

*Neotoma lepida*. By B. J. Verts and Leslie N. Carraway

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*Neotoma lepida* Thomas, 1893

Desert Woodrat

*Neotoma lepida* Thomas, 1893:235. Type locality restricted by Goldman (1932:61) to "Somewhere on 'Simpson's Route' between Camp Floyd (a few miles west of Utah Lake) [= Fairfield, Toole County], Utah, and Carson City, [Douglas County, Nevada]."

*Neotoma desertorum* Merriam, 1894:125. Type locality "Furnace Creek, Death Valley, [Inyo County,] California."

*Neotoma bella* Bangs, 1899:66. Type locality "Palm Springs, Riverside Co., California."

**CONTEXT AND CONTENT.** Order Rodentia, suborder Sciurognathi, family Muridae, subfamily Sigmodontinae, genus *Neotoma*, subgenus *Neotoma* (Musser and Carleton 1993). Musser and Carleton (1993:687) considered *Neotoma* to be within the neotomine Sigmodontinae but chose to use only "informal adjectival construction" for the names of tribes. Twenty-three subspecies of *N. lepida* (Fig. 1) are recognized currently (Musser and Carleton 1993):

*N. l. abbreviata* Goldman, 1909:140. Type locality "San Francisco Island (near San Jose Island), off east coast of southern Lower California [Baja California Sur, Mexico]."

*N. l. arenacea* Allen, 1898:150. Type locality "San José del Cabo, Lower California [Baja California Sur, Mexico]."

*N. l. aridicola* Huey, 1957:287. Type locality "Gulf of California, Baja California, Mexico."

*N. l. californica* Price, 1894:154. Type locality "Bear Valley, San Benito County, California."

*N. l. egressa* Orr, 1934:109. Type locality "One mile east of El Rosario, 200 feet altitude, Lower California [Baja California, Mexico]."

*N. l. felipensis* Elliot, 1903:217. Type locality "San Felipe, Gulf of California, Lower California [Baja California, Mexico]."

*N. l. gilva* Rhoads, 1894:70. Type locality restricted by Goldman (1932:63) to "Banning, Riverside County, California." (*sola* Merriam is a synonym.)

*N. l. grinnelli* Hall, 1942:369. Type locality "Colorado River, 20 miles above (by river, but about 12½ miles north by air-line) Picacho, Imperial County, California."

*N. l. insularis* Townsend, 1912:125. Type locality "Angel del la Guardia Island, [Baja California, Mexico]."

*N. l. intermedia* Rhoads, 1894:69. Type locality "Dulzura, San Diego Co., Cal[ifornia]."

*N. l. latirostra* Burt, 1932:180. Type locality "Danzante Island (latitude, 25°47'N., longitude, 111°11'W.), Gulf of California, Lower California [Baja California], Mexico."

*N. l. lepida* Thomas, 1893:235, see above (*bella* Bangs and *desertorum* Merriam are synonyms).

*N. l. marcosensis* Burt, 1932:179. Type locality "San Marcos Island (latitude 27°13'N., longitude, 112°05'W.), Gulf of California, Lower California [Baja California Sur, Mexico]."

*N. l. marshalli* Goldman, 1939:357. Type locality "Carrington Island, Great Salt Lake, [Toole County,] Utah (altitude about 4,500 feet)."

*N. l. molagrandis* Huey, 1945:307. Type locality "Santo Domingo Island (lat. 28°15'N.), Baja California, Mexico (more precisely, at the site of the old well near the edge of a mesa-like shelf, some 3 miles inland from the landing beach, elevation about 50')."

*N. l. nevadensis* Taylor, 1910:289. Type locality "Virgin Valley, Humboldt Co., Nevada, altitude 4,800 ft."

*N. l. notia* Nelson and Goldman, 1931:108. Type locality "La Laguna, Sierra de la Victoria, southern Lower California [Baja California Sur], Mexico (altitude 5,500 feet)."

*N. l. nudicauda* Goldman, 1905:28. Type locality "Carmen Island, Lower California [Baja California Sur], Mexico."

*N. l. perpallida* Goldman, 1909:139. Type locality "San Jose Island, off east coast of Lower California [Baja California Sur], Mexico."

*N. l. petricola* von Bloeker, 1938:203. Type locality "Abbott's Ranch, 670 feet altitude, Arroyo Seco, Monterey County, California."

*N. l. pretiosa* Goldman, 1909:139. Type locality "Matancita (called also Soledad), about 50 miles north of Magdalena Bay, Lower California [Baja California Sur], Mexico (altitude 100 feet)."

