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Neotoma albigula.

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Neotoma albigula Hartley, 1894

White-throated Woodrat

Neotoma albigula Hartley, 1894:157. Type locality near Tucson, Pima Co., Arizona.

Neotoma latifrons Merriam, 1894:121. Type locality Querendaro, Michoacán.

Neotoma leucodon Merriam, 1894:120. Type locality San Luis Potosí, San Luis Potosí.

Neotoma venusta True 1894:354. Type locality Carrizo Creek, Imperial Co., California.

Neotoma cumulator Mearns, 1897:503. Type locality old Fort Yuma, Imperial Co., California, on right bank of Colorado River.

Neotoma montezumae Goldman, 1905:29. Type locality Zimapan, 7,500 ft, Hidalgo.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Sigmodontinae, Genus *Neotoma*, Subgenus *Neotoma*. Fifteen subspecies are currently recognized (Hall and Genoways, 1970).

N. a. albigula Hartley, 1894:157. See above (*angusticeps* Merriam is a synonym).

N. a. brevicauda Durrant, 1934:65. Type locality Castle Valley, about 15 mi NE Moab, Grand Co., Utah.

N. a. durangae J. A. Allen, 1903:602. Type locality San Gabriel, Durango.

N. a. laplataensis F. W. Miller, 1933:2. Type locality near Bondad, La Plata Co., Colorado.

N. a. latifrons Merriam, 1894:121. Type locality Querendaro, Michoacán.

N. a. leucodon Merriam, 1894:120. Type locality San Luis Potosí, San Luis Potosí (*montezumae* Goldman and *zacatecae* Goldman are synonyms).

N. a. mearnsi Goldman, 1915:135. Type locality Tinajas Altas, Gila Mts., Yuma Co., Arizona.

N. a. melanura Merriam, 1894:126. Type locality Ortiz, Sonora.

N. a. melas Dice, 1929:3. Type locality Malpais Spring, malpais lava beds near Carrizozo, Lincoln Co., New Mexico.

N. a. robusta Blair, 1939:3. Type locality Limpia Canyon, 4,300 ft, 16 mi N Fort Davis, Jeff Davis Co., Texas.

N. a. seri Townsend, 1912:125. Type locality Tiburón Island, Gulf of California, Sonora.

N. a. sheldoni Goldman, 1915:136. Type locality Pápago Tanks, Sierra Pinacate, Sonora.

N. a. subsolana Alvarez, 1962:141. Type locality Miquihuana, 6,400 ft, Tamaulipas.

N. a. venusta True, 1894:354. See above (*cumulator* Mearns and *grandis* Elliot, 1904, are synonyms).

N. a. warreni Merriam, 1908:143. Type locality Gaume Ranch, 4,600 ft, northwest corner Baca Co., Colorado.

DIAGNOSIS. *Neotoma albigula* is a medium-sized woodrat with the following diagnostic cranial characters (Fig. 1): skull smooth, with a short relatively broad rostrum; supraorbital region less arched than cranial region; dorsal margin of foramen magnum deeply concave; maxillovomerine notch interrupting the nasal septum, and anterior palatal spine pointed; posterior margin of the palate usually concave; large sphenopalatine vacuities and shallow anterointernal M1 re-entrant angle. The dorsal pelage is brown, usually overlaid with black (Fig. 2); the throat and pectoral regions are pure white to the base of the hairs. The tail is distinctly bicolored, brownish or dusky above and whitish below (Findley et al., 1975; Hall, 1981; Lechleitner, 1969).

Neotoma albigula and *N. micropus* are closely allied (Anderson, 1969). In Colorado, populations of these species show only very slight morphological differences, apparently leading to their hybridization in northern Baca County (Finley, 1958). Anderson (1969) predicted a possible future fusion of *N. floridana*, *N. micropus*, and

