

Ammospermophilus leucurus. By Mark C. Belk and H. Duane Smith

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Ammospermophilus leucurus (Merriam, 1889)

White-tailed Antelope Squirrel

Tamias leucurus Merriam, 1889:20. Type locality "San Gorgonio Pass [Riverside Co.], California."

Ammospermophilus leucurus: Mearns, 1907:299. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Tribe Marmotini, Subtribe Ammospermophilina (Hafner, 1984). A key to the five species of *Ammospermophilus* is presented in Best et al. (1990). Nine subspecies of *A. leucurus* are recognized (Hall, 1981) as follows:

- A. l. canfieldae* Huey, 1929:243. Type locality "Punta Prieta, Lower [Baja] California."
- A. l. cinnamomeus* (Merriam, 1890:52). Type locality "Echo Cliffs, Painted Desert [Coconino Co.], Arizona."
- A. l. escalante* (Hansen, 1955:274). Type locality "2 mi. SE Escalante, 5400 ft., Garfield Co., Utah."
- A. l. extimus* Nelson and Goldman, 1929:281. Type locality "Sacaton, 15 mi. N Cape San Lucas, Lower [Baja] California."
- A. l. leucurus* (Merriam, 1889:20), see above.
- A. l. notom* (Hansen, 1955:274). Type locality "Notom, Wayne Co., Utah."
- A. l. peninsulae* (J. A. Allen, 1893:197). Type locality "San Telmo, Lower [Baja] California."
- A. l. pennipes* Howell, 1931:162. Type locality "Grand Junction, Colorado."
- A. l. tersus* Goldman, 1929:435. Type locality "lower end Prospect Valley, Grand Canyon, Hualpai Indian Reservation, Arizona, altitude 4500 ft."

DIAGNOSIS. Diagnostic characteristics of *A. leucurus* include white median on underside of tail with only one black subterminal band, and presence of fully formed anterior premolars. *A. leucurus* differs from *A. nelsoni* in having narrower zygomatic arches and smaller auditory bullae (Hall, 1981).

GENERAL CHARACTERS. Like other members of the genus, *A. leucurus* (Fig. 1) is a medium-sized ground squirrel with short, rounded ears and relatively long legs compared to other terrestrial sciurids (Bryant, 1945). It has 10 mammae and internal cheek pouches used to carry food items (Hall, 1946). The dental formula is $i\ 1/1, c\ 0/0, p\ 2/1, m\ 3/3$, total 22 (Burt and Groszheider, 1964). Means and ranges (in parentheses) of measurements (in mm) for 10 adult *A. l. leucurus* (five males and five females) from San Gorgonio Pass, Riverside Co., California (type locality) are: total length, 216.3 (211-223); length of tail vertebrae, 67.5 (63-71); length of hind foot, 38.3 (37-40); length of ear from notch, 9 (8.5-10; Howell, 1938). Means and ranges (in parentheses) of cranial measurements (in mm) of 11 adults (eight males and three females) from the same location are: greatest length of cranium, 38.8 (37.3-40); palatilar length, 17.6 (16.8-18.5); zygomatic breadth, 22.6 (21.7-23.5); cranial breadth, 18.4 (17.8-19.3); interorbital breadth, 9.7 (8.8-10.4); postorbital constriction, 13.9 (13.1-14.9); length of nasals, 11.4 (10.7-12); length of maxillary toothrow, 6.7 (6.1-7; Howell, 1938).

Males average slightly larger than females in total length and weight. Means (ranges in parentheses) of measurements (in mm) for six male and six female *A. l. leucurus*, respectively, collected near Searchlight, Clarke Co., Nevada, are: total length, 212 (188-220), 210 (202-216); length of tail, 56 (42-71), 61 (55-66); length of hindfoot, 36 (35-38), 37 (36-38); weight (in g), 111.1 (103.7-116.8), 100.6 (96.2-104.5; Hall, 1946). Average size of races generally increases toward the east and south of the species' range, grading from the smaller *A. l. leucurus* and *A. l. tersus* to the more

robust *A. l. cinnamomeus* and *A. l. pennipes*. Color of the dorsal pelage also varies from grayish to brown to cinnamon among subspecies (Howell, 1938). Winter pelage typically is darker and grayer in all subspecies. Underparts are creamy white, and there are two white stripes on the back (extending from shoulder to rump). The tail is dark above, whitish below, and with one subterminal black band (Hall, 1981; Hoffmeister, 1986). The skull (Fig. 2) has long, well-inflated bullae, and a relatively flattened braincase.

DISTRIBUTION. *Ammospermophilus leucurus* is a conspicuous desert species characteristic of the Sonoran life zone, but occasionally is found in the lower transition life zone (Hall, 1981; Howell, 1938). Its range (Fig. 3) extends from southeastern Oregon and southwestern Idaho through most of Utah and Nevada (excepting the northeastern one-fourth of Utah), includes western Colorado, northwestern New Mexico, northern Arizona, interior, central, and southern California, and extends along the length of Baja California (Hall, 1981; O'Farrell and Clark, 1984). Two specimens of *A. leucurus* were collected from Isla San Marcos, Baja California Sur, Mexico (D. J. Hafner, pers. comm.).