*N. l. ravida* Nelson and Goldman, 1931:107. Type locality "Comondú, southern Lower California [Baja California Sur], Mexico (altitude 700 feet)."

*N. l. vicina* Goldman, 1909:140. Type locality "Espíritu Santo Island, off east coast of southern Lower California [Baja California Sur], Mexico."

**DIAGNOSIS.** *Neotoma lepida* (Fig. 1) is a relatively small (total length usually <300 mm) rat-like rodent with a relative short, bicolored tail (ca. 75% of length of head and body) covered with short (ca. 6 mm) hairs; long vibrissae; long, lightly furred ears (only slightly shorter than length of hind feet); long, soft pelage; and wide sphenopalatine vacuities. It usually can be distinguished from sympatric and parapatric congeners by these characters combined with 1 or more of the following: hairs of underparts white with those on throat lead-colored basally; greatest length of skull usually <42 mm; baculum long (>10 mm), slender (0.45–1.1 mm in diameter at midlength), ventrally curved, and tipped distally with cartilaginous spine and proximally with a dumbbell-shaped bony expansion that tapers abruptly; length of glans penis 10 times its greatest diameter; anterior lingual reentrant angle on M1 absent or only slightly developed; postero-labial fold on M3 (Fig. 2) directed medially and almost meeting lingual fold; 2nd loph on M3 usually broad labially and at nearly a right angle to long axis of tooth (Burt and Barkalow 1942; Hall 1946; Hoffmeister 1986; Hoffmeister and de la Torre 1960; Hooper 1960; Verts and Carraway 1998).

**GENERAL CHARACTERS.** Dorsal pelages among desert woodrats range from pale, buffy gray to dark gray and from cinnamon to nearly black. Depending on the color of substrate, considerable variation in pelage color may occur within an area of



FIG. 1. Photograph of *Neotoma lepida*. Photograph reprinted from Verts and Carraway (1998) with permission of the photographer, Ronn Altig.

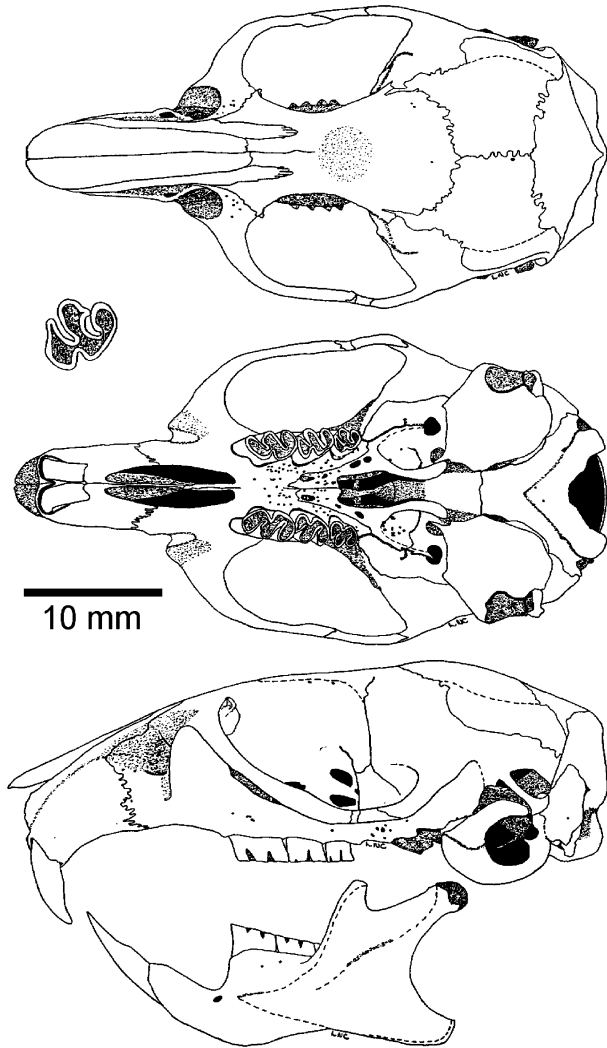


FIG. 2. Dorsal, ventral, and lateral views of cranium, lateral view of mandible, and occlusal view of M3 of an adult male *Neotoma lepida* (Oregon State University, Department of Fisheries and Wildlife [OSUFW] 5621) from Steens Mt., T30S, R31E, Sec. 14, Harney Co., Oregon. Greatest length of skull is 39.28 mm. Skull plate reprinted from Verts and Carraway (1998) with permission of the University of California Press.