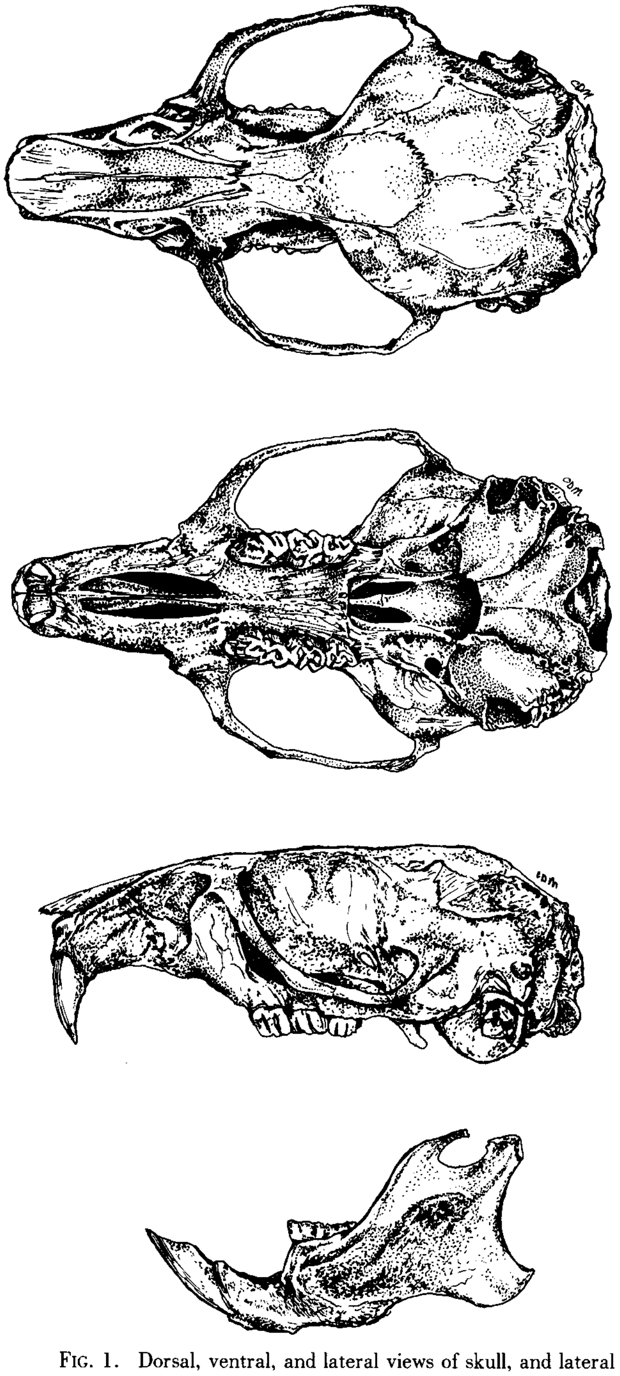

FIG. 1. Dorsal, ventral, and lateral views of skull, and lateral view of mandible of an adult male *Neotoma albigula* from 4.2 mi S and 0.8 mi W Kenton, Cimarron Co., Oklahoma; occipitonasal length = 46.7 mm. Illustrations by C. McCallister.

FIG. 2. Adult *Neotoma albigula* from immediately south of Tucson, Pima Co., Arizona. Photograph by C. R. Williams.

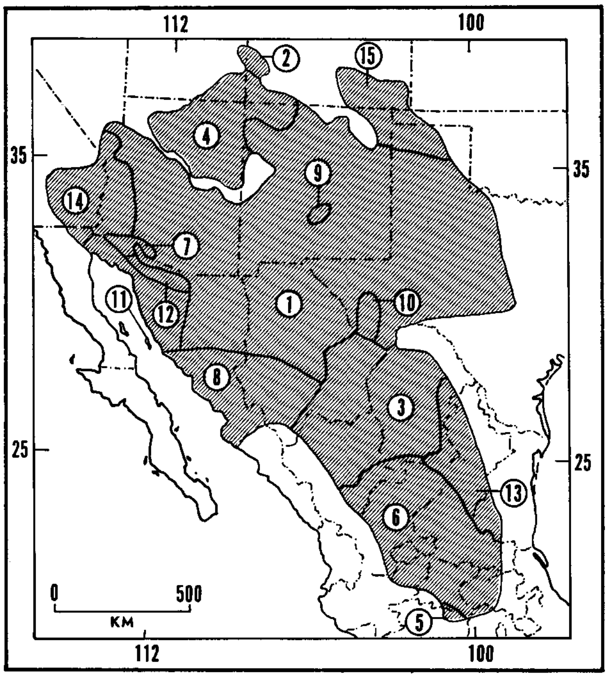

FIG. 3. Geographic distribution of *Neotoma albigula* and subspecies (from Hall, 1981): 1, *N. a. albigula*; 2, *N. a. brevicauda*; 3, *N. a. durangae*; 4, *N. a. laplataensis*; 5, *N. a. latifrons*; 6, *N. a. leucodon*; 7, *N. a. mearnsi*; 8, *N. a. melanura*; 9, *N. a. melas*; 10, *N. a. robusta*; 11, *N. a. seri*; 12, *N. a. sheldoni*; 13, *N. a. subsolana*; 14, *N. a. venusta*; 15, *N. a. warreni.*

