

*Spermophilus mohavensis*. By Troy L. Best

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***Spermophilus mohavensis* Merriam, 1889**  
Mohave Ground Squirrel

*Spermophilus mohavensis* Merriam, 1889:15. Type locality "Mojave River, California." Restricted to "near Rabbit Springs, about 15 miles east of Mohave River at Hesperia, in San Bernardino County" (Grinnell and Dixon, 1918:667).

**CONTEXT AND CONTENT.** Order Rodentia, Suborder Sciuromorphi, Family Sciuridae, Subfamily Sciurinae, Genus *Spermophilus*, Subgenus *Xerospermophilus*. The genus *Spermophilus* contains 38 species (Wilson and Reeder, 1993). *S. mohavensis* is monotypic (Hall, 1981).

**DIAGNOSIS.** The range of *S. mohavensis* lies completely within the distribution of *Ammospermophilus leucurus* (Bartholomew and Hudson, 1960). Compared with *S. mohavensis*, *A. leucurus* has distinctive white stripes on the sides (Jameson and Peeters, 1988). The only congeners that occur in the same region of California as *S. mohavensis* (Fig. 1) are *S. beecheyi* and *S. tereticaudus*. Compared with *S. beecheyi* (total length, 357-500 mm), *S. mohavensis* (total length, 210-230 mm) is smaller, upperparts are plain and not variegated, and upper incisors are slender and not distinctly recurved (Hall, 1981).

The ranges of *S. mohavensis* and *S. tereticaudus* abut, but do not overlap, along a broad front of ca. 240 km (J. R. Gustafson, in litt.; Hafner, 1992). Compared with *S. tereticaudus*, *S. mohavensis* is most easily distinguished by its tail, which has a white undersurface, is shorter, and is more broadly haired (flatter) than in *S. tereticaudus*. Claws of *S. mohavensis* are stouter, cheeks are brownish instead of white, quantity of winter pelage is greater, and general tone of coloration always is decidedly dark (Grinnell and Dixon, 1918). *S. mohavensis* also is significantly larger than *S. tereticaudus* in 18 of 20 cranial characters (except postorbital and interorbital breadths). Averages (in mm) of the most divergent measurements for *S. mohavensis* and *S. tereticaudus*, respectively, are: condylobasal length, 35.4, 32.8; condyloincisor length, 34.2, 31.3; bullar breadth, 18.6, 17.6; nasal length, 12.7, 11.2; width at masseteric tubercles, 9.6, 8.8; rostral width, 6.7, 6.1; length of diastema, 9.0, 7.9; length of articular process, 17.5, 15.7; length of coronoid process, 13.6, 12.1 (Hafner, 1992). In addition, there is a consistent difference in diploid number of chromosomes (2N) between *S. mohavensis* (2N = 38) and *S. tereticaudus* (2N = 36). A narrow zone of hybridization, shown by allozymes, is found at one ecologically disturbed site near Helendale, San Bernardino Co. (Hafner, 1992; Hafner and Yates, 1983).

**GENERAL CHARACTERS.** The Mohave ground squirrel is a brown-colored ground squirrel, without stripes or conspicuous markings on the body, but with a short, broadly haired tail (Grinnell and Dixon, 1918). In unworn winter pelage (March), upperparts are uniform pale drab, with a tinge of pale vinaceous-cinnamon that is strongest on the forehead. Front feet are pale pinkish-cinnamon, and hind feet are pale buff, washed with pale pinkish-cinnamon or pinkish buff. Dorsally, the tail is fuscous, overlaid with creamy white. Ventrally, the tail and underparts are creamy white. In summer pelage (May), upperparts are drab or yellowish (Howell, 1938).

The skull of *S. mohavensis* (Fig. 2) is smooth, and the shelf of the palate is produced backward in the median line in the form of a long, slender spine (Merriam, 1889). The braincase is short and broad, the rostrum is short, and the nasals end nearly in line with the premaxillae. The zygomata are heavy, widely expanded, and twisted so that they occupy a position about midway between vertical and horizontal. The postorbital processes are broad at the base, narrowing rapidly to a slender tip, which is depressed. The incisors are moderately short, stout, and slightly recurved. The

auditory bullae are broad, evenly rounded, and considerably inflated (Howell, 1938).

The sexes appear alike (Grinnell and Dixon, 1918) and there is little variation among ages (Merriam, 1889). Averages and ranges of external measurements (in mm) are ( $n = 11$ —Howell, 1938): total length, 223 (210-230); length of tail, 66 (57-72); length of hind foot, 36 (32-38). Average (in mm) of cranial measurements are ( $n = 54$ —Hafner, 1992): condylobasal length, 35.4; condyloincisor length, 34.2; zygomatic breadth, 24.0; bullar breadth, 18.6; nasal length, 12.7; postorbital breadth, 12.7; interorbital breadth, 8.7; width at masseteric tubercles, 9.6; rostral width, 6.7; bullar length, 9.6; interbullar width, 3.6; occlusal length of maxillary tooth-row, 7.9; length of diastema, 9.0; palatal width at M3, 4.4; palatal width at P4, 5.5; width of P3, 1.1; width of M1, 2.4; length of articular process, 17.5; length of coronoid process, 13.6; width of angular process, 8.6. Depending upon time of year, mass is 70-300 g (Bartholomew and Hudson, 1961; Jameson and Peeters, 1988; P. Leitner, pers. comm.; Recht, 1977). During years with high winter precipitation and high primary productivity in Inyo Co., pre-estivating individuals often have a mass of 200-275 g and some >300 g (P. Leitner, pers. comm.).

**DISTRIBUTION.** The Mohave ground squirrel inhabits a 20,000-km<sup>2</sup> area in the northwestern corner of the Mojave Desert (Hafner, 1992; Fig. 3). The range of *S. mohavensis* includes parts of Inyo, Kern, Los Angeles, and San Bernardino counties, California (J. R. Gustafson, in litt.; Hall, 1981; Zembal and Gall, 1980). The Mohave ground squirrel occupies the lower Sonoran life zone in the Mojave Desert at elevations of 610-1,800 m (Grinnell, 1933; Grinnell and Dixon, 1918; J. R. Gustafson, in litt.; Howell, 1938; Ingles, 1965).

**FOSSIL RECORD.** The genus *Spermophilus* evolved by the early Pleistocene (Black, 1972). Fossils that may represent *S. mohavensis* have been recovered in late Quaternary deposits in the Mojave Desert, California (Goodwin and Reynolds, 1989).