≤250 km<sup>2</sup> (Lieberman and Lieberman 1970). Underparts and dorsal surface of feet are white; white hairs of throat have lead-colored bases. Pes is naked on outer side of plantar surface to tarsometatarsal joint. Like other members of the genus *Neotoma*, rostrum is slender; cheek teeth are rooted, hypsodont, flat-crowned, and prismatic with puddles of dentine extending the full width of grinding surfaces; M3s are smaller than M2s; and 2 pairs of mammae, both inguinal, are present. Scales on tail are less evident than in *Rattus*. Pes is pentadactyl, but manus has only 4 digits; skull (Fig. 2) is narrow interorbitally; frontoparietal ridges are absent; and incisive foramina are long and narrow, extending posteriorly to level of M1s (Bailey 1936; Goldman 1910; Hall 1946; Hoffmeister 1986). Desert woodrats with congenitally split ears are known (Dingman 1970).

Ranges of maximum body dimensions (in mm, *n* not available) of females and males (in parentheses) for all subspecies except *N. l. californica* were: total length, 281–392 (276–407); length of tail, 122–192 (119–198); length of hind foot, 27–38 (28–38); and length of ear from notch, 27–38 (28–38). With few exceptions, maximum dimensions tended to increase from north (Oregon–Nevada) to south (Baja California Sur—Alvarez-Castañeda and Cortés-Calva 1999; Durrant 1952; Hall 1946; Nelson and Goldman 1931; Orr 1934; Smith 1991; Taylor 1910; Verts and Carraway 1998; von Bloeker 1938). Ranges of maximum body mass (in g, *n* not available) of females and males (in parentheses) for 13 races from throughout

the species' range were: 122–240 (132–350—Hall 1946; Smith 1991; Verts and Carraway 1998). Ranges of maximum skull dimensions (in mm, *n* not available) of females and males (in parentheses) for 5 northern races were: greatest length of skull, 35.9–41.2 (38.8–46.0); basilar length, 30.6–36.3 (33.8–36.0); basal length, 36.3 (40.8); length of maxillary toothrow, 8.2–8.8 (7.9–9.1); zygomatic breadth, 19.9–22.3 (20.5–23.8); breadth of braincase, 16.6 (17.5); least interorbital breadth, 5.1–5.6 (5.2–5.9); skull depth, 13.1–14.0 (13.8–15.7); length of nasals, 14.2–16.3 (15.1–17.4); length of incisive foramen, 8.7–9.5 (8.0–9.5); and length of palatal bridge, 7.1–8.4 (7.2–7.8—Durrant 1952; Hall 1946; Taylor 1910; Verts and Carraway 1998). Ranges of maximum skull dimensions (in mm) reported for 4 races (sexes combined) from the Baja California peninsula were: greatest length of skull, 45.3–47.5; length of maxillary toothrow, 9.2–9.3; zygomatic breadth, 23.3–23.5; least interorbital breadth, 6.4–6.7; mastoid breadth, 18.1–18.6; rostral breadth, 5.2–5.4; and length of mandibular toothrow, 8.5–9.0 (Alvarez-Castañeda and Cortés-Calva 1999). We reported maximum values for body and skull dimensions and body mass because some minimum values (thus, averages also) might include either juvenile or damaged specimens.

Within *N. lepida* 2 morphotypes exhibiting penial differences are present (Mascarello 1978). The western type, distributed in Nevada and eastern California, is characterized by a cord (baculum) length (in mm) of  $11.01 \pm 0.6$  *SD* (range, 9.83–12.04; *n* = 30) and a protractile tip with a shallow cleft. The Baja type, distributed in the Baja California peninsula and western California is characterized by a cord length of  $15.52 \pm 1.4$  *SD* (range, 12.12–18.49; *n* = 29) and a protractile tip with a deep cleft. Averages and ranges (in parentheses) of dimensions (in mm) for bacula of 5 *N. l. lepida* were (Burt and Barkalow 1942): cord length, 11.26 (10.20–12.20); dorso-ventral diameter of base, 1.15 (0.99–1.25); lateral diameter of base, 1.98 (1.80–2.20); dorso-ventral diameter at midshaft, 0.50 (0.45–0.55); and lateral diameter at midshaft, 0.67 (0.61–0.70). The same dimensions for 11 *N. l. pretiosa* were: 18.01 (17.0–20.2), 1.53 (1.12–1.79), 2.51 (2.20–2.79), 0.77 (0.61–0.80), and 0.92 (0.81–1.10). These dimensions for 1 *N. gilva* were: 17.05, 1.32, 2.50, 0.60, and 0.70; for 1 *N. l. marcosensis* were: 18.55, 1.56, 2.40, 0.73, and 0.90; and for 2 *N. l. felipensis* were: 14.30–15.60, 1.00–1.30, 2.10–2.18, 0.64–0.65, and 0.70–0.80. These dimensions (8.40, 1.22, 2.00, 0.58, and 0.76) for 1 individual of the small island race *N. l. insularis* are considerably smaller than for either of the 2 recognized morphotypes of *N. lepida*.