N. albigula into one species. Interspecific relationships were also considered by Zimmerman and Nejtek (1977) in a starch-gel electrophoretic study encompassing 19 populations of *N. albigula*, *N. micropus*, and *N. floridana*. The study revealed 9 of 20 loci were fixed for the same allele in all three species. The very high coefficients of genetic similarity (average S value of 0.765) also support the view of the genetic relatedness of these species. Zimmerman and Nejtek (1977) estimated that *N. albigula* diverged from the parental form approximately 155,000 years ago. The genus *Neotoma* was last revised by Goldman (1910) who, in addition to providing keys at the subgeneric, specific, and subspecific levels, also included extensive information concerning the distributions, habits, and characters of woodrats.

GENERAL CHARACTERS. *Neotoma albigula* has soft and short fur. Because of molting and the worn condition of the pelage in summer, insulation is somewhat reduced during warmer months (Finley, 1958). This species has relatively long ears and a long-haired but not bushy tail; the soles of the hind feet are naked to the heel (Lechleitner, 1969). Vorhies and Taylor (1940) observed tail autotomy in *N. albigula*.

The average external dimensions (in mm) reported by Bailey (1931) were: total length, 328; length of tail, 152; length of hind foot, 33.5; length of ear from notch, 30. The average adult female mass is 188 g. Males are consistently larger than females and average 36 g heavier. Average skull measurements (in mm) of adult specimens from eastern Pima and northwestern Cochise counties, Arizona, are (Hoffmeister, 1986; sample size in parentheses): greatest length of skull, 43.56 (21); condylobasal length, 40.88 (24); basilar length, 35.45 (24); zygomatic breadth, 22.01 (25); interorbital breadth, 5.63 (26); nasal length, 16.29 (24); incisive foramina, 8.80 (27); length of palatal bridge, 7.46 (27); length of alveolar maxillary toothrow, 8.52 (27); mastoidal breadth, 17.62 (23); rostrum breadth, 7.29 (26); rostrum depth, 7.21 (27).

Alvarez (1963) reported an average mass for five pregnant females of 196.7 g (range, 183 to 207), whereas nine adult males and six nonpregnant females averaged 215.6 (175 to 250) and 162.5 (155 to 175) g, respectively. Crown-rump length of embryos taken from the pregnant females averaged 22.2 mm.

There is substantial interpopulation variation in *N. albigula*, which has led to the designation of various subspecies. In western Arizona, for example, *N. albigula* is represented by populations (*N. a. venusta*) which have a larger, more angular skull than *N. a. albigula*. Dichromatic specimens have been obtained from Rio Puerco and San Rafael, New Mexico. Another variant is the form occurring on the western slopes of the Sierra Madre in southern Sonora and southwestern Chihuahua (*N. a. melanura*), which is intermediate both in color and cranial characters between *N. a. albigula* and populations occurring further south (Goldman, 1910).

DISTRIBUTION. *Neotoma albigula* occurs in a wide variety of habitats throughout its geographic range (Brown, 1968). It is found from southeastern California and southeastern Utah, to central Texas, northeastern Michoacán, and Hidalgo, Mexico (Fig. 3). *N. albigula* is sympatric with *N. stephensi* in northern Arizona (Freeman, 1974). In southern Utah, Colorado, and northern Arizona, *N. albigula* is sympatric with *N. cinerea*. In Texas, three species, *N. mexicana*, *N. albigula*, and *N. micropus*, have overlapping ranges extending from the Guadalupe and Davis mountains westward (Davis, 1966; Genoways et al., 1979; Hall, 1981). In New Mexico, *N. albigula* mainly occupies the Upper Sonoran zone, but in places its range may extend into the edge of the Lower Sonoran (Bailey, 1931). In southwestern and southeastern Colorado, *N. albigula* occurs at elevations as high as 2,135 m (Armstrong, 1972; Lowe, 1964). In Chihuahua, Mexico, *N. albigula* is sympatric with *N. mexicana* in some areas, and occurs with *N. micropus* in the northern part of the state. *N. goldmani* occurs with *N. albigula* in eastern Chihuahua (Anderson, 1972).