FOSSIL RECORD. Earliest fossils of the genus *Ammospermophilus* are of late Miocene-early Pliocene age (Savage and Russell, 1983). James (1963) described *A. fossilis* from Clarendonian deposits in Cayuma Valley, California, and concluded the genus probably originated in early Miocene. Based on "aberrant" features of the dentition, he reasoned that *A. fossilis* was not in the direct line leading to present species. Gustafson (1978) described *A. hanfordi* from early Pliocene deposits in Washington, noting it was the largest *Ammospermophilus* species recorded, but it appears similar to present species in form. Miller (1980) described *A. jeffriesi* of middle-late Pliocene age from the cape region, Baja California Sur, Mexico. Zakrzewski (1969) tentatively referred a partial mandible of late Pliocene age to *Ammospermophilus*, and noted its similarity to *A. leucurus*. Skull fragments of early Pliocene age from the Juntura Basin, Oregon, originally referred to *Citellus juntuensis* by Shotwell et al. (1963), were later tentatively referred to as *Ammospermophilus* by Black (1963) based on dental characters. *A. leucurus* is known in the fossil record from Centipede Cave, Texas (outside the current range) and from Crystal Ball Cave, Utah, both late Pleistocene in age (Heaton, 1985; Kurtén and Anderson, 1980; Savage and Russell, 1983), and from Holocene sites in Arizona (Hoffmeister, 1986; Lindsay and Tessman, 1974; Mead and Phillips, 1981), Nevada, and California (Goodwin and Reynolds, 1989; Harris, 1985).

FORM AND FUNCTION. *Ammospermophilus leucurus* molts twice a year (Hoffmeister, 1986; Howell, 1938), excepting the tail hair, which appears to molt only during autumn (Hall, 1946). Timing of the molt ranges from April to July in spring and August to November in autumn, varying according to geographic location and altitude (Howell, 1938). Summer pelage is shorter and coarser than winter pelage (Hoffmeister, 1986).

Bacula of *Ammospermophilus leucurus* are small and distinctly shaped (Bryant, 1945; Burt, 1960). Measurements (in mm) of bacula from two *A. leucurus* collected in Nevada are: length, 2.0, 2.1; width of base, 1.0, 1.0; width of distal end, 1.6, 1.7 (Burt, 1960).

The white-tailed antelope squirrel discriminates some colors; it is sensitive to blue wavelengths, less so to yellow, but apparently has no ability to discriminate green and red areas of the spectrum (Crescitelli and Pollock, 1965, 1972). Cone receptors predominate in the retina, but, as in some other ground-dwelling sciurids, a few rods are present (Fisher et al., 1976).

Ammospermophilus leucurus is diurnally active, and does not hibernate or estivate (Hall, 1981; Hudson, 1962). Its ability to thrive in a hot, dry, desert environment can be attributed to inter-related physiological, ecological, and behavioral adjustments pro-



FIG. 1. Photograph of adult *Ammospermophilus leucurus*, from Clear Lake, Millard Co., Utah.

moting water conservation and allowing thermoregulation under extreme conditions (Bartholomew and Dawson, 1968; Hudson, 1962).

Unlike many heteromyid rodents, *A. leucurus* cannot survive indefinitely without free water; death from water deprivation occurs after 8–35 days (Maxson and Morton, 1974). Water turnover at 20–25%/day is typical of desert-dwelling sciurids, but is greater than in heteromyid rodents (Yousef et al., 1974). The white-tailed antelope squirrel can withstand dehydration of 20–25% of field weight, and it regains weight quickly when water becomes available (Bartholomew and Hudson, 1959). During periods of negative water balance, it conserves plasma volume better than non-desert sciurids (Hartman and Morton, 1973). Lung morphology characterized by relatively few goblet cells appears to aid in decreasing water loss from pulmonary tissues (Babero et al., 1973). Under extreme heat stress, *A. leucurus* salivates profusely to avoid heat prostration; this behavior, commonly seen in animals confined in traps, probably is rare under normal conditions (Hudson, 1962).

The white-tailed antelope squirrel has efficient kidneys and can produce urine with 12.2 times greater osmolarity than plasma, comparing favorably with other desert rodents. It can maintain body weight with a daily water ration as little as 2–5% of body weight (Hudson, 1962; Maxson and Morton, 1974). This minimum water requirement fluctuates seasonally in accordance with available water in the environment (Karasov, 1983a; Maxson and Morton, 1974). Captive squirrels readily drink saline solutions, and can maintain body weight on concentrations up to 0.8 M (about 1.4 times as concentrated as sea water; Bartholomew and Hudson, 1959).

Active body temperature in *A. leucurus* is 38°C, but it is labile and fluctuates with environmental temperature (Chappell and Bartholomew, 1981a, 1981b). Rhythmic fluctuations in body temperature of the white-tailed antelope squirrel coincide with periods of activity (Kramm, 1972). It tolerates hyperthermia well, allowing body temperatures up to 43.6°C with no ill effects. This allows it to store heat over a longer period while active above ground (Chappell and Bartholomew, 1981a, 1981b). During winter, it minimizes energy cost by decreasing body temperature during the night to 31–33°C (Chappell and Bartholomew, 1981b; Karasov, 1983b). *A. leucurus* tolerates cold poorly. If exposed to low temperatures, it sometimes becomes torpid as a last resort, but it cannot arouse from torpor unless ambient temperature rises above 20°C (Kramm, 1972). When arousing from torpor it does not reduce posterior blood flow by differential vasoconstriction as hibernating species do, although, paradoxically, isolated hearts of *A. leucurus* behave the same as hearts of hibernators, continuing to beat regularly at temperatures as low as 0–2°C (Lyman, 1964).