**DISTRIBUTION.** *Neotoma lepida* occurs from southeastern Oregon, southwestern Idaho, and extreme northeastern California south through Nevada, western Utah, California south of San Francisco, and Baja California peninsula, Mexico (Fig. 3). The species also occurs on several islands in the Gulf of California and the Pacific Ocean near Baja California peninsula, Mexico. Individuals were captured at 2,440 m in Nevada (Linsdale 1938) and 2,900 m in California (Bole 1938).

**FOSSIL RECORD.** Fossil remains of *N. lepida* were recovered at 4 Late Wisconsinan–Early Holocene deposits in California, 14 sites in Nevada, and 2 caves in Utah; none was extralimital (Faunmap Working Group 1994).

**FORM AND FUNCTION.** Dental formula is *i* 1/1, *c* 0/0, *p* 0/0, *m* 3/3, total 16 (Hall 1981). Tracheae range from 0.82 to 0.88 mm in diameter and contain pseudostratified columnar ciliated cells 15–48 μm tall. The 15–20 cartilagenous plates are 77–125 μm in diameter. Parabasal cells containing 4 chromatin granules are numerous, but globlet cells are absent. Basement membrane is ca. 7 μm thick. Mucosa contains thick elastic reticular fibers and numerous capillaries. Submucosa also has thick elastic fibers, macrophages, seromucous glands, and abundant large blood vessels (Babero et al. 1973). Low ciliated columnar cells 26–34 μm tall line the bronchioles; low basal cells are abundant around the 1-μm-thick basement membrane. Small venules permeate tissue forming the gland-free submucosa. Terminal bronchioles are 192–336 μm wide proximally and narrow to 113–117 μm distally. Cells forming distal portions of terminal bronchiole are rounded and without cilia. Lining of respiratory bronchioles contains cuboidal cells with indistinct cilia but prominent basal bodies. Each bronchiole bifurcates distally, each branch of which is subdivided into 2–3 alveolar ducts. Ducts bifurcate with each branch further subdivided into 2–3 atria (Babero et al. 1973). Both ducts and atria have thick