FOSSIL RECORD. Biochemical data suggest that *N. albigula* diverged from the parental stock approximately 155,000 years BP during the late Sangamon interglacial or early Wisconsin glaciation (Zimmerman and Nejtek, 1977). Speciation may have occurred in response to vegetational changes during the Wisconsin glaciation. Hibbard (1967:128) suggested that "the stock that gave rise to *Neotoma* must have separated off from a generalized cricetine in the Upper Miocene." Woodrats of the *N. floridana*-group (containing *N. angustipalata*, *N. floridana* and *N. micropus*) occurred on the Great Plains by late Illinoian (Birney, 1973). *N. albigula* could have diverged from this stock during this period, and it would therefore seem appropriate to include *N. albigula* and related species (that is, *N. palatina*, *N. nelsoni*, and *N. varia*) in the *N. floridana*-group (Birney, 1973). Kurtén and Anderson (1980) reported fossil *N. albigula* from New Mexico and Texas, with the oldest occurrence being Illinoian in age from Slaton, Texas. Mead et al. (1983) collected 35 packrat middens (species not indicated) from 17 localities in the Sonoran Desert of southwestern Arizona and southeastern California. *N. albigula* remains are listed only from Wolcott Peak: C14 5,020 ± 80 to 14,500 ± 800. The paleo-community associated with this midden was pinyon-juniper (*Pinus-Juniperus*) and oak (*Quercus*) woodland. Radiocarbon dating and analysis of plant and animal associates showed the middens were between 32,000 and 1,500 years old. A late Pleistocene fauna from San Josecito Cave, Nuevo Leon, Mexico, included remains of *N. albigula* (Jakway, 1958). *Neotoma* remains found at Tequesquinahua, 3.2 km NW Tlalnepantla, Mexico, included three molars that generally resemble extant *N. albigula* and *N. micropus* (Alvarez, 1966).

FORM. Markedly different melanistic color patterns for *N. albigula* occur on lava beds. In Texas, animals are characterized by having a blackish dorsum with dark gray on the sides; the tail is nearly black, slightly darker dorsally. The ventrum is completely dark except for three areas that are white: a spot in the inguinal region, a thin line on the inside of the hind limbs, and a thoracic-jugular patch (Blair, 1954). A black race also evolved on the Carrizozo malpais of New Mexico; individuals are black except for a white throat patch (Findley et al., 1975; Hooper, 1941). In this lava association, *N. albigula* was one of the most abundant resident mammals (Blair, 1943).

Howell's (1926) myological study indicated that *N. albigula* is intermediate in form between *Homodontomys* and *Teonoma*. For the osteological comparisons, *N. albigula* resembled *Homodontomys* in 21 points, *Teonoma* in 12, and was intermediate in 7. In digestive and urogenital comparisons, *N. albigula* also occupied an intermediate position relative to the development of non-muscular soft parts.

The baculum of *N. albigula* is broadly U-shaped in cross-section at its promixal end, and has a knob on the distal end (Burt and Barkalow, 1942). Near the middle, it is nearly circular in cross section. Its shaft curves slightly downward from proximal to distal end. Average measurements (in mm) of 15 bacula (including *N. a. albigula*, *N. a. melanura*, and *N. a. robusta*) were: lateral diameter (at base), 3.17; dorsoventral diameter (near midpoint), 0.61; lateral diameter (near midpoint), 0.67. Hooper (1960) emphasized that *N. albigula*, *N. floridana*, *N. micropus*, and *N. mexicana* have similar phallic morphology. The glans in these species is "robust and oblong, its length twice the greatest diameter and approximately ⅖ the hind foot length" (Hooper, 1960:4).

FUNCTION. Selective advantage is conferred to larger woodrats in cold climates because of their greater surface-to-mass ratio; the opposite is true of desert animals, where small size is favored because of the importance of heat dissipation (Brown and Lee, 1969). Scholander (1955) and McNab (1971) pointed out that the physiological and ecological generalizations often associated with Bergmann's Rule are questionable since many of the characters studied in analyses of body size in small mammals are not significant in heat exchange. Homeothermy in these animals is maintained by adjustments of insulation and metabolic heat production (Brown and Lee, 1969). In low desert areas, these rats face summer temperatures that frequently are only a few degrees below lethal limits. They survive because they have a reduced amount of pelage and an efficient vascular system (Brown, 1968); they avoid high environmental temperatures by remaining in their burrows.