**FORM AND FUNCTION.** Length of tail of the Mohave ground squirrel is ca. 50% of the length of head and body. The feet are large, claws are long and moderately curved, thumbs have a large blunt claw, palms of the forefeet are naked, and soles of the hind feet are densely haired to the claws. The pelage is rather coarse (Merriam, 1889). Maximum length of dorsal guard hairs is 10 mm, and width is up to 90  $\mu$ m (Mayer, 1952). Guard hairs are not uniform in color; the distal, middle, and proximal parts of these hairs are brown-black, translucent, and tan, respectively. The extent of piloerection governs the extent of hair overlap, resulting in differing appearance of prebasking and postbasking individuals (Recht, 1977).



FIG. 1. *Spermophilus mohavensis* in California City, Kern Co., California. Photograph by R. Patrick.

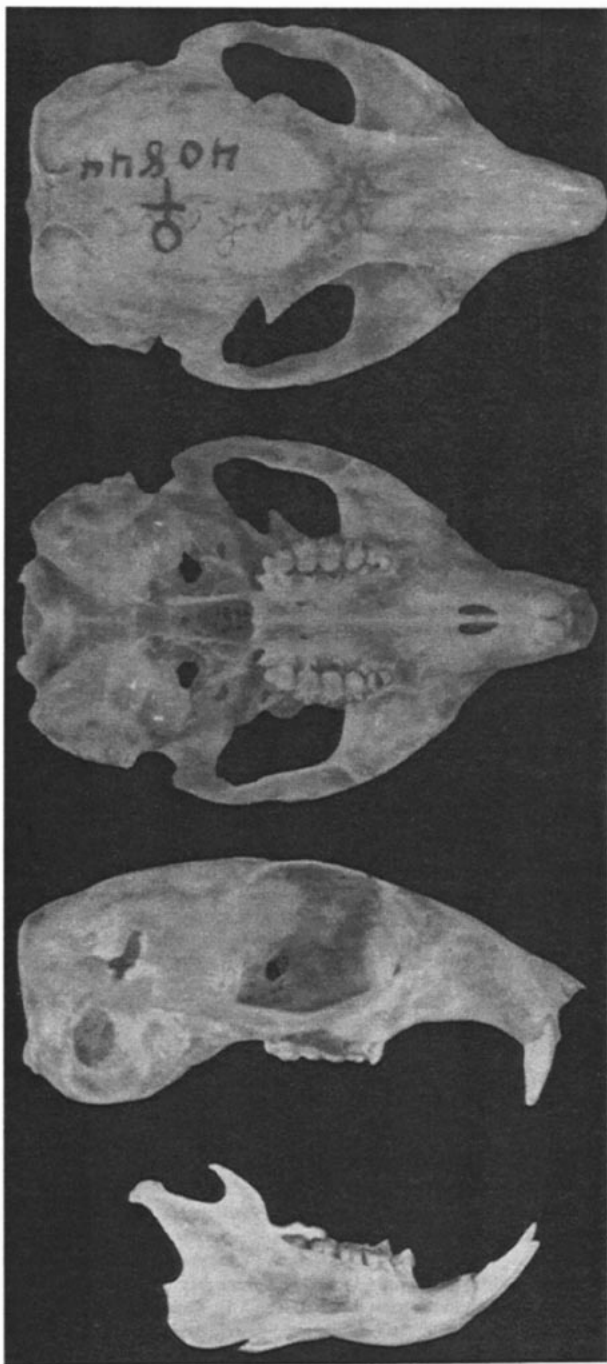


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Spermophilus mohavensis* from Owens Lake, Inyo Co., California (female, United States National Museum of Natural History 40844). Greatest length of cranium is 38.8 mm.

On 3-12 May, *S. mohavensis* showed the process of molt from winter to summer pelage. Patches of worn and yellowed winter hairs remained on the fore back and rump. The tail seemingly is not included in the spring molt; old tail hairs become crinkled and broken at the ends. The white of the underside is dingy, and a dark subterminal band is present around the end of the tail (Grinnell and Dixon, 1918). A female on 12 May had new pelage covering the head, shoulders, and most of the back (Howell, 1938).

Vibrissae of *S. mohavensis* conform to the general rodent arrangement. The posterior mystachials are longest. A row of superciliary vibrissae extends dorsocaudad from the anterior angle of each eye. A vertical series of genals is present near the center of each cheek. The carpal vibrissae are well developed. An ulnar vibrissa

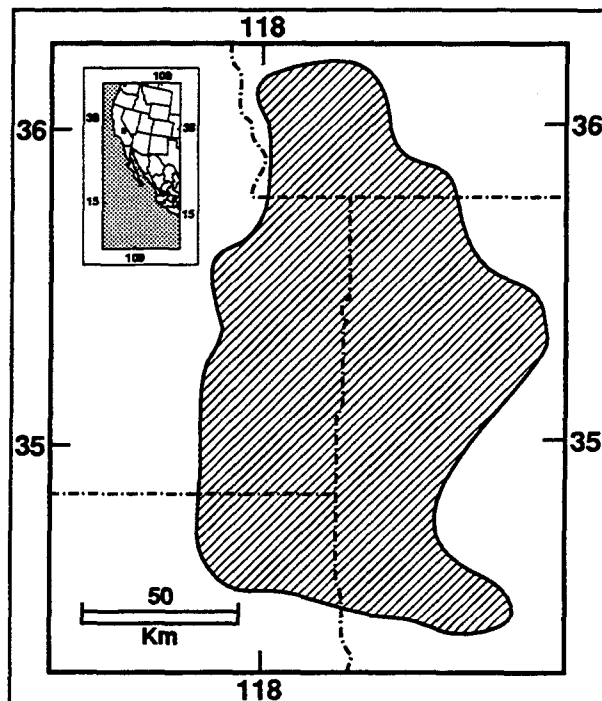


FIG. 3. Distribution of *Spermophilus mohavensis* in California (J. R. Gustafson, in litt.; Hall, 1981; Zembal and Gall, 1980).

is present on the outer side of the forearm proximal to the carpus (Bryant, 1945).

The rhinarium of the Mohave ground squirrel is shallow, broad, and convex. The round nares open anterolaterally from under the margin of the septum and are separated partially from a lateral groove by a small dorsal fold. The naris and lateral groove in combination are comma shaped. When the tip of the muzzle is drawn downward, the supranarial border covers the nares and the openings are reduced to convex slits (Bryant, 1945).