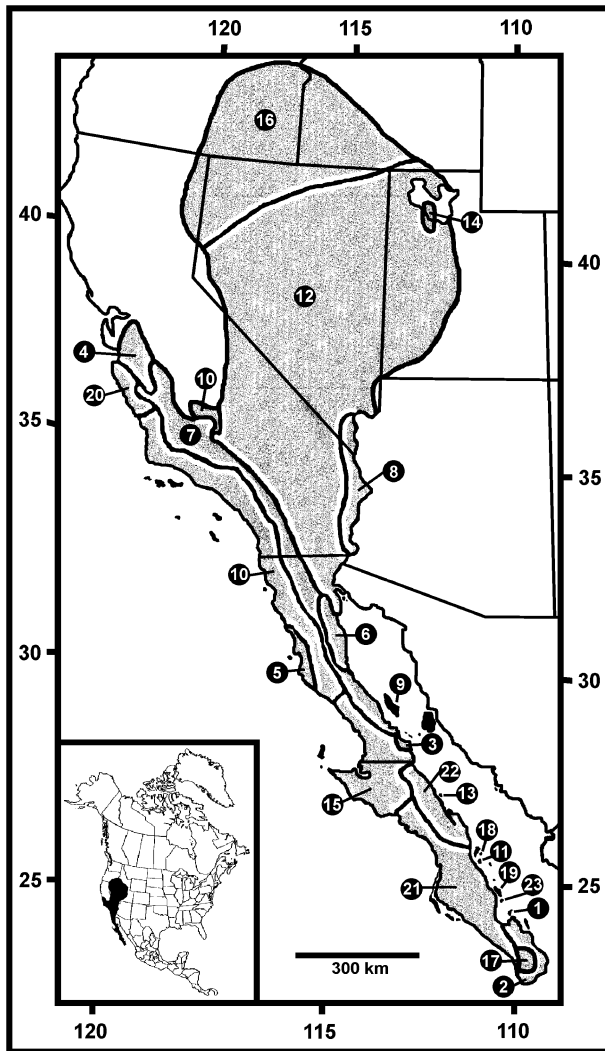


FIG. 3. Distribution of *Neotoma lepida*. Subspecies are 1, *N. l. abbreviata*; 2, *N. l. arenacea*; 3, *N. l. aridicola*; 4, *N. l. californica*; 5, *N. l. egressa*; 6, *N. l. felipensis*; 7, *N. l. gilva*; 8, *N. l. grinnelli*; 9, *N. l. insularis*; 10, *N. l. intermedia*; 11, *N. l. latirostra*; 12, *N. l. lepida*; 13, *N. l. marcosensis*; 14, *N. l. marshalli*; 15, *N. l. molagrandis*; 16, *N. l. nevadensis*; 17, *N. l. notia*; 18, *N. l. nudicauda*; 19, *N. l. perpallida*; 20, *N. l. petricola*; 21, *N. l. pretiosa*; 22, *N. l. ravida*; and 23, *N. l. vicina*. Map redrawn from Hall (1981:759, map 435) with modifications based on Koop et al. (1985), Mascarello (1978), and Musser and Carleton (1993).

walls of squamous or cuboidal epithelium. Atria, 88–157  $\mu\text{m}$  in diameter and containing capillaries within their walls, are separated by thick septa of cuboidal cells, elastic fibers, and capillaries. Alveoli are thick walled, 35–250  $\mu\text{m}$  in diameter, and lined with cells with spherical nuclei (Babero et al. 1973). The relatively small-diameter atria are considered to be involved in water economy (Babero et al. 1973).

In comparison with those of 78 other species of rodents, the sudoriferous glands of oral lips and angle are small, sebaceous glands are moderate, and mucous glands are extremely large (Quay 1965). Basihyal is small (5.2 mm wide, 1.3 mm thick through entoglossal process), thyrohyals are straight and slender without flare or trochanters (4.4 mm long, 9.8 mm wide), and ceratohyals are boot-shaped (2.2 mm long); arch of basihyal and thyrohyals is 4.4 mm long (Sprague 1941).

In comparison with 9 other species of *Neotoma*, the glans penis of *N. lepida* has the longest distal tract (22.5 mm), longest glans (19.4 mm), longest baculum (14.4 mm, but 17.6 mm including cartilagenous tip), and smallest diameter (2.1 mm). Glans is a gently curved simple cylinder with a finely annulated surface (resembling an earthworm), a bifurcate tip, and short tubercles, each

in a circular pit, on basal one-fourth (Hooper 1960). Uniqueness of the glans penis supports Burt and Barkalow's (1942) contention that the species should be segregated subgenerically (Hooper 1960).

For specimens ( $n = 5$ ) of *N. lepida* in which body mass averaged ( $\pm SE$ ) 98.9  $\pm$  8.9 g (Karasov and Diamond 1985; Karasov et al. 1986), length of the small intestine averaged 42  $\pm$  3 cm with a surface area of 39.6  $\pm$  3  $\text{cm}^2$ ; the same dimensions for the large intestine were 32.1  $\pm$  1 cm and 49.2  $\pm$  5  $\text{cm}^2$ . Microscopic area of the small intestine (including villi and ridges) was 506  $\pm$  57  $\text{cm}^2$  (Karasov and Diamond 1985). The 1.3:1 ratio of length of intestinal segments in favor of the small intestine is contradictory to the 0.5:1 ratio reported by Hoffmeister (1986) and to that depicted by Karasov et al. (1986:601, figure 1). At death, the digestive tracts of captive *N. lepida* fed alfalfa pellets and water ad lib. contained an average of 3.45 g of digesta: 27  $\pm$  1% was in the stomach, 15  $\pm$  3% was in the small intestine, 23  $\pm$  2% was in the cecum, and 35  $\pm$  1% was in the large intestine. Passage of 50% of digesta markers required 3–5 h; dry matter digestibility ( $n = 4$ ) was 55  $\pm$  2% (Karasov et al. 1986). Average ( $\pm SE$ ) percent digestibility was 56  $\pm$  3% for ash, 69  $\pm$  2% for nitrogen, 34  $\pm$  2% for neutral detergent fiber (plant cell walls), and 70  $\pm$  2% for neutral detergent-soluble fraction (plant cell contents—Karasov and Diamond 1985; Karasov et al. 1986).