Olfaction in woodrats influences their social interactions. Males have specialized midventral glands used for deposit of scent in specific localities. The ventral gland is only moderately or poorly developed in most females. Scent is used in social functions involving sexual and agonistic interactions, in courtship, in hierarchic organization, and perhaps in territoriality. It also provides cues for sex and species recognition. Males may use olfactory clues present in feces and urine outside dens to distinguish sex of occupants. Thus, they probably reduce energetic costs of agonistic encounters by avoiding other males (August, 1978; Howe, 1977).

The ability of *N. albigula* to survive in its arid habitat is aided by behavioral adaptations such as nocturnality, diurnal residence within a den, and choice of succulent foods that satisfy water needs (Lee, 1963; Schmidt-Nielsen and Schmidt-Nielsen, 1952). Water consumption by *N. albigula* is inversely related to its availability in the habitat (Boice, 1969; Boice and Boice, 1968). A comparative analysis of water conservation in desert mammals showed that woodrats are highly vulnerable to desiccation, and they are no better able to concentrate urea and electrolytes in the urine than many rodents occurring in more mesic habitats (Schmidt-Nielsen et al., 1948). Woodrats need more water than kangaroo rats (*Dipodomys*) and pocket mice (*Chaetodipus* and *Perognathus*) and obtain water from their food. During the driest parts of the year, water-rich cacti constitute approximately 90% of the diet. *Neotoma* display a habitat-related physiological adaptation; they may safely consume oxalic acid, a component of cactus that is highly toxic to other mammals (Schmidt-Nielsen, 1964).

ONTOGENY AND REPRODUCTION. Males have enlarged testes during periods of sexual activity. In females, an enlarged or congested uterus indicates either the approach of sexual activity or recent parturition (Vorhies and Taylor, 1940).

Richardson (1943:130) noted that the gestation period in *N. albigula* is ". . . at least 37, perhaps more than 38, days . . . ." This contradicts Feldman's (1935) observation that gestation is less than 30 days. Litter size is usually two young, with a maximum of three (Feldman, 1935; Richardson, 1943).

Birth requires from 45 to 65 s. *N. albigula* adopts a nearly quadrupedal position during birth, and the tail is elevated and parallel to the substrate. There are no abdominal contractions. Placentas weighed 0.85 g, are 7 mm thick, and are immediately consumed after parturition (Bleich and Schwartz, 1975).

The timing of breeding varies geographically. *N. albigula* in Coahuila may breed at any time of the year (Baker, 1956). Immature animals were trapped from January to April, in June, September, and December; pregnant females were captured from March through May, and in July. It seems probable that more than one litter is raised in a season (Baker, 1956). The breeding season of *N. a. venusta*, in San Diego Co., California, is from January to July (Schwartz and Bleich, 1975; Vorhies and Taylor, 1940). Vorhies and Taylor (1940) reported a female in her den with two neonates and three half-grown animals.

Newborns averaged 10.9 g (Richardson, 1943). The mother aids in excretion and defecation by stimulating the genital region or by compressing the abdomens of neonates with her forefeet. The young initiate foot-thumping behavior at the age of 26 days. Eating and manipulating cholla (*Opuntia bigelovii*) begins at 17 to 55 days. During this time the young also learn to extract cholla thorns from their flesh. Enlargement of testes begins at 9 or 10 weeks (Richardson, 1943). Lactation persists until 20 to 25 days after birth. Males and females do not exhibit differential growth; onset of maturity, both in size and sexual development, occurs at approximately 300 days of age. Two captive females, however, reached sexual maturity at 80 and 87 days of age, respectively, while males attained sexual maturity at 101 days (Schwartz and Bleich, 1975). Characteristics of sexual maturity include swollen vulva, perforate vagina, and scrotal testes (Schwartz and Bleich, 1975).

Live-trapping records suggest that males have a greater probability of survival than females (Rainey, 1965). This may be a result of the increased hazards encountered by females with young. The age of one captive female was estimated at 60 months (Landstrom, 1971).