The white-tailed antelope squirrel exhibits a series of integument modifications that possibly aid in reducing water loss and blocking solar radiation. These include increased thickness of the epidermis, less dense connective tissue, greater cell content in the dermis, and increased melanization (Quay, 1964).

Daily energy expenditure of free living *A. leucurus* (measured with doubly-labeled water) varies from 1,340 kilojoules $\text{kg}^{-1} \text{day}^{-1}$

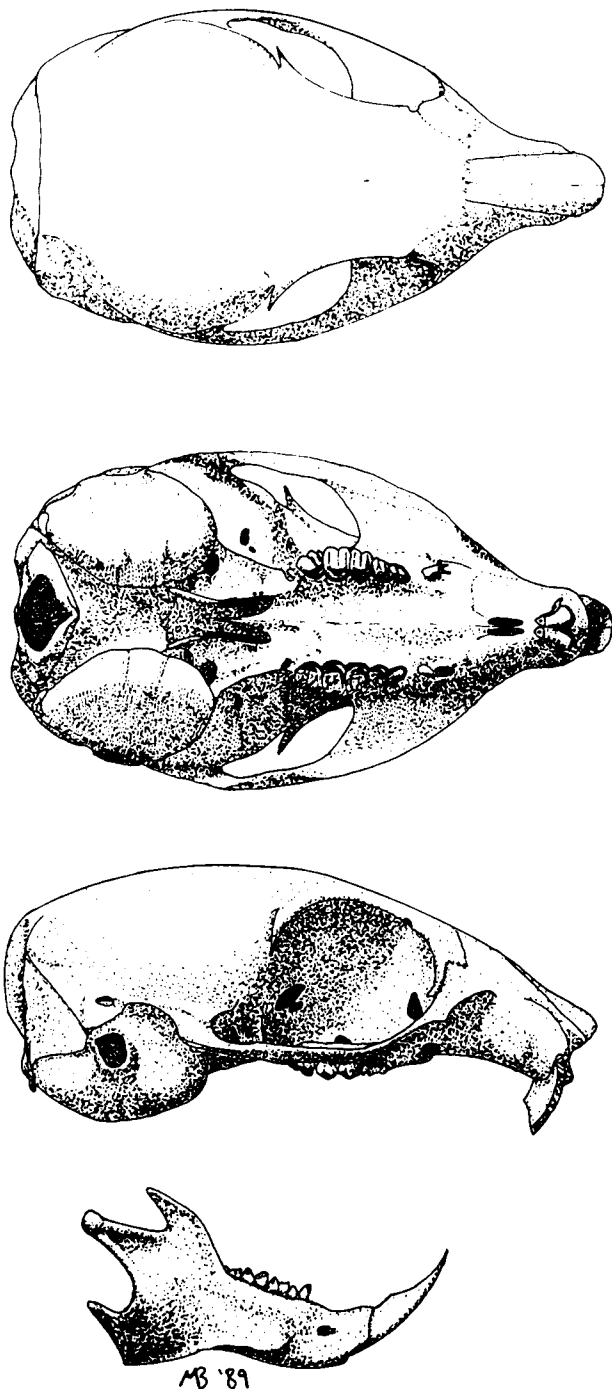


FIG. 2. Dorsal, ventral, and lateral views of the skull and lateral views of the mandible of an adult male *Ammospermophilus leucurus* (Brigham Young University, Monte L. Bean Museum 4122) from Nevada Atomic Test Site, Nye Co., Nevada. Occipitonasal length is 37.5 mm.

in April to 970 kilojoules $\text{kg}^{-1} \text{day}^{-1}$ in October; resting metabolic rate during daytime also varies seasonally from 22.1 joules $\text{g}^{-1} \text{h}^{-1}$ in August to 19.1 joules $\text{g}^{-1} \text{h}^{-1}$ in January, but most of the variance in daily energy expenditure is attributable to different thermoregulatory costs among seasons. Cost of activity is estimated at about 50% of total energy expenditure (Karasov, 1981).

Basal metabolic rate of *A. leucurus* at 30°C is about 0.8 ml $\text{O}_2 \text{g}^{-1} \text{h}^{-1}$ (Hudson and Deavers, 1976); change in metabolic rate with temperature can be described by the following: metabolic rate (in ml $\text{O}_2 \text{g}^{-1} \text{h}^{-1}$) = $3.49 + (-0.202)t - 20.84$, where t is temperature in °C (Dawson, 1955). Typical of many desert-dwelling sciurids, basal metabolic rate is lower than predicted based on body

size. Thyroidectomy decreases basal metabolic rate only slightly (13–15%), indicating a relatively inactive thyroid (Hudson and Deavers, 1976). Levels of plasma thyroxin (Scott et al., 1976; Yousef et al., 1984) and plasma corticosterone (Vanjonack et al., 1975) also are lower in *A. leucurus* than in non-desert sciurids, but thyroid activity is not decreased as much as in another desert-dwelling sciurid, *Spermophilus tereticaudus* (Yousef, 1975; Yousef et al., 1974). Decreased metabolic rate may be adaptive in hot desert environments (Hudson and Deavers, 1976). Physiological changes in liver and kidney of heat- and cold-acclimated *A. leucurus* are similar to other rodents; that is, there is increased size and function with cold acclimation and decreased size and function in heat acclimated animals (Balcer and Chaffee, 1982, 1984; Balcer et al., 1978). In contrast to hibernating sciurids, *A. leucurus* shows little change in mass of brown oxidative tissue or activity of oxidative enzymes in response to heat or cold acclimation (Balcer and Chaffee, 1981). Heat acclimation increases intestinal serosal transport, explaining how body weight can be maintained even though basal metabolism is decreased (Yousef et al., 1984). Thermal sensitivity of gut contractions in *A. leucurus* is lower than in many small mammals (Studier et al., 1977).