The eyes are large and have a small, black-tipped plica semilunaris under the anterodorsal surface of the upper eyelid. The iris and pupil are round, eyes are surrounded by a pale-colored ring (Bryant, 1945), and eyelids are white (Merriam, 1889). The auricula of the ear is reduced to an oval, thickened rim, and there is no antitragus or intertragal notch (Bryant, 1945).

The highest point of the moderately convex dorsal profile of the skull is situated slightly posterior to the plane of the postorbital processes. From this point to the rostrum, the skull of *S. mohavensis* is nearly flat. The downward inclination of the rostrum is about the same as that of the cranium posterior to the highest point. The rostrum is short in comparison with length of skull. From the dorsal view, the cranium is nearly quadrate. The inclination of the posterior wall of the orbit is dorsal. The parietal ridges are inconspicuous and broadly lyre-shaped (Bryant, 1945).

The diastemal part of the mandible is slender, rounded laterally, concave above and below, and flattened medially. The alveolar border is level with or below the level of the anterior tip of the mandible. The anterior margin of the alveolar surface passes ventrad to join the diastemal part in a gradual curve. The ventral mandibular incisure is deep and acutely arched (Bryant, 1945).

The dental formula of the Mohave ground squirrel is  $i\ 1/1, c\ 0/0, p\ 2/1, m\ 3/3$ , total 22 (Hall, 1981). As in other sciurids, the upper toothrows are farther apart than lower toothrows. Thus, it is impossible for the two series to be in perfect occlusion at the same time. Nevertheless, arrangement of cusps is such that an excellent lateral-grinding movement is assured. When teeth are meshed, transverse ridges prevent a fore-and-aft movement of the mandible. When gnawing is desired, this mechanical condition is overcome by lowering the mandible and pushing the lower incisors forward to make contact with the upper incisors. These relationships account for fore-and-aft gnawing movements and transverse grinding movements (Bryant, 1945).

Alveoli of the upper incisors open cranioventrally in the anterior

ends of the premaxillae. Incisors pass through the lateral parts of the premaxillae and maxillae, and terminate medial to the infraorbital foramina. Upper incisors are shorter, stouter, and more curved than lower ones. Anterior surfaces usually are more rounded than lateral surfaces, and medial surfaces are flat. Each lower incisor extends posteriad through the ventral part of the body of the mandible and terminates at the base of the condyloid process. A small tubercle on the lateral surface of the ramus marks the point of termination (Bryant, 1945).

Ratios (in percent) of parts of the skeleton of *S. mohavensis* are: length of cervical vertebrae to length of vertebral column, 14.2; length of thoracic vertebrae to length of vertebral column, 39.7; length of lumbar vertebrae to length of vertebral column, 34.8; length of sacrum to length of vertebral column, 11.7; length of scapula to length of vertebral column, 16.6; width of scapula to length of scapula, 53.8; length of humerus to length of vertebral column, 22.4; length of radius to length of vertebral column, 18.7; length of humerus to length of humerus and radius, 54.5; length of olecranon to length of ulna, 15.6; length of os coxae to length of vertebral column, 25.8; length of femur to length of vertebral column, 26.7; length of tibia to length of vertebral column, 27.2; length of femur to length of femur and tibia, 49.1; length of sternum to length of vertebral column, 21.1. These ratios are similar to those of congeners (Bryant, 1945).

Aestivation in the Mohave ground squirrel shows the classical criteria for hibernation: body temperature near ambient temperature; oxygen consumption markedly reduced; prolonged periods of apnea; a torpor more pronounced than deep sleep; arousal, either spontaneous or induced, accompanied by activation of major heat-producing mechanisms. Furthermore, physiological and behavioral performance is qualitatively similar over body temperatures of 10–27°C. Physiological and behavioral differences between aestivating and hibernating Mohave ground squirrels are matters of degree and appear simply to be functions of body temperature, the level of which is determined by environmental temperature (Bartholomew and Hudson, 1960). Therefore, the term aestivation is used to refer to the annual period of torpor.

*Spermophilus mohavensis* becomes fat before entering aestivation (Bartholomew and Hudson, 1961). Large amounts of stored fat are used during aestivation and to supply metabolic water in periods of drought (Pengelley and Kelly, 1966). The Mohave ground squirrel can add 100–200 g to its body mass before retiring underground (Bartholomew and Hudson, 1961; P. Leitner, pers. comm.). Average gain in mass of adults is 0.8–2.5 g/day and of juveniles 0.5–1.8 g/day. The Mohave ground squirrel enters aestivation at ca. 165–300 g, and emerges at 70–80 g (P. Leitner, pers. comm.; Recht, 1977).

In the laboratory, continuous aestivation is never >2 weeks in *S. mohavensis*. There is no significant difference in periods of continuous aestivation at 3 and 12°C. During aestivation, body temperature is 8–10°C at 3°C, and 12°C at an ambient temperature of 12°C. Each arousal from aestivation is complete, i.e., the active homothermic temperature of 37–38°C is regained before re-entry into aestivation. Urination invariably takes place before the animal enters aestivation again (Pengelley and Kelly, 1966).

During dormancy, heart rate of the Mohave ground squirrel is greatly reduced (Bartholomew and Hudson, 1961). In the laboratory, perfused and isolated hearts have been exposed to temperatures of 0–25°C; at 0–2°C, the heart ceases to beat (Lyman, 1964).

Body temperature of *S. mohavensis* usually is greater than environmental temperature, although when active its temperature fluctuates sharply (Bartholomew and Hudson, 1961). In the laboratory, the Mohave ground squirrel spontaneously enters torpor at room temperature and spends much of the summer, autumn, and winter in a dormant condition. During periods of normal activity, its metabolism averages ca. 0.8 cm<sup>3</sup> of oxygen g<sup>-1</sup> h<sup>-1</sup> and its body temperature averages 35.8°C (range, 35.2–36.1°C). *S. mohavensis* may become torpid over a range of ambient temperatures of 10.6–27.1°C. When entering torpor at ambient temperatures of 22–26°C, the Mohave ground squirrel assumes the usual sleeping posture, oxygen consumption declines rapidly, and body temperature approximates environmental temperature within 3–4 h. Thereafter, oral and rectal temperatures vary directly with ambient temperature. Body temperature increases more slowly, and levels of body temperature characteristic of normal activity usually are attained in 45–60 min. Typically, rectal and oral temperatures are within 0.5°C of each other during arousal. Behavioral capacities of an individual

increase steadily as body temperature rises and appear normal at 30°C (Bartholomew and Hudson, 1960).