ECOLOGY. *Neotoma albigula* is primarily found in arid regions, and is often, but not obligately, associated with clumps of prickly pear (*Opuntia*; Armstrong, 1972; Blair, 1954). Vorhies and Taylor (1940) stated that this cactus usually determines the abundance of *N. albigula* in southern Arizona. Woodrats are usually few in number where *Opuntia* is scarce. *N. albigula* is most abundant in natural and modified pinyon-juniper habitats (Turkowski and Watkins, 1976). Large quantities of dead trees enhance woodrat populations by providing cover and material for house construction. Olsen (1973) hypothesized that shelter-site selection by *N. albigula* is based upon the quantity of ground-level vegetation available for cover. Vorhies and Taylor (1940) had also suggested that the abundance of woodrats is determined by the number of bushes suitable for shelter.

In west Texas *N. albigula* primarily occupies rocky areas (Bailey, 1905), whereas in the Lower Sonoran Zone of Arizona it has been found in nearly every type of habitat (Vorhies and Taylor, 1940). In the Tularosa Basin of New Mexico, *N. albigula* were relatively rare in grassy-wash associations, and were more abundant on rocky-mountain slopes (Blair, 1943). A survey of mammals in Guadalupe Mountains National Park, Texas, showed that *N. albigula* occurred around the perimeter of the mountains and on the floors of the Upper Dog and West Dog canyons (Genoways et al., 1979). In this region, *N. albigula* may be limited more by the presence of two other species of woodrats (*N. mexicana* and *N. micropus*) than by specific habitat conditions (Cornely, 1979).

Neotoma albigula is nocturnal and during the day it retires into rock crevices, caves, hollow trees, abandoned buildings, or dens and burrows constructed by the woodrats themselves. These locations provide stable temperatures (Brown, 1968) and protect them from some predators.

According to Ekkens (1974), the most abundant material composing a den is usually jumping cholla. He found that the interior portions of the lodge included sticks, leaves, cactus pads (*Opuntia engelmanii* and *O. versicolor*), and remains of cactus fruits (*O. engelmanii, Carnegiea gigantea*, and *Ferocactus wislizenii*). Bottle caps, bones, pieces of charcoal, empty rifle shells, palo verde beans, and green leaves also were found. Lechleitner (1969) noted that these lodges have more than one entrance and contain a large central chamber located above ground. The nest, contained in this chamber, is 15 to 25 cm in diameter. Vorhies and Taylor (1940) indicated that nests are of slightly flattened spherical shape, lined with grasses, and are kept free of feces. The nest is used by the young, and also year-round as a resting and sleeping place for the female woodrat. The dens of *N. albigula* may be as large as 2 mm in diameter and 60 cm in height. Successive generations may inhabit the same construction.

Some *N. albigula* do not construct elaborate dens; instead they use rock crevices for shelter, filling them with sticks, cacti, and other objects (Cornely, 1979). Runways radiate from the nest to a mean distance of 6 m, are approximately 10 cm in width, and are lined with cholla joints (Hill, 1942). Hill (1942) suggested that the animals can run over cholla spines without injury. *N. albigula* have been observed to climb freely in both cholla and prickly pear, and to run over and transport cholla joints without sustaining injury (Vorhies and Taylor, 1940).

Many vertebrates are known to use woodrat lodges for shelter (Kingsley and Kurzius, 1978; Ryckman et al., 1981; Vorhies and Taylor, 1940), including lizards (*Coleonyx variegatus, Callisaurus draconoides, Uta stansburiana*), tree frogs (*Hyla*), opossums (*Didelphis*), shrews (*Notiosorex, Sorex*), rodents (*Peromyscus, Microtus*), skunks (*Mephitis*), and rabbits (*Sylvilagus*). Five classes of arthropods (Crustacea, Diplopoda, Chilopoda, Arachnida, and Insecta) also are found commonly in woodrat houses (Rainey, 1965; Ryckman et al., 1981). Vorhies and Taylor (1940) noted that Microlepidoptera are among the most abundant invertebrate inhabitants of woodrat dens.