Average body mass of groups of desert woodrats acclimated to 5°C ( $n = 6$ ) and 35°C ( $n = 10$ ), and controls held at 28°C ( $n = 13$ ), for 4 weeks with ad lib. food and water did not differ significantly from that of the groups initially. However, average ( $\pm SE$ ) food intake (g/day) was 11.1  $\pm$  1.3, 2.7  $\pm$  0.3, and 3.8  $\pm$  0.3; body temperature (°C rectally) averaged 33.0  $\pm$  0.3, 37.9  $\pm$  0.2, and 36.0  $\pm$  0.2; average plasma glucose (mg/100 ml) was 105.4  $\pm$  6.9, 97.1  $\pm$  8.4, and 109.9  $\pm$  4.3; and average in vitro glucose absorption (mg glucose 100 g tissue<sup>-1</sup> h<sup>-1</sup>) was 49.2  $\pm$  9.8, 102.3  $\pm$  11.8, and 44.0  $\pm$  4.3 for the 3 groups, respectively. The increase in serosal transfer of glucose may not represent an increase in glucose metabolism because the gut wall was "much thinner" in heat-acclimated woodrats and "much thicker" in cold-acclimated woodrats than in controls (Chu et al. 1979:484). Alterations in glucose transport during heat acclimation may compensate for reduced food intake (Chu et al. 1979). Cold acclimation also increased oxygen consumption, rates of secretion and turnover of thyroxine, and plasma T<sub>3</sub>; body temperature declined 2°C, but plasma T<sub>4</sub> and hematocrit did not change significantly. Heat acclimation caused a decline in oxygen consumption, rates of secretion and turnover of thyroxine, plasma T<sub>3</sub> and T<sub>4</sub>, and hematocrit (Yousef and Johnson 1978).

Ranges in mass of the liver, kidney, and intrascapular brown fat relative to body mass (as estimated from graphs) of wild-caught desert woodrats sampled monthly throughout the year from a California population were: 3.8–5.3%, 1.0–1.4%, and 0–0.8%, respectively. In late summer, all 3 values and specific activity of Na<sup>+</sup>-K<sup>+</sup>-ATPase in liver and kidney were lowest (Davis and Hillyard 1983). As temperatures cooled in autumn, relative mass of liver and Na<sup>+</sup>-K<sup>+</sup>-ATPase in both liver and kidney increased significantly. During December–January, when ambient temperature (T<sub>a</sub>) was lowest, relative mass of intrascapular brown fat increased and remained elevated through spring. Thus, desert woodrats may reduce metabolic heat production in the vicera (a major source of metabolic heat) in summer and increase heat production rapidly as T<sub>a</sub> declines in autumn. During winter, when brown-fat is capable of sufficient thermogenesis, the relative mass of vicera and its capability for thermogenesis decline (Davis and Hillyard 1983).

Mean dry mass of desert woodrats ( $n = 13$ ) from southern California was 25.9 g, with 14.7% ash and 8.1% fat. Mean ( $\pm 2 SE$ ) chemical composition (mg/g dry mass) of the woodrats was: N, 116  $\pm$  4.7; Ca, 38.2  $\pm$  2.0; S, 33.0  $\pm$  4.6; P, 21.9  $\pm$  1.1; K, 13.0  $\pm$  0.5; Na, 3.94  $\pm$  0.47; Mg, 1.32  $\pm$  0.09; Fe, 230  $\pm$  22; Al, 166  $\pm$  16; Zn, 66.1  $\pm$  5.2; Sr, 57.5  $\pm$  7.7; Mn, 4.5  $\pm$  1.2; Ba, 42.3  $\pm$  5.7; B, 6.1  $\pm$  0.7; and Mo, 2.6  $\pm$  0.1 (Wiener et al. 1977).

Average ( $\pm SE$ ) dry biomass of *N. lepida* ( $n = 17$ ) from a xeric habitat in California was 24.16  $\pm$  3.61 g, of which 7.64  $\pm$  1.40% was fat and 14.72  $\pm$  0.99% was ash. Energy density for average dry biomass was 20.13  $\pm$  0.25 kJ/g, and for average ash-free dry biomass it was 23.16  $\pm$  0.17 kJ/g. *N. lepida* had the lowest percent fat and energy density for ash-free dry biomass and the highest dry biomass among 16 species tested (Kaufman et al. 1975).

Mean hemoglobin concentration (g%) of *N. lepida* averaged

ca. 12.2 in summer ( $n = 10$ ) and ca. 15.7 in winter ( $n = 3$ ). The log of mean hemoglobin concentration in relation to log of mean body mass was the lowest among 7 species of desert rodents in both summer and winter (Lee and Brown 1970). Plasma corticosterone levels in samples collected on 4 successive days from specimens ( $n = 10$ ) held captive 2–4 weeks averaged ( $\pm SE$ )  $105 \pm 15.4$  ng/ml and comprised an average of  $99.6 \pm 0.7\%$  of glucocorticoids secreted by the adrenal cortex. Levels decreased by 48% from day 1 to day 3. Relatively low corticosterone level may function as an adaptive thermoregulatory mechanism by decreasing endogenous heat production and conserving water (Vanjonack et al. 1975).