Aestivating individuals are most readily distinguished from sleeping animals by respiratory pattern. Torpid individuals show prolonged periods of apnea, while sleeping animals do not. Oxygen consumption during torpor usually is uniform and is 0.1–0.2 cm<sup>3</sup> g<sup>-1</sup> h<sup>-1</sup>, but may increase to 0.4 cm<sup>3</sup> g<sup>-1</sup> h<sup>-1</sup>. Duration of torpidity varies from 8 h to several days. Aestivating individuals occasionally shift position or change posture without arousing (Bartholomew and Hudson, 1960).

When an aestivating Mohave ground squirrel starts to arouse, its oxygen consumption rises rapidly and may increase 10–20 fold in <15 min. The peak of oxygen consumption usually is reached within 20 min of the start of arousal. Oxygen consumption then declines to the normal resting level in ≥2 h. Thus, during much of the period of arousal from aestivation, oxygen consumption actually is decreasing from its initial peak while body temperature increases. With onset of arousal, breathing of an animal aestivating at ≥20°C immediately becomes continuous and within 5–10 min reaches the normal rate of ca. 80–90/min. Thereafter, it usually remains relatively constant in rate, but may increase in amplitude. At body temperatures <20°C, periods of apnea continue to occur even while the animal is arousing. Toward the end of arousal, breathing rate sometimes becomes conspicuously depressed and respiratory movements become deep and heavy (Bartholomew and Hudson, 1960).

The time required for body temperature to rise to levels characteristic of normal activity depends largely on initial body temperature, but rate of increase shows nonsignificant correlation with body temperature at the start of arousal. Rate of temperature change varies in the same individual between arousal times. At ambient temperatures of 22–27°C, maximum rate of increase in body temperature above ambient temperature was 0.4°C/min, while minimum rate was 0.1°C/min. Body temperature at termination of arousal is 33–38°C. Usually, *S. mohavensis* shivers strongly during arousal. Occasional slight quivering of the anterior parts of the body occur at body temperatures as low as 16°C. Strong, sustained shivering usually does not begin until body temperatures of 23–24°C are attained. Shivering appears first anteriorly and then spreads to posterior parts of the body. Shivering does not continue after body temperature reaches 35°C (Bartholomew and Hudson, 1960).

Continuous records of body temperature may be obtained by inserting a vinyl-sheathed copper-constantan thermocouple through the rectum to a depth of 5–6 cm, securing the leads to the tail with tape, and attaching them to a recording potentiometer. Oral temperatures may be determined manually by a thermocouple or by a quick-acting thermometer (Bartholomew and Hudson, 1960).

Specimens of *S. mohavensis* can be preserved for study by embalming with trioxitone (formaldehyde, denatured alcohol, zephiran chloride, and water). After 7 days, specimens were in excellent condition (Loomis, 1960).

**ONTOGENY AND REPRODUCTION.** Males of *S. mohavensis* typically emerge from aestivation in February, up to 2 weeks before females. Males may establish and defend a territory against other males, and females may enter the territory of a male and occupy burrows close to the burrow of the male. The male and a female may enter his burrow, where they may remain for several hours. Presumably, copulation occurs in the burrow. After emerging from the burrow, the female remains another day or so in the male's territory, then leaves to establish a home range. Other females repeat the sequence of individually entering the male's burrow, spending a short period of time, and then departing (J. R. Gustafson, in litt.; M. A. Recht, in litt.).

There are pregnant females from February to May (Bartholomew and Hudson, 1960; Booth, 1968; Jameson and Peeters, 1988; Pengelley, 1966, 1969). On 29 March, a female had six embryos that were 31–36 mm in length. On 12 April, another was lactating, and her uterus showed that she recently had given birth (Burt, 1936). After a gestation period of 29–30 days, young are born in the female's burrow (J. R. Gustafson, in litt.; M. A. Recht, in litt.). Litter size is 4–9 (Booth, 1968; Jameson and Peeters, 1988; Pengelley, 1966), sex ratio of neonates is 1:1, and mass at birth is 4–5 g (Pengelley, 1966).

At birth, young Mohave ground squirrels are fetal-like in appearance, being non-pigmented except for the eyeball showing through the skin. They are blind and have pinnae, but the auditory meatus is closed. Vibrissae are present, and small hairs occur on the head.

Neonates are capable of a high-pitched squeaky vocalization, apparently associated with suckling, and the righting reflex is well developed. They also can move by a wriggling motion with the assistance of fore and hind limbs. Onset of skin pigmentation begins on the 8th day, ears open in 17–19 days, eruption of lower incisors occurs in 19–25 days, eruption of upper incisors in 27–28 days, eyes open in 30–31 days, and weaning occurs in 32 days (Pengelley, 1966). Young have been born and successfully raised in the laboratory, where they were weaned at 6 weeks of age (Pengelley, 1969).

*Spermophilus mohavensis* may respond to drought by failing to reproduce. Prolonged periods of drought result in extinction of local populations. During droughts, no young may be born for several years. Survival of adults is reduced by poor conditions of habitat, and the remaining adults eventually die due to old age and predation. In years of low precipitation and reduced growth of plants, females survive the aestivation period by suspending reproductive activity and entering aestivation as soon as they can build up adequate fat reserves. The alternative, waiting until after young are weaned in dry years to begin accumulating fat, would doom females that reproduced because they would lack sufficient time to gain mass (J. R. Gustafson, in litt.; P. Leitner and B. M. Leitner, in litt.).

**ECOLOGY.** The Mohave ground squirrel occurs in a region characterized by hot, rainless summers and mild winters with light precipitation. This diurnal rodent is not exposed to prolonged low temperatures, although nighttime temperatures in winter may fall below freezing, days usually are mild. Seasonal dormancy does not appear to be an adaptation for avoidance of low temperatures, but appears to be an adaptation to seasonally restricted food and water (Bartholomew and Hudson, 1960).

*Spermophilus mohavensis* occurs in a variety of habitats, from creosotebush (*Larrea divaricata*) and saltbush (*Atriplex*) communities at low elevations to rich Joshua tree (*Yucca brevifolia*) and monotypic blackbrush (*Coleogyne ramosissima*) habitats at elevations >1,500 m (Grinnell, 1933; Ingles, 1965; E. V. Wessman, in litt.). In Inyo Co., the Mohave ground squirrel occurs in shadscale (*Atriplex confertifolia*) and creosotebush communities where perennial plant cover is 10–19%. One Mohave ground squirrel was observed in steeply sloping and rocky terrain (Zemal and Gall, 1980). Near Palmdale, *S. mohavensis* usually is found on the lower desert, but penetrates the Joshua tree belt in certain places. It occupies areas where soil is sandy or sand mixed with gravel, with a sparse growth of shrubby plants. The terrain usually is fairly level, with a few shallow ravines. The area is covered with shrubs, but is fairly open. Small bushes are 6–9 m apart and not >0.6 m in height. *S. mohavensis* was never observed in the foothills (Burt, 1936).