In an area of 1.7 ha in Arizona, Hanson (1957) found 27 dens, of which 78% were in active use (an average of 12.6/ha). In contrast, an average of only 5.7 dens/ha was found on 304 ha in southeastern Arizona and southwestern New Mexico; 91.4% of these were in use (Monson and Kessler, 1940). In a 4-year study of species composition and density of several rodent populations in the Chihuahuan Desert in southern New Mexico, Whitford (1976) found that *N. albigula* and *N. micropus* maintained nearly constant population densities. His study elucidated density differences between resident populations in the playa, a clay bottom depression with a vine mesquite (*Panicum obtusum*) cover, and the bajada, an area dominated by creosotebush (*Larrea tridentata*). In the former, the population of *Neotoma* was approximately 1/ha, while in the latter it remained constant at about 2/ha from 1971 to June 1973, after which it increased to 8/ha.

Vorhies and Taylor (1940) noted that 43.8% of the annual diet of *N. albigula* is composed of cacti. The mean daily consumption of cactus is approximately 60% of the woodrat's body mass (Spencer and Spencer, 1941). *Opuntia* is likely to be both a water source as well as a food source for woodrats (Olsen, 1976). Water, and not food, may be the limiting factor for populations of woodrats in certain regions. When *Opuntia* is not readily available, other food sources, such as juniper, are used as food items (Finley, 1958). Near Two Buttes, Colorado, juniper and soapweed (*Yucca glauca*) were the alternative food sources (Freeman, 1974). Other foods include yucca blades, shrubs, grasses, and husks of juniper berries (Lechleitner, 1969).

Ecological distribution of woodrats is determined primarily by climbing ability, house construction ability, and diet. *N. mexicana* inhabits steep cliffs and rocky slopes, whereas *N. albigula* builds dens on moderately rocky slopes, and *N. micropus* resides on plains and in areas lacking rocks (Armstrong, 1972; Dice, 1942; Finley, 1958; Wright, 1973). Variation in vegetation and soil type was correlated with the degree of coexistence of *N. albigula* and *N. micropus* in Mesilla Valley, southern New Mexico (Wright, 1973); competitive exclusion of *N. micropus* by *N. albigula* may be occurring. In southern New Mexico, Dice (1942) trapped *N. albigula* primarily in the sabinal belt, which is dominated by pinyon pine (*Pinus edulis*) and junipers (*Juniperus monosperma*). In addition, Dice (1942) found melanistic populations (*N. albigula melas*) to be confined to the black-lava rocks of the Tularosa Malpais. In northern Arizona the altitudinal range of *N. albigula* extends up to about 2,150 m; however, an adult female was trapped at 2,499 m in the Santa Rita Mts., Pima Co. (Vorhies and Taylor, 1949). In northern Arizona *N. albigula* competes with *N. stephensi* for food and cover, and may successfully exclude it through active aggression (Freeman, 1974).

Predators of *N. albigula* may include weasels (*Mustela*), skunks (*Spilogale, Mephitis*), badgers (*Taxidea*), foxes (*Vulpes, Urocyon*), bobcats (*Lynx*), raccoons (*Procyon*), and rattlesnakes (*Crotalus*; Ryckman et al., 1981; Vorhies and Taylor, 1940). *Neotoma* skulls frequently are found in pellets of horned owls (*Bubo*; Goldman, 1910; Vorhies and Taylor, 1940). Humans also consume woodrats (Dalquest, 1953; Mearns, 1907; Vorhies and Taylor, 1940).

Woodrat activity significantly increases the quantity of total soluble salts (calcium, magnesium), bicarbonate, and nitrate ions in the soil (Greene and Reynard, 1932). This is attributed to the excreta of the animals and to materials the animals carry into their burrows. Another consequence of burrowing activity upon the soil is increased aeration and water percolation.

Trypanosoma cruzi, the agent of Chagas disease, is carried by triatomid bugs (Triatominae); these ectoparasites are common occupants of woodrat dens (Ekkens, 1981). Of 79 *Neotoma* dens surveyed, 67 (79.7%) contained one or more species of *Triatoma* (Ekkens, 1974). Other associated parasites are *Paratriatoma hirsuta* (Ryckman et al., 1965) and the small eyeless flea *Anomiopsyllus* sp. (Barnes et al., 1977).

BEHAVIOR. *Neotoma albigula* is primarily nocturnal, although there have been several reports of daytime activity, usually within the den. This species remains active throughout the year. Justice (1960) noted that even when kept in total darkness, captive animals had persistent daily endogenous cycles of slightly less than 24 h. Lunar periodicity was not noted.

