Cynomys*, and probably *S. columbianus*, establish territories that may include ranges of several females (Dunford, 1977*c*). Dunford (1975, 1977*a*) found in a high density population that aggression by residents can prevent outsiders from establishing territories but cannot force offspring to leave their natal areas. Aggression affects dispersal in arctic ground squirrels (*S. parryii*) and marmots (*Marmota*), but not in most other ground squirrels. Population densities in Dunford's (1977*a*) study were not limited by behavioral mechanisms when food was plentiful and predation rates were low.

Little mention of interspecific competition is made, although *S. tereticaudus* is sympatric in parts of its range with *Ammospermophilus harrisii*, *A. leucurus*, *S. spilosoma*, *S. variegatus*, *S. mohavensis*, and *S. lateralis*. Dunford (1977*a*) observed an aggressive encounter between a round-tailed ground squirrel and a Western pocket gopher (*Thomomys bottae*). *S. tereticaudus* may compete with *T. bottae* and with white-throated woodrats (*Neotoma albigula*) for burrow space, especially during inclement weather (Dunford, 1977*a*). Behavioral interactions between *S. tereticaudus* and the Mongolian gerbil (*Meriones unguiculatus*) in enclosures began with roll fights, usually initiated and won by *S. tereticaudus*. Gerbils were able, however, to occupy squirrel nest boxes after 24 h in four trials (Fisler, 1977).

GENETICS. The diploid (2n) chromosome number in *S. tereticaudus* is 36 (Hafner and Yates, 1983; Ingles, 1965; Nadler, 1962); FN = 68 (Hafner and Yates, 1983). Autosomes are metacentric or submetacentric. The X chromosome is submetacentric and of medium size. The Y chromosome is acrocentric and also medium sized (Nadler, 1962). In a study of seven populations throughout the range of *S. tereticaudus*, Hafner and Yates (1983) found no intra- or interpopulational variations in chromosome number. Giemsa-banding patterns of *S. tereticaudus* are more similar to those of *S. townsendii* than to those of *S. beecheyi*, *S. lateralis*, or *S. saturatus* (Gibson, 1985).

Albinism has been reported for one individual (Turkowski and Parker, 1967). No records of melanistic individuals have been reported.

REMARKS. The species name, from the Latin *tereticaudus*, means "round-tailed" (Jaeger, 1961). Vernacular names for these squirrels include Yuma round-tailed ground squirrel (*S. t. tereticaudus*), Palm Springs round-tailed ground squirrel (*S. t. chlorus*), Arizona round-tailed ground squirrel (*S. t. neglectus*), and Trinidad Valley round-tailed ground squirrel (*S. t. apricus*).

Elliot (1904) suggested that intergradation occurred between *S. tereticaudus* and *S. mohavensis* at one site in California, whereas Grinnell and Dixon (1918) and Howell (1938) suggested that the two were full species. Karyotypic and electrophoretic analyses at several sites in California and Mexico indicated two distinct chromosomal populations. Hybridization occurs only in a restricted area that has been ecologically disturbed (Hafner and Yates, 1983).

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