Hemoglobin concentration varies between 15.5 g/100 ml in winter and 13.4 g/100 ml in summer, apparently in response to environmental temperatures (Lee and Brown, 1970). Bile acid composition is similar to other desert rodents; cholic acid is most common (75%) followed by chenodeoxycholic acid (19%) and deoxycholic acid (6%; Yousef et al., 1973). Whole body content of ash and fat averages 15.0 and 12.3%, respectively (Weiner et al., 1977). Dry-weight caloric density for *A. leucurus* is 4.97 ± 0.08 kcal/g and live-weight caloric density is 1.2–1.3 kcal/g based on 75% water composition (Kaufman et al., 1975).

ONTOGENY AND REPRODUCTION. *Ammospermophilus leucurus* in southern Nevada breeds from February to June with a peak in February and March (Bradley, 1967; Bradley and Mauer, 1973; Hall, 1946; Hoffmeister, 1986; Smith and Jorgensen, 1975). However, in California there is a protracted mating period with nearly all mating occurring during the first 2 weeks of March (Kenagy and Bartholomew, 1985). The annual reproductive cycle is relatively insensitive to photoperiodic changes; rather ovarian and testicular cycles are controlled by a strong endogenous rhythm (Kenagy, 1978, 1981; Kenagy and Bartholomew, 1979). In California, mass of testes begins to increase in early November with expansion of the seminiferous tubules. By December the germinal epithelium has developed and spermatogenesis begins. Spermatogenesis and testis size peak in February (representing a 35-fold increase in size). Size of epididymides and seminal vesicles peaks 1 month later at the height of the breeding season. After mating, the testes regress rapidly. Mature sperm are present for about 5 months, but sex-accessory glands remain undeveloped for most of this time (Kenagy and Bartholomew, 1985). Mean time between annual peaks in testicular size was 423 days for six individuals kept in 12L:12D conditions, and 358 days for four individuals kept in constant light conditions (Kenagy, 1981). Uterine and ovarian mass and activity follows a clear annual cycle, peaking during the breeding season. Fat tissue associated with the uterus and ovaries increases for several months prior to mating, then decreases to a minimum during pregnancy (Kenagy and Bartholomew, 1985).

In California, *A. leucurus* has a synchronous and uniform reproductive pattern. Nearly 100% of males and females are reproductively active every year. Environmental fluctuations (or experimentally-increased food supply) have no effect on timing of reproduction, but litter size is adjusted by as much as two young per litter according to annual environmental productivity. *A. leucurus* allocates energy to reproduction in small amounts over several months. Thus, pulses of primary production are averaged over a relatively long period and reproduction occurs during early spring when, on average, available energy is at a maximum (Kenagy and Bartholomew, 1985).

Both male and female *A. leucurus* reproduce first at 1 year of age (Kenagy and Bartholomew, 1985). Probably, only one relatively large litter per year is produced (Kenagy, 1981; Kenagy and Bartholomew, 1985); however, Bailey (1931:96) observed "half-grown young" in late August, and suggested that a second litter is sometimes produced in New Mexico. Litter sizes range from 5 to 14, and average about eight (Grinnell and Dixon, 1919; Hall, 1946; Howell, 1938; Kenagy, 1981; Kenagy and Bartholomew, 1985; Maxwell and Morton, 1975; Pengelly, 1966; Smith and Jorgensen,