Minimal metabolic rates ( $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) were 0.79 in low desert ( $n = 7$ ), 0.79 in higher desert ( $n = 11$ ), and 0.72 in coastal areas ( $n = 7$ ). At  $6^\circ\text{C}$  the values were 2.38, 2.20, and 1.90 for the 3 areas, respectively (Brown and Lee 1969; Lee 1963).

Total lung volume averaged ( $\pm SE$ )  $4.55 \pm 0.26$  ml, and total alveolar surface area averaged  $0.218 \pm 0.006 \text{ m}^2$  for 3 wild-caught desert woodrats with an average body mass ( $W$ ) of  $146 \pm 14$  g. Standard oxygen consumption ( $\text{ml/min}$ ) was  $0.0602 \times W^{0.727}$ , and maximum oxygen consumption was  $0.499 \times W^{0.678}$  (Lechner 1978).

Body temperature of captives ( $n = 12$  individuals; 26 measurements) measured from 0830 to 1000 h at a  $T_a$  of  $22^\circ\text{C}$  averaged ( $\pm SD$ )  $36.8 \pm 0.75^\circ\text{C}$  for a desert race (*N. l. lepida*) and  $36.7 \pm 0.78^\circ\text{C}$  for a coastal race (*N. l. intermedia*). Temperature of *N. lepida* nests containing young ( $n = 22$  measurements) averaged ( $\pm SE$ )  $28.6 \pm 0.27^\circ\text{C}$  (Schwartz and Bleich 1976). Body temperature of juveniles increased slightly between 3 and 25 days of age ( $Y = 0.1124X + 33.831$ ), and loss of body temperature declined with age when young were placed in a chamber at  $6.9\text{--}8.0^\circ\text{C}$  ( $Y = 22.665 + 0.958X - 0.0178X^2 + 1.175 \times 10^{-4}X^3$ ). Although morphological development may be prolonged in *N. lepida*, thermoregulatory development is more rapid than in the somewhat larger *N. albigula* (Schwartz and Bleich 1976).

Average ( $\pm SE$ ) evaporative water losses ( $\text{mg g}^{-1} \text{ h}^{-1}$ ) of summer-caught ( $n = 10$ ) and winter-caught ( $n = 10$ ) desert woodrats maintained in captivity at a  $T_a$  of  $30 \pm 0.5^\circ\text{C}$  and a relative humidity of 20% were  $1.44 \pm 0.10$  and  $1.23 \pm 0.07$ , respectively. Average maximum chloride concentrations ( $\text{mEq/l}$ ) of urine ( $n = 10$  and  $n = 9$ ) collected within 6 h from desert woodrats to which 3.0 ml of a solution of 3 M NaCl/100 g body mass was administered by lavage were  $232.2 \pm 14.0$  and  $236.9 \pm 22.3$  for the 2 groups, respectively. In neither test were differences between groups significant (Stallone 1979). Average ( $\pm SE$ ) evaporative water loss and chloride concentration of summer-caught desert woodrats acclimated to winter conditions were  $1.21 \pm 0.05$  ( $n = 10$ ) and  $303.6 \pm 32.3$  ( $n = 9$ ), but for winter-caught animals acclimated to summer conditions the values were  $0.88 \pm 0.05$  ( $n = 10$ ) and  $466.7 \pm 20.9$  ( $n = 9$ ). Seasonal values for both concentrations were significantly different. The lesser evaporative water loss of summer-acclimated animals was not a result of a reduced metabolic rate because oxygen consumption of animals in this group was not significantly different from that of the other group (Stallone 1979).

Daily water consumption of captive individuals maintained at  $20\text{--}23^\circ\text{C}$  and 50–80% relative humidity averaged 18.0 ml/day for a coastal race (*N. l. intermedia*), whereas those of a desert race (*N. l. lepida*) drank an average of 35.9 ml/day (Lee 1963). Deprived of water, individuals of the desert race ( $n = 10$ ) lost 6.3% of body mass/day (MacMillen 1964) and weighed only 84% of the initial body mass ( $n = 9$ ) in 4 days (MacMillen and Christopher 1975); all were dead by 5.3 days (MacMillen 1964). Loss totaled 32.5% of body mass for the desert race and 28.8% for the coastal race for individuals that died of water deprivation (Lee 1963). When succulent vegetation was absent, woodrats required ca.  $5 \text{ cm}^3$  water/day to maintain body mass; thus, they must consume plants with an average ( $\pm SE$ ) of at least  $0.65 \pm 0.03 \text{ cm}^3/\text{g}$  of dry mass (Karasov 1989).