Feldman (1935) noted that captive *N. albigula* have no social life other than during mating and rearing of young. Foot-thumping frequently precedes copulation. There is minimum tactile contact during copulatory lock and the male shows no clasp of the female. A mean duration of 30.1 s per lock was recorded. Because a locked pair is highly susceptible to predation, the locking copulatory pattern may have evolved in those rodents in which copulation occurs in a relatively safe place, such as in the den (Dewsbury, 1975; see also Dewsbury, 1971, 1974). The minimum-area home range of *N. albigula* in a cholla-forest habitat was estimated by Boggs (1974) to be approximately 161 ± 19 m^2, or 486 ± 49 m^2, assuming home ranges were circular. Many home ranges overlapped those of neighbors from 1 to 100%, but the animals were observed to defend their nest area. Nests were separated by an average of 12 m. Social hierarchy seems to be influenced by factors such as sex, age, weight, residency, and experience. Male and female *N. albigula* do not show any significant differences in movement patterns related to spatial utilization (Bateman, 1967). Trapping revealed that home ranges of woodrats were much smaller than those of *Peromyscus eremicus*, but these results may be misleading, as the vertical component of the activity area of woodrats was not evaluated.

Through interspecific pairings of males, Howe (1978) showed that there are no qualitative differences in agonistic behavior among different *Neotoma* species. *N. albigula* may be dominant to the smaller *N. stephensi*, whereas *N. mexicana* probably outcompetes *N. albigula*. Freeman (1974) found that in behavioral laboratory studies *N. albigula* exhibited aggressive behavior, but *N. stephensi* did not.

Foot-thumping behavior (mentioned above in association with copulatory activity) was also noted by Bleich and Schwartz (1975), who assumed this to be a reaction to fear. However, foot-tapping and thumping have also been interpreted as being a means of communication among woodrats (Vorhies and Taylor, 1940). Behavioral reactions of *N. albigula* to gopher snakes (*Pituophis melanoleucus*) and to gila monsters (*Heloderma suspectum*) could be divided into three phases: 1) orientation and perception of stimuli by the woodrat; 2) alarm reaction and thumping of hind feet; 3) panic as stimuli intensified, resulting in random, fast movements (Richardson, 1942). In experimental manipulations involving young rats with unopened eyes, snakes were always treated as inanimate objects. Thumping of hind feet was observed in a young animal of 26 days whose eyes had been open for 11 days. Introduction of other reptiles such as lizards (*Cnemidophorus tessellatus*, *Callinsaurus draconoides*, *Sceloporus magister*, *Phrynosoma*) and desert tortoises (*Gopherus agassizii*) into woodrat cages produced little or no alarm reactions. A combination of at least two stimuli (for example, sight and odor) was necessary to produce the typical alarm reaction (Richardson, 1942).

GENETICS. The autosomes include two large and two small pairs of distinctly biarmed chromosomes (2n = 52; fn = 58). The X-chromosome is large and submetacentric, whereas the Y-chromosome, usually large and subtelocentric, was acrocentric in two Texas specimens (Baker and Mascarello, 1969).

The nearly identical G-banding patterns in the euchromatic portions of chromosomes in *N. micropus* and *N. albigula*, except for some extra heterochromatin in the latter species, suggest a close phylogenetic association (Mascarello et al., 1974). Mascarello and Hsu (1976) maintained that the fundamental karyological difference between *N. albigula* and *N. micropus* lies in the presence of heterochromatic second arms on the two largest autosomes of *N. albigula*. An analysis of chromosomal patterns of 160 specimens of *N. albigula* and *N. micropus* from southeastern Colorado suggested these species are hybridizing (Huheey, 1972). Vertical starch-gel electrophoresis of serum proteins revealed several hybrid band patterns. Hemoglobins, although analyzed, proved to be highly polymorphic and did not yield any correlation patterns with either species. Further support for the occurrence of hybridization was provided by the esterase and morphological intermediates. Huheey (1972) indicated that evidence for hybridization appears to be limited to southeastern Colorado, and that it is most extensive in the region of Two Buttes. Zimmerman and Nejtek (1977) suggested that *N. albigula*, *N. micropus*, and *N. floridana* are semispecies. The high coefficients of genetic similarity of these species reflect the small degree of differentiation between them.

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