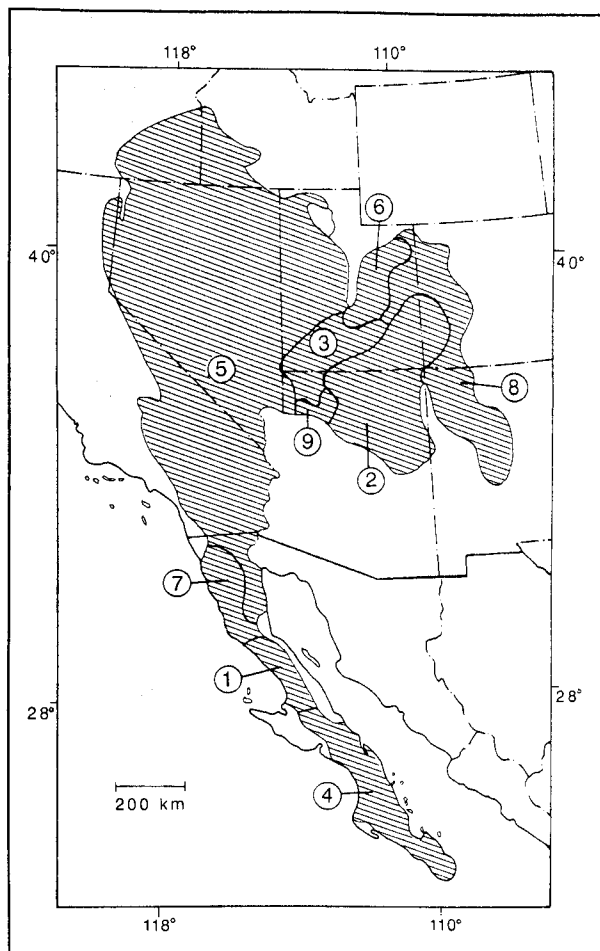


FIG. 3. Distribution of *Ammospermophilus leucurus* (modified from Hall, 1981, and O'Farrell and Clark, 1984): 1, *A. l. canfieldae*; 2, *A. l. cinnamomeus*; 3, *A. l. escalante*; 4, *A. l. extimus*; 5, *A. l. leucurus*; 6, *A. l. notom*; 7, *A. l. peninsulae*; 8, *A. l. pennipes*; 9, *A. l. tersus*.

1975). There were two incidences of embryo resorption (one embryo per litter) out of 14 litters examined in California (Kenagy and Bartholomew, 1985). Gestation lasts 30–35 days in Nevada (Smith and Jorgensen, 1975) and California (Kenagy and Bartholomew, 1985). Maxwell and Morton (1975) reported average birth weight as 2.9 g (range, 2.0–3.6 g), and Pengelly (1966) reported birth weight as 3–4 g (in four litters) and a sex ratio at birth of 1:1.1 (males to females). Both studies were conducted in California.

Ammospermophilus leucurus is born proportionately larger (percent adult weight), but grows and develops slower than many other terrestrial sciurids including *Spermophilus beldingi*, *S. lateralis*, *S. tereticaudus*, and *S. mohavensis* (Maxwell and Morton, 1975; Pengelly, 1966). The growth-rate constant for *A. leucurus* is 0.054 compared to 0.071 for *S. beldingi*, which occupies high elevations. Correspondingly, young *A. leucurus* do not acquire complete thermoregulatory capability until 45 days after birth compared to 24 days in *S. beldingi*. Shivering occurs first at day 25 and adult pelage is present by 35 days after birth (Maxwell and Morton, 1975). The developmental sequence of four litters from California was as follows: pigmentation, 9 days; lower incisor eruption, 19–25 days; upper incisor eruption, 29–30 days; ears open, 24–32 days; eyes open, 34–36 days; weaned (minimum), 65 days (Pengelly, 1966). Young first appear on the surface in mid-May 1–2 weeks before weaning (Kenagy and Bartholomew, 1985).

Reproductive investment for a litter at birth, measured as mass of young produced, averages 24% of adult female mass; at emergence, investment increases to about 300% of maternal mass. This is a proportionately greater investment than that made by heteromyid rodents (Kenagy and Bartholomew, 1985). Since *A. leucurus* does not hibernate, estivate, or store body fat, growth of young would

not be constrained by these behaviors; that is, there is no need for rapid growth and fat deposition in preparation for hibernation (Maxwell and Morton, 1975). Rather, relatively slow growth and long dependence on maternal milk may be advantageous to young in arid environments (Pengelly, 1966).

ECOLOGY. *Ammospermophilus leucurus* is a conspicuous inhabitant of desert habitats from valley floors to the juniper belt (Hoffmeister, 1986; Jorgensen and Hayward, 1965). It is common in shrubby areas with sandy to rocky soil (Armstrong, 1979; Robey et al., 1987). Dominant shrubs of habitat occupied by white-tailed antelope squirrels in Utah and Nevada include sagebrush (*Artemisia*), greasewood (*Sarcobatus*), shadscale (*Atriplex*), creosotebush (*Larrea*), and occasionally juniper (*Juniperus*; Bradley and Mauer, 1973; Honeycutt et al., 1981). Common herbaceous plants and grasses include the following: *Opuntia*, *Yucca*, *Fraseria*, *Gutierrezia*, *Grayia*, *Lycium*, *Kochia*, *Salsola*, *Coleogyne*, *Chrysothamnus*, *Bromus*, and *Oryzopsis* (Armstrong, 1979; Honeycutt et al., 1981; Jorgensen and Hayward, 1965; Robey et al., 1987). *A. leucurus* is a generalist with respect to plant species and soil type (Bradley and Mauer, 1973). In central Utah, it occupies a broad habitat niche centered far from the mean habitat sampled (Robey et al., 1987).