The Mohave ground squirrel is omnivorous (Morton, 1979), but is a short-term dietary specialist during the activity season (Recht, 1977). For example, in Inyo Co. in late March, the diet was >95% leaves of *Grayia spinosa*. In April, the diet was 68% forbs with *Monardella exilis*, *Gilia*, and *Linanthus aureus* each contributing significantly. In June, seeds of *Lycium* were ca. 74% of the diet. At times, the diet was composed of 70–85% arthropods and seeds of *Opuntia*; the arthropods primarily were caterpillars (Lepidoptera), which were present in large numbers (J. R. Gustafson, in litt.; P. Leitner and B. M. Leitner, in litt.). In Los Angeles Co., four plants with water content of 6–16% (*Lycium*, *Coreopsis*, *Amsinckia*, and *Salsola*) comprised the major food resources. These plants were not used simultaneously, but usually were eaten at different times depending upon their water content. Except for *Lycium* (10% of vegetative cover), these represented the most abundant vegetation (60–90% of vegetative cover) when they were present. At the time *Lycium* was consumed, tiny grasses comprised the bulk of vegetative cover, but were not eaten by *S. mohavensis*. Other foods included *Atriplex*, *Larrea*, *Eriogonum*, *Malacothrix*, *Stephanomeria*, and Cruciferae (Recht, 1977).

Fruits of the Joshua tree are a favorite food of *S. mohavensis* (Jameson and Peeters, 1988), but may not be important in the diet in all parts of the range (J. R. Gustafson, in litt.; P. Leitner et al., in litt.). In Inyo Co., nearly one-half of the Mohave ground squirrels were seen far from the nearest Joshua tree. However, when seeds of the Joshua tree were available, they were heavily utilized and appeared to be a preferred food. In one area of ca. 0.39 km<sup>2</sup> (ca. 3.2 km by 122 m), 30 fruiting Joshua trees were found; 16 *S. mohavensis* and 21 *Ammospermophilus leucurus* were counted at fruit clusters there on 3 July at 1445–1550 h (Zemal and Gall, 1980).

Analyses of feces indicated that forbs composed ca. 50–85% of the diet. Plants eaten included *Astragalus lentiginosus*, *Eremalche exilis*, *Schismus arabicus*, *Baileya pleniradiata*, *Langloisia matthewsii*, *Gilia*, *Atriplex*, and flowers and seeds of various composites. One fecal sample contained 62% mycorrhizal fungi and another contained 45% creosotebush. In 35 of 47 fecal samples, the samples tended to be dominated by a single item. Overall, forbs provided significant amounts of foliage to the diet, as well as some seeds; grasses and shrubs made smaller contributions. Arthropods (mostly grasshoppers, ants, and beetles) were a small, but consistent (5–8%), component of the diet (J. R. Gustafson, in litt.; P. Leitner and B. M. Leitner, in litt.). In captivity, *S. mohavensis* can subsist on a diet of commercial rat chow, sunflower seeds, and water ad lib. (Bartholomew and Hudson, 1960; Lyman, 1964; Pengelley, 1969; Pengelley and Kelly, 1966).

Burrows of the Mohave ground squirrel often are placed in the soil of desert washes beneath clumps of desert willows (*Chilopsis linearis*—Elliot, 1904) and near plants it consumes (Bartholomew and Hudson, 1961). There are three types of burrows; a home burrow, an aestivation burrow, and an accessory burrow. The home burrow is where the squirrel goes each evening and emerges each morning. Upon entering the burrow to retire for the day, it will push up a soil plug to close the burrow opening. This soil plug is removed upon emergence in the morning. These burrows usually are located on the boundary of the home range rather than in the center. Occasionally, the site of the home burrow is shifted to a new area. The aestivation burrow is excavated over several days, and may be either an enlarged, existing burrow or a new burrow. The accessory burrow also may be either an existing or a freshly excavated burrow and may serve in social interactions, escape, or thermoregulation, but the most frequent use is for thermoregulation. These burrows are used extensively in midday to cool off (Recht, 1977).

Burrows are ca. 5.5 m in length and 1 m in depth (Bartholomew and Hudson, 1961), and enter the ground at an angle of ca. 35°. Dirt taken from the burrow apparently is scattered, because little or none occurs at the entrance. A burrow excavated near Palmdale had two openings. One of these was nearly round, but the other was slightly oval. They measured 5 cm in the smaller and 6.4 cm in the greatest diameter. The openings were 1.4 m apart and the simple tunnel was 30 cm below the surface at the deepest point. Above the tunnel was an enlarged chamber, but there was no nest material. It is possible that the burrow was not complete, as a female did more digging near the entrance (Burt, 1936). In Kern Co., the entrance to one burrow was under a creosotebush, and a second burrow was located in the open ca. 6 m from the creosotebush. A *S. mohavensis* entered one opening and ca. 30 min later reappeared at the other entrance. This ground squirrel appeared at irregular intervals from 1130–1330 h to feed near the burrow entrance (Chesmore and Carroll, 1976).

Size of home range does not differ between sexes, but adult Mohave ground squirrels occupy smaller home ranges than juveniles (Recht, 1977). During a drought in Inyo Co., average size of home range was 0.71–1.92 ha. There was little overlap of home ranges, and even small areas of overlap usually were not occupied simultaneously by two individuals (J. R. Gustafson, in litt.; P. Leitner et al., in litt.). During adverse years, size of home range does not increase; there simply are fewer individuals per hectare (J. R. Gustafson, in litt.). Radiotelemetry has been used to study home range, foraging areas, and activity patterns of the Mohave ground squirrel (Recht, 1977).

Populations of *S. mohavensis* usually are small and scattered (Burt, 1936; Zemal and Gall, 1980), but may be locally abundant in early summer (Hafner, 1992; Zemal and Gall, 1980). Densities may be 0.04–6.00/ha, and may average ca. 0.4 adult female/ha of suitable habitat (J. R. Gustafson, in litt.; P. Leitner and B. M. Leitner, in litt.; Recht, 1977). Populations around alfalfa fields probably are large due to abundant food (E. V. Wessman, in litt.). Near Palmdale, the Mohave ground squirrel was not numerous in spring; no more than 2–3/km were observed along a roadway, and often none for 3–5 km. It is distinctly less numerous than *Ammospermophilus leucurus*. During the mating season, two Mohave ground squirrels may be found close together, but more than two have not been observed within a radius of 0.4 km (Burt, 1936).

*Spermophilus tereticaudus* may be expanding its range at the expense of the parapatric *S. mohavensis*. The current species-contact boundary is remarkably coincident with the Pleistocene full-pluvial network of lakes and rivers in the region. The selection of

gravelly soils by *S. mohavensis* and sandy soils by *S. tereticaudus* is apparent at sympatric sites, such as Coyote Dry Lake, but both soil types are found throughout the Mojave Desert (Hafner, 1992).

The range of *S. mohavensis* lies completely within the distribution of *Ammospermophilus leucurus*. *A. leucurus* does not aestivate or hibernate, but remains active aboveground all year. *S. mohavensis* stays underground and presumably dormant, except during the most favorable part of the year; spring and early summer. Thus, in the area of sympatry during the more demanding and difficult parts of the year (late summer, autumn, and early winter), only *A. leucurus* is active (Bartholomew and Hudson, 1960). *S. mohavensis* also occurs in the same habitat as *Spermophilus beecheyi* (Burt, 1936), *Perognathus longimembris*, *Dipodomys deserti*, *D. merriami*, *D. microps*, *Peromyscus eremicus*, *P. maniculatus*, *Onychomys torridus*, *Neotoma lepida* (E. V. Wessman, in litt.), and *Perognathus parvus* (Hafner, 1992).

Natural predators of the Mohave ground squirrel probably include common diurnal avian and mammalian predators of the Mojave Desert. These are the golden eagle (*Aquila chrysaetos*), prairie falcon (*Falco mexicanus*), red-tailed hawk (*Buteo jamaicensis*), badger (*Taxidea taxus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), and Mojave rattlesnake (*Crotalus scutulatus*—J. R. Gustafson, in litt.). Although tested repeatedly, there is no laboratory-confirmed evidence that plague (*Yersinia pestis*) occurs in *S. mohavensis* (Nelson, 1980; Wayson, 1947). No external or internal parasites are known.

*Spermophilus mohavensis* has been captured in oat-baited rat-traps set beneath creosotebushes on gravelly soil (Grinnell and Dixon, 1918), in 7.6 by 8.9 by 22.9-cm Sherman live traps baited with rolled oats and set in the shade of shrubs (E. V. Wessman, in litt.; Zembal and Gall, 1980), and in open wire-mesh traps, baited with canned apricots, peaches, or plums. The open wire-mesh traps were placed upwind within 3 m of feeding squirrels (Recht, 1977). The Mohave ground squirrel also has been captured in Sherman live traps using a mixture of peanut butter, shredded coconut, and coconut extract as bait, and by using birdseed, bacon, or oranges as bait (D. F. Hoyt, in litt.).

The range of *S. mohavensis* borders the populous and rapidly expanding Los Angeles metropolitan area (Hafner, 1992). The major cause of decline in populations of the Mohave ground squirrel has been destruction of its habitat by humans for the purpose of development for urban, suburban, agricultural, military, or other use. Because virtually any plant community in its range provides habitat, destruction or damage to any plant community results in loss of habitat for this species (J. R. Gustafson, in litt.). *S. mohavensis* also may be associated with alfalfa fields where it seems dependent on the fields for food, and could be exterminated easily by rodent-control programs (D. F. Hoyt, in litt.).

Due to limited distribution, encroaching urban development in its range, and suspected population declines, *S. mohavensis* is listed as a threatened species by the California Fish and Game Commission (J. R. Gustafson, in litt.; Hafner, 1992). The Mohave ground squirrel has been listed as a category-two species by the United States Department of the Interior, Fish and Wildlife Service (Drewry, 1991).

**BEHAVIOR.** *Spermophilus mohavensis* is placid, docile, sedentary, and can be approached easily in the wild. Except during the breeding season, the Mohave ground squirrel is solitary. In captivity, *S. mohavensis* is so intolerant of conspecifics that it must be housed individually (Bartholomew and Hudson, 1960, 1961).

The Mohave ground squirrel is an aestivator that emerges earlier in the southern part of the Mojave Desert than farther north (Jameson and Peeters, 1988). *S. mohavensis* emerges from dormancy in midwinter, breeds, and gives birth before midspring. It takes advantage of green vegetation available in spring and early summer, becomes fat by the beginning of hot weather, and aestivates underground until the following January or February. Five to 6 months of activity are followed by 6–7 months of aestivation. The succulent greens it seems to prefer cannot be stored; hence, fat provides energy during dormancy (Bartholomew and Hudson, 1960; Egoscue, 1975).

*Spermophilus mohavensis* is active aboveground during the day. It emerges from its burrow near sunrise and forages throughout the day, even when air temperature may reach  $\geq 43^{\circ}\text{C}$  and soil temperature may be  $>66^{\circ}\text{C}$  (Bartholomew and Hudson, 1961). In cloudy weather, the Mohave ground squirrel is less active than on

clear, warm days. On 5 April, only two *S. mohavensis* were observed in 6 h on a cloudy day; it was more numerous on previous clear days (Burt, 1936).

The Mohave ground squirrel typically emerges from its burrow in the morning and sits just outside the entrance to bask in direct sunlight. It sits on its rump, hind limbs flexed, with the paws of the hind feet ventrad. The palmar surfaces of the forefeet are ventrad and forelimbs are extended, raising the body to ca.  $30^{\circ}$  angle with the substrate. The head is held horizontally and the tail lies flat on the substrate (either straight or curved to the side). Later in the basking sequence, the sitting posture may be replaced by a prone posture, with forelimbs extended forward and hind limbs flexed as in the sitting posture. The head is held horizontally between extended forelimbs, either above or resting on the substrate. Throughout the basking sequence, there are changes in orientation with respect to the sun. These positional changes alternately direct one side, the back, or the other side toward the sun. The amount of time in each position is about equal. When a Mohave ground squirrel emerges from its burrow to begin basking, pelage on the side, back, and rump is fully piloerected. This piloerection reveals the darkly pigmented skin underneath the pelage and gives the squirrel a fuzzy appearance. At the end of the basking sequence, the pelage is not erect; it appears glossy and much paler. As the squirrel presents one side toward the sun, the pelage is piloerected on that side, but not on the other side. The boundary between the two sides forms a midsagittal line down the back of the basking squirrel (Recht, 1977).