Ammospermophilus leucurus is omnivorous, feeding on (in descending order of abundance) green vegetation, seeds, insects, and vertebrate flesh according to seasonal availability and water content (Bradley, 1968a; Karasov, 1983a, 1985). In southern Nevada, green vegetation, chiefly from *Oenothera*, *Eriogonum*, and *Erodium*, is most commonly eaten from December to May. Seeds, mainly from *Ephedra*, *Yucca*, and *Opuntia*, are eaten all year, but less commonly in March and April. Arthropods are most commonly eaten in late summer and autumn; grasshoppers (Orthoptera) are dominant in the diet in spring and summer, and beetles (Coleoptera) are more commonly eaten in autumn. Jerusalem crickets (*Stenopelmatus fuscus*) and ants (family Formicidae) also are common in the diet. Small vertebrates are eaten throughout the year in small quantities (Bradley, 1968a). Bradley (1968a) and Karasov (1985) suggested that vertebrate flesh was obtained as carrion; however, Morgart (1985) observed a white-tailed antelope squirrel catch and consume an adult pocket mouse (Perognathinae), suggesting that squirrels are capable of preying on small vertebrates. Water content of at least 0.9 cm³/g dry mass, nitrogen requirement of 500 mg kg⁻¹ day⁻¹, and dry matter digestibility of about 50% are constraints affecting diet choice. For 4–6 months after winter rains these constraints are unimportant because of the abundance of green vegetation providing sufficient water and nitrogen. At this time, it feeds primarily on vegetation, but seeds, arthropods, and vertebrates are consumed as encountered. By late summer, plants become so dry that they no longer satisfy water or nitrogen requirements; seeds contain only about 0.1 cm³ water/g dry mass, so arthropods (containing 1.5–4.0 cm³ water/g dry mass) are selected to supplement water in the diet during autumn. Seeds also are selected at this time because they have high digestibility requiring fewer arthropods to maintain water balance (Karasov, 1982, 1983a, 1985).

The white-tailed antelope squirrel showed low persistence on a study site in southern Nevada as follows: 52.9%, <50 days; 68.6%, <100 days; 86.3%, <200 days; 96.1% for <400 days. Population density ranged from 0.35 squirrels/ha in autumn to 0.06 squirrels/ha in late spring (Bradley, 1967). Population density in Utah varies widely among years, with high densities often followed by a population crash (Fautin, 1946; Hardy, 1945). Densities of *A. leucurus* are low relative to other desert rodents (Bradley, 1967; Hall, 1946), but because of its relatively larger body size it represents an important portion of the small mammal biomass in desert communities. In southern Nevada, it makes up 2.9% of rodents by number (fourth most abundant) but 6.7% of biomass, second only to *Dipodomys merriami* (Bradley and Mauer, 1973). In California, it constitutes >50% of total rodent biomass (Chew and Butterworth, 1964). *A. leucurus* is sparsely distributed in northern Nevada where it occupies a secondary role to *Perognathus parvus* and *Dipodomys microps* in the small mammal community (O'Farrell and Clark, 1986). The white-tailed antelope squirrel is commonly associated with various species of kangaroo rats (*Dipodomys*), pocket mice (*Perognathus* and *Chaetodipus*), woodrats (*Neotoma*), and deer mice (*Peromyscus*; Bradley and Mauer, 1973; Chew and Butterworth, 1964; Robey et al., 1987).

Because it inhabits sparsely populated desert areas, *A. leucurus*

rarely comes in contact with cultivated crops. However, if available, it will feed on ripening grain, alfalfa, grapes, and seeds of melons and corn (Hoffmeister, 1986; Howell, 1938; Kenagy and Bartholomew, 1985). The ecology of *A. leucurus* appears to be unaffected by manmade constructions such as campgrounds and roads (Clevenger and Workman, 1977; Garland and Bradley, 1984). It is captured with equal efficiency by Victor rat traps, Victor mouse traps, Museum Special traps, and Sherman live traps (Wiener and Smith, 1972).

Potential predators include desert-dwelling, diurnal raptors, coyotes (*Canis latrans*), foxes (*Vulpes velox*), badgers (*Taxidea taxus*), and many snakes (Fautin, 1946; Hall, 1946). Endoparasites include seven protozoans, *Entamoeba citelli*, *Chilomastix magna*, *Hexamastix muris*, *Hexamites teres*, *Monocercomonoides pilleata*, *M. robustus*, and *Tritrichomonas muris* (Evans, 1955; Jenkins and Grundmann, 1973); four cestodes, *Hymenolepis citelli*, *H. diminuta*, *Taenia hydatigena*, and *T. rileyi* (Grundmann, 1958; Mead et al., 1986); one acanthocephalen, *Moniliformis clarki* (Jenkins and Grundmann, 1973); and seven nematodes, *Citellina triradiata*, *Physaloptera massino*, *Spirura infundibuliformis*, *S. leucurusi*, *Rictularia coloradoensis*, *Sublura nevadense*, and *Syphacia citelli* (Babero, 1973; Grundmann, 1957; Jenkins and Grundmann, 1973). The nematode *C. triradiata* is the most common endoparasite of *A. leucurus*, both in number of hosts infected and number of individuals per host (Grundmann, 1957; Grundmann et al., 1976; Jenkins and Grundmann, 1973). In a survey done by Jenkins and Grundmann (1973) 71.5% of white-tailed antelope squirrels were parasitized; this relatively high level of infection is due to the high incidence of *C. triradiata*. Insects serve as intermediate hosts for many of these endoparasites, and squirrels become infected by eating insects (Grundmann et al., 1976).