Morning and afternoon patterns of activity by *S. mohavensis* are similar, but differ from activity at midday. When the morning sand and air temperatures in the sun reach  $46.5$  and  $35.5^{\circ}\text{C}$ , respectively, a sharp decrease of activity in the sun occurs. This decrease continues simultaneously with an increase of activity in shade. Sand and air-shade temperatures are considerably lower than their corresponding sun temperatures ( $33$  and  $29^{\circ}\text{C}$ , respectively). In morning, the transition from activities in sun to those in shade involves an increasing amount of time spent in shade until all activity is in shade. Shade in bushes is  $2^{\circ}\text{C}$  cooler than in open shade, and burrows are even cooler. In afternoon, there is an increase in activity in the sun as daily cooling takes place. By performing daily activities in the sun, shade, bushes, or in burrows, *S. mohavensis* can remain active throughout the hot summer day and remain within its thermoneutral zone. Apparently, there also is a seasonal change in foraging behavior. July appears to be a transition period between when Mohave ground squirrels crawl inside bushes and feed and when they emerge from burrows, run out into the open sun, forage briefly, and return with a mouthful of food. They pause in the shade of the burrow entrance to eat the food before entering the burrow. As temperatures increase in August, activity is more concentrated in shaded areas and in the burrow (Recht, 1977).

Mohave ground squirrels will cool in the shade after they have been active in direct sunlight. Typically, squirrels run from direct sunlight into the shade of nearby bushes. Initially, they lay prone with forelimbs extended forward (palmar surface ventrad). The head usually is held horizontally just above the extended forelimbs. After briefly lying prone, squirrels will rise to a partially sitting posture and briefly dig in the soil with the forefeet to create a small depression. They then push the head through this depression, with the soil riding up on the lateral surface of the muzzle. The neck is pushed through this depression and the chest region comes to rest in it. Forefeet are extended forward (palmar surface ventrad), and the head is rested on the soil between them. The hind limbs sometimes remain flexed, but usually they are extended posteriad (plantar surface dorsad). The tail is flat on the substrate and usually is directed posteriad, but occasionally is curved laterally. The squirrels usually reposition themselves once or twice during a cooling bout by arising to a partial-sitting posture, redigging the depression, and lying in it again (Recht, 1977).

*Spermophilus mohavensis* rarely runs for any great distance, as usually it is near the entrance to a burrow. When danger threatens, it enters a burrow and almost immediately sticks its head out again for observations. Instead of entering the burrow, the Mohave ground squirrel sometimes crouches low on its belly and is relatively inconspicuous against the sandy background, which closely matches its pelage color (Burt, 1936).

When running slowly from bush to bush, the tail is carried over the back in the same manner as is characteristic of *A. leucurus*, but the white underside of the tail is not as conspicuous as it is in *Ammospermophilus*. *S. mohavensis* does not twitch its tail as does



*Ammospermophilus*. If startled while feeding, the Mohave ground squirrel rises upon its hind feet to gain a better view of the surrounding territory. When sitting in this position, the forelegs hang limply along the ventrolateral part of the body (Burt, 1936).

In Inyo Co., the Mohave ground squirrel often is conspicuous when engaged in harvesting seeds of Joshua trees. It may be engaged in this harvest for hours at a time. Individuals were observed perched high in the tops of Joshua trees almost continuously during daylight hours, from ca. 3 h after sunrise to 1 h before sunset. One *S. mohavensis* was observed for 4 h, during which time it worked on a clump of fruits and made frequent journeys down the tree to a burrow located at the base of the trunk. These trips to the burrow occurred at ca. 15–20-min intervals, and the animal remained in the burrow for an average of 4 min each time. This behavior was observed for several other Mohave ground squirrels, and clearly suggested hoarding. Two were observed carrying seeds into burrows (Zemal and Gall, 1980).

There is a significantly higher level of aggression in *S. mohavensis*, both intraspecifically and interspecifically, than in *A. leucurus* (Adest, 1972; Zemal and Gall, 1980). In Inyo Co., only one *S. mohavensis* was observed at a time in a single Joshua tree, whereas as many as seven *A. leucurus* were observed together in the same tree. *A. leucurus* was subordinate to *S. mohavensis* in each of 27 agonistic encounters between individuals of the two species during confrontations in Joshua trees. Individuals of both species frequently were observed in the same tree; aggression occurred invariably except in large trees with two or more widely spaced fruit clusters. In one small Joshua tree possessing one trunk and one cluster of fruits, one *A. leucurus* managed to feed only while the *S. mohavensis* using this tree was in a burrow located at the base of the tree. The sight of *S. mohavensis* coming up the tree elicited a hasty retreat down the tree by *A. leucurus*. The same *A. leucurus* attempted to climb the tree many times, appearing unaware that the *S. mohavensis* was perched at the fruit cluster. In 102 min, *A. leucurus* was displaced 18 times (Zemal and Gall, 1980).

The nocturnal burrow sometimes is far from the area in which a Mohave ground squirrel spends the day feeding and nesting. One individual traveled ca. 400 m between its nocturnal burrow and the area in which it usually was found during the day. This area had a relatively dense stand of Joshua trees, and the Mohave ground squirrel may have traveled this relatively long distance to feed on fruits of Joshua trees. Other *S. mohavensis* moved 200–250 m from their nocturnal burrows to daily feeding areas (J. R. Gustafson, in litt.; P. Leitner et al., in litt.). On 12 April, a female was observed from 0900–1530 h. During the 6.5 h of observation, she entered four burrow systems, remaining a few minutes in each. The last burrow entered had been plugged partially and it was necessary for her to remove some loose earth from the entrance. As she entered the burrow, she kicked back loose earth with her hind feet and partially plugged the opening from within (Burt, 1936).

*Spermophilus mohavensis* uses specific runways to commute to and from foraging sites. The runways are paths of barren sand that branch across the habitat in an arterial network, connecting areas of frequent use. Activities of Mohave ground squirrels took place within 30 cm on either side of these runways (Recht, 1977).