Ectoparasites include 23 fleas, *Foxella ignota*, *Rhadinopsylla heiseri*, *R. fraterna*, *Meringis dipodomys*, *M. parkeri*, *Megarthroglossis smiti*, *M. spenceri*, *Stenistomera alpina*, *Thrassis francisi*, *T. pandorae*, *T. bacchi*, *Diamanus montanus*, *Orchopeus leucopus*, *Oropsylla idahoensis*, *Opisthocrostitis tuberculatus*, *O. hirsutus*, *O. labis*, *Dactylopsylla ignota*, *Malareus sinomus*, *Monopsyllus wagneri*, *Pulex irritans*, *Echidnophaga gallinacea*, and *Hoplopsylla anomalous* (Hansen, 1954; Jenkins and Grundmann, 1973; Parker and Howell, 1959; Stark, 1958; Tipton et al., 1979); 3 lice, *Enderleinellus suturalis*, *Neohaematopinus citellinus*, and *N. laeviusculus* (Hansen, 1954; Jenkins and Grundmann, 1973); 5 mites, *Haemolaelaps glasgowi*, *Hirstionyssus incomptus*, *H. tricanthus*, *Dermadelema furmani*, and *Trombicula* sp. (Allred, 1962; Hansen, 1954; Jenkins and Grundmann, 1973; Pomeroy and Loomis, 1984); 4 ticks, *Dermacentor parumapertus*, *Ixodes kingi*, *I. angustus*, and *Ornithodoros parkeri* (Hansen, 1954; Jenkins and Grundmann, 1973; Johnson, 1966); and 2 dipteran larvae from the families Cecidomyiidae and Mycetophyllidae (Jenkins and Grundmann, 1973). In central Utah, numbers of the most common flea found on the white-tailed antelope squirrel, *T. bacchi*, peak in April and January, and numbers of *H. anomalous* (the second most common flea) peak in August (Parker, 1958). From a sample of 71 *A. leucurus* collected in central Utah, an average of 58 ectoparasites (fleas, lice, ticks, and mites) per individual were recorded. All individuals were parasitized (Johnson et al., 1968). *A. leucurus* is susceptible to a disease, of unknown cause, that causes open sores, permanent scars, and loss of large patches of skin and hair, but does not seem to cause mortality or decreased activity (Long, 1940).

BEHAVIOR. Activity patterns of *A. leucurus* are strongly influenced by thermoregulatory constraints. During summer, daily activity follows a bimodal pattern peaking in mid-morning and late afternoon with a lull during midday when temperatures are extreme (Chappell and Bartholomew, 1981a, 1981b; Karasov, 1981). Correspondingly, it is most active from 10–32°C (Bradley, 1967). When active at high temperatures, it moves rapidly while above ground, running through open areas and pausing to forage in the shade of shrubs and rocks (Chappell and Bartholomew, 1981b; Karasov, 1981). Individuals may spend up to one-fourth of activity time moving (Karasov, 1981). Because of the rapid rate of heat gain from the environment when temperatures are high, metabolic heat generated by activity contributes relatively little to total heat gain. Thus, individuals actually gain less heat by running about than by moving more slowly and increasing time spent in open areas with high solar radiation (Chappell and Bartholomew, 1981a, 1981b). When critical temperatures are reached, squirrels retreat to a burrow

and sprawl flat on the floor with their sparsely haired ventral surface in contact with the substrate to quickly unload excess heat via convection (Bartholomew and Dawson, 1968; Chappell and Bartholomew, 1981a, 1981b; Karasov, 1981). A typical cycle of heat gain and loss takes a minimum of 15–20 min. According to this pattern of behavior, the ratio of time spent active to time spent inactive should be about 1:1. However, several behavioral adaptations act to decrease the rate of heat gain and thus increase this ratio to >1. Selective use of shade, body orientation, and self-shading using the large, white tail decrease solar radiation experienced by the squirrel (Chappell and Bartholomew, 1981a, 1981b; Karasov, 1981). While foraging, the white-tailed antelope squirrel often climbs into bushes where airflow increases the rate of convective heat loss. These behaviors coupled with tolerance of hyperthermic body temperatures greatly increase the time that can be spent above ground (Bartholomew and Dawson, 1968).

In winter, when temperatures are low, daily activity is unimodal beginning about 1 h after sunrise with constant activity throughout the day and ending about 1 h before sunset. The white-tailed antelope squirrel favors open areas in winter, basking in the sun during much of the day to absorb solar radiation (Chappell and Bartholomew, 1981a, 1981b). During inclement weather, activity is greatly reduced (Bradley, 1967).

Circadian activity rhythms of *A. leucurus* have received much attention (De Coursey, 1973; Kenagy, 1978; Kramm, 1973, 1976; Pohl, 1983). The period of free-running cycles is relatively constant throughout the year and over a wide range of light intensities (Kenagy, 1978). When confined in constant light or dark conditions, the period of free-running cycles increases linearly (Kramm, 1973, 1976). Upon re-exposure to a light-dark schedule, the activity phase is either advanced or delayed to coincide with the lights on or lights off signal (De Coursey, 1973; Kramm, 1973, 1976). Pohl (1983) showed that 1-h light pulses also were effective in entraining circadian activity rhythms of at least 50% of the squirrels in his study. In a study on the effect of light intensity on activity of *A. leucurus*, time spent running peaked between light levels of 1,300–17,000 lux (17,000 lux is equal to light intensity at about 30 min after sunrise and 30 min before sunset). Running speed peaked between light intensities of 2,600–17,000 lux (Kavanau and Rischer, 1972). One captive *A. leucurus* greatly increased its activity during and after a partial solar eclipse, probably because increasing light levels following the eclipse simulated conditions following sunrise (Kavanau and Rischer, 1973).

Home ranges of nine individuals in southern Nevada averaged 6 ha (Bradley, 1967). Estimates using different methods of calculation ranged from 3–8 ha, but Bradley believed the estimate of 6 ha by the minimum home range plus method was most accurate. Home ranges on disturbed and undisturbed areas on the Nevada Test Site (calculated using a probability-density function) were 7.8 ha and 4.7 ha, respectively (Jorgensen and Hayward, 1965). These estimates of home range are large in comparison to estimates for other rodents (Bradley, 1967). Average range of movement (greatest distance between captures) on the Nevada Test Site for males and females, respectively, was 117 and 101 m. In nuclear-disturbed areas, the average range of movement for both sexes was 161 m compared to 88 m in undisturbed areas (Allred and Beck, 1963). Average daily movement in southern Nevada (greatest distance between multiple captures on the same day) was 87.5, 103, and 147.5, based on two, three, and four captures, respectively. Daily range (calculated from daily movement) averaged 1.61 ha, and fluctuated with seasonal changes in food availability and breeding behavior with most movement occurring from July to October (Bradley, 1967). Radio-collared individuals in California traveled an average of 1.0 km/day; the longest daily movement reported was 2.6 km by a male in April (Karasov, 1981). *A. leucurus* has better homing ability than *Spermophilus tereticaudus*, with 23 of 38 individuals (60.5%) returning from 0.8 km, and, of those that returned, 13 of 15 (86.6%) successfully homed from a 1.6 km displacement. Percent of *S. tereticaudus* returning from 0.8 km and 1.6 km displacements were 37.9 and 0%, respectively (Bradley, 1968b).

Ammospermophilus leucurus utilizes many burrows scattered throughout the home range as daytime retreats (Bradley, 1967; Karasov, 1981). Often it occupies different burrows on different nights with as many as six (Bradley, 1967) or seven (Karasov, 1981) burrows used over the course of a few weeks. Burrows used by *A. leucurus* usually are abandoned burrows of kangaroo rats (*Dipodomys*), and are most commonly found in sandy or conglomerate

soils both under shrubs and in the open (Bradley, 1967). Entrances to nest burrows often are close to shrubs and the tunnels descend about 45.7 cm in depth; a nest chamber, 13–20 cm in diameter, lined with dried plant material, rabbit fur, and other shredded materials is located near the center of the burrow system. Small seed caches, but no feces or discarded food materials, are found at the end of blind side tunnels. Escape burrows are variable, but usually about 3 m long and 25–38 cm deep with no nest or food caches (Bradley, 1967). Four summer burrows in California ranged from 25 to 38 cm deep, compared to one burrow excavated in April that was 66 cm deep (Karasov, 1981).

Because of the diurnal activity of *A. leucurus*, as opposed to nocturnal activity by most other desert rodents, social interaction between it and other desert-dwelling species is uncommon. It is probably behaviorally dominant to smaller desert rodents, and it has been reported to prey on some (Morgart, 1985). In arena encounters, *A. leucurus* attacked and defeated Mongolian gerbils (*Meriones unguiculatus*). However, after 24 h, gerbils had evicted squirrels from nest boxes (Fisler, 1977).

White-tailed antelope squirrels form stable, linear hierarchies of dominance rather than defending exclusive territories. This dominance system is maintained by visual and tactical cues. Greetings usually take the form of naso-nasal or naso-oral touching with variations depending on the rank of individuals. A direct approach without hesitation and greeting with naso-oral or double naso-oral (kiss) is typical of individuals secure in their position in the hierarchy and occasionally used in male-female courtship. A hesitancy greeting by young animals or animals of uncertain rank is characterized by stretching the body full length low to the ground with the head far forward, followed by a retreat by the subordinate. When dominance is contested, agonism can increase from lunging and side displays to boxing and roll fights. Tooth chattering, low growls, and chirps often accompany agonistic behavior. Changes in dominance can occur gradually over the course of several days or may result from one agonistic encounter. Juvenile squirrels initially do not respond to social signals by adults, but learn signals gradually over the course of 2–3 weeks (Fisler, 1976). Alarm vocalizations are characterized as shrill rapid chitters (Howell, 1938) or trills (Bolles, 1988; Fisler, 1976). These trills are heard when predators are near and at other times for no obvious reason, particularly in the spring (Fisler, 1976). Alarm calls of *A. leucurus* and *A. harrisi* are pure-toned, high-pitched, relatively long trills compared to other members of the genus. High-pitched trills are characteristic of antelope squirrels found in open habitats; other species of *Ammospermophilus* (*A. nelsoni*, *A. interpres*, and *A. insularis*) found in closed habitats had shorter, harsher, lower-pitched calls (Bolles, 1988). Based on comparisons with other sciurids, Bolles (1988) suggested that long, high-pitched calls of *A. leucurus* and *A. harrisi* are of recent origin, accompanying the development of deserts in North America.

GENETICS. Members of the genus *Ammospermophilus* have a diploid number of 32 chromosomes. They also have unusually large chromosomes due to large amounts of heterochromatin and satellite DNA, about 70% more than is found in *Spermophilus spilosoma*. *A. leucurus* has four pairs of chromosomes with interstitial blocks of constitutive heterochromatin, three pairs of chromosomes with prominent blocks of heterochromatin in the distal portions of their long arms, and one pair of chromosomes in which only the distal extremes of the short arms are euchromatic. Three chromosomes have identical heterochromatin-banding patterns among all five species of *Ammospermophilus* (Mascarello and Mazrimas, 1977). Highly repeated sequences of alpha-satellite DNA in *A. leucurus* are similar to *Dipodomys ordii* and other rodents (Fry and Salser, 1977).

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