When foraging, *S. mohavensis* moves about slowly and cautiously among the vegetation, sampling a bite of food here and there. During early spring, food is composed almost entirely of tender green vegetation that is just beginning growth. At 0900 h, a female was feeding around a small patch of green vegetation, where she remained for 50 min. Apparently, she was undisturbed by a human observer in an automobile 5 m away. While feeding, she crawled along among the vegetation, bit off a green stem or leaf, held it in her forefeet, and ate it while sitting partially erect. She then would crawl farther and repeat the process. Most of the time she was relatively inconspicuous. While searching for food in this manner, her tail was almost constantly moving slowly from side to side. When she sat, her tail was brought against her back. She fed almost continuously for 50 min, but may have been feeding prior to these observations. The only interruptions in her feeding were when she stopped to scratch herself or to investigate noises. At 0950 h, she started away, running slowly for short distances and stopping often to investigate a potential food plant. She entered a burrow 10 min later, which was ca. 95 m in a straight line from where she was first observed, but she travelled a rather zigzag course. After 10 min in the burrow, she appeared again and began searching for food, occasionally sampling food items. She spent much of the time exploring and climbing over fallen trunks of a dead Joshua tree. She climbed into small

bushes five or six times to eat green buds, but never ascended >30 cm from the ground. During this time (2.5 h), she covered an area within a radius of ca. 23 m and entered three more burrows. At 1530 h, she was still foraging (Burt, 1936).

A female Mohave ground squirrel darted into a burrow as she was approached by a human observer, but in ca. 2 min she emerged and started feeding on green vegetation. When approached again, she went into another burrow, emerged again, washed her pelage, and renewed her feeding activities. When examined closely, the cheekpouches were filled with finely chewed green vegetation. During 45 min, her activities were confined to an area 9 m in diameter. At no time was she >1.5 m from a burrow entrance. One of the burrows entered had the general appearance of a kangaroo rat (*Dipodomys*) burrow. This female was near a highway, and whenever an automobile passed, she crouched for a moment, then continued foraging. However, if a motorcycle passed or a horn was heard, the Mohave ground squirrel immediately reacted by twitching, and then cautiously looked in the direction of the sound (Burt, 1936).

One *S. mohavensis* was feeding near its burrow; at short intervals, it stopped feeding and scratched various parts of its body. The squirrel spent 5 min scratching itself and washing its pelage. Washing of the pelage is accomplished in a manner similar to that used by domestic cats. After thoroughly washing its face and underparts, the Mohave ground squirrel resumed feeding on green vegetation around its burrow (Burt, 1936).

Home ranges of *S. mohavensis* are relatively stable until late June. Until this time, home ranges are separate or nearly so, and few agonistic encounters occur. Smaller home ranges are occupied by dominant animals, usually adults. Larger home ranges, at least twice as large as those occupied by dominant animals, are occupied by subordinate squirrels, usually juveniles. Home ranges of individuals may shift during the activity season to allow access to areas with adequate food. Because the home range of an individual is an arterial network of pathways, construction of a typical polygonal home range does not accurately represent the area actually used. Home ranges of juveniles form a cluster around the home range of an adult. Within 2 days after adults enter aestivation, juveniles take possession of the former home ranges of adults (Recht, 1977).

Adult Mohave ground squirrels behave agonistically to juveniles, excluding them from those portions of habitat with densest vegetation. Juveniles apparently must spend more energy in foraging than adults (Recht, 1977). In captivity, the mother makes no attempt to defend the young (Pengelley, 1966).

In captivity, *S. mohavensis* is extremely lethargic, spends much of its time asleep or torpid, and becomes extremely fat, but tends to lose some mass during spring. In captivity, it is active and shows no signs of dormancy from March to August, but during the remainder of the year the Mohave ground squirrel is intermittently torpid at room temperature despite the continuous availability of food and water, and despite frequent disturbances associated with maintenance of other experimental animals in the same room. In the laboratory during late summer, autumn, and winter, the Mohave ground squirrel assumes a sleeping position with feet and head tucked under the body as it enters torpor. At body temperatures as low as 10°C, *S. mohavensis* responds to touch by withdrawal. No vocalization can be elicited at body temperatures <21°C, but vocalization occurs in response to all disturbances at body temperatures >25°C. At body temperatures <15°C, the Mohave ground squirrel is unable to right itself when placed on its back. At a body temperature of 20°C, it is capable of poorly coordinated crawling and slow, jerky walking. At this temperature, *S. mohavensis* often attempts to dig. At 27–28°C, its walking and digging activities appear normal and coordinated. By the time body temperature reaches 32–33°C, behavior appears normal (Bartholomew and Hudson, 1960).

The call of *S. mohavensis* may consist of a low whistle, uttered at long intervals (Elliot, 1904), a shrill whistle, or a high-pitched peep with a slight rasping effect; similar to a horned lark (*Eremophila alpestris*), but not as smooth (Burt, 1936). The Mohave ground squirrel has been kept as a pet; when handled, it chitters and rarely bites (Ross, 1930).

**GENETICS.** The karyotype has a diploid number of 38 chromosomes and a fundamental number of 70 chromosomal arms. The X chromosome is metacentric and the Y chromosome is a small acrocentric (Fig. 4). Based on 24 genic loci, *S. mohavensis* has a mean proportion of loci heterozygous per individual of 0.033, and the proportion of loci polymorphic per population is 0.250 (Hafner and Yates, 1983).

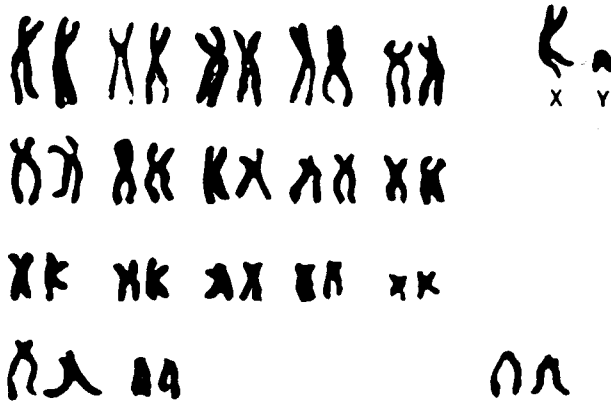


FIG. 4. Karyotype of a male *Spermophilus mohavensis* from ca. 15 km NNE Johannesburg, San Bernardino Co., California (D. J. Hafner, pers. comm.; Hafner and Yates, 1983).

**REMARKS.** *Spermophilus* is from the Greek *sperma* and *philos* meaning seed loving (Jaeger, 1955). The specific epithet *mohavensis* refers to its range in the Mojave Desert, California. *S. mohavensis* also has been referred to as the Mohave Desert spermophile (Elliot, 1905) and Mohave Desert ground squirrel (Grinnell, 1933).

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T. L. BEST, DEPARTMENT OF ZOOLOGY AND WILDLIFE SCIENCE AND ALABAMA AGRICULTURAL EXPERIMENT STATION, 331 FUNCHESS HALL, AUBURN UNIVERSITY, ALABAMA 36849-5414.