Under laboratory conditions, urine osmotic concentrations averaged ( $\pm SD$ )  $396 \pm 236 \text{ mOsm/l}$  for *N. lepida* ( $n = 10$ ) provided water ad lib. but  $2,436 \pm 445 \text{ mOsm/l}$  when deprived of water ( $n = 9$ ). Under field conditions when rainfall was 103 mm in 1 year but only 21 mm in the next, blood plasma osmotic concentrations were "fairly stable" at ca.  $350 \text{ mOsm/l}$ , and urine osmotic concentrations "remained quite dilute" at ca.  $1,000\text{--}2,000 \text{ mOsm/l}$  irrespective of rainfall (MacMillen and Christopher 1975:126). The "uniformly low concentrations [reflect] the succulent, low-proteinaceous nature of its diet" (MacMillen and Christopher 1975:132).

**ONTOGENY AND REPRODUCTION.** In the San Gabriel Mountains, California, the breeding season of *N. lepida* based on the occurrence of pregnant or lactating (or both) females extended from November to May; females produced 1–4 (mean, 2.7) litters per breeding season with juvenile females born early in the season becoming reproductively active later in the same season (MacMillen 1964). In southwestern Utah females taken in February, March, May, and July had an average of 2.9 embryos (Long 1940). In southern Nevada 9 of 13 adult females collected in June were pregnant with an average of 3.1 embryos; 1 pregnant female was lactating (Deacon et al. 1964). In the same region, in May and June, 3 pregnant females each with 4 embryos were collected; 1 of the females collected in June also was nursing 4 quarter-grown young (Burt 1934). During a drought in the Mohave Desert, California, desert woodrats ceased to reproduce; none in reproductive condition was captured during a 20-month period (Smith 1995a).

In captivity, average litter size of *N. l. lepida* from Utah ( $n = 100$ ) was 2.3 (mode = 2; range, 1–5—Egoscue 1957). Based on 1,297 litters, maximum litter size = 5, maximum litters/year = 11, maximum young/year = 37, maximum litters/lifetime = 29, maximum young/lifetime = 82, and maximum age at birth of last litter = 3 years + 4 months (Egoscue et al. 1970). Gestation period is 30–36 days (Egoscue 1957).

Average litter size was 2.6 (range, 1–5) for wild-caught pregnant *N. l. lepida* from California ( $n = 19$ ) maintained in captivity. Selection for litter size likely is related to maternal nutrition because an average of 4.5 young/litter were born to females ( $n = 4$ ) from mesic desert woodlands, whereas an average of only 2.1 young/litter were born to females ( $n = 15$ ) from the less-productive scrub vegetation on the desert floor (Cameron 1973).

In Utah the average mass of neonates ( $n = 100$ ) born in captivity was 10.4 g; dorsum was pigmented and tips of hairs were visible. Two young (1 of each sex) that averaged 12.3 g with 26-mm tails, 13.5-mm hind feet, and 6-mm ears at birth averaged 23.5 g with 38.5-mm tails, 21.5-mm hind feet, and 12-mm ears at 10 days of age. Eyes and ears opened at 10 days postpartum, although 11–13 days was given as the range for opening of the eyes (Egoscue 1957). Rainey (1965) described the birth of 4 premature young *N. l. lepida* from California; 2 thought to be males weighed 4.4 and 4.8 g and measured 34.0- and 38.9-mm crown-rump length with 15.1- and 15.3-mm tails and 7.5- and 8.3-mm hind feet, respectively. Vibrissae were 2 mm long, but no other hair was noted. The young exhibited a suckling response when the nose was touched (Rainey 1965).

At birth, incisors of *N. lepida* (Egoscue 1957) are splayed with posteriorly directed tips forming a hexagonal opening in anterior aspect (Hamilton 1953:186, plate II). Nipples of neoparturient females are gripped in the hexagonal opening between the recurved incisors so securely that separation of nursing young and maternal females is difficult. Although in captivity young desert woodrats nursed for ca. 4 weeks, by 12 days postpartum, the incisors were no longer effective in maintaining a hold (Egoscue 1957). In females with small litters only the posterior pair of mammae provided milk. Young began to consume solid food at ca. 3 weeks of age (Egoscue 1957).

In California, average ( $\pm SE$ ) mass of young born to wild-caught pregnant females was  $10.5 \pm 0.2$  g for litters of 1 ( $n = 6$ ) and  $10.7 \pm 0.4$  g for litters of 2 ( $n = 3$ ), but declined to  $8.8 \pm 0.1$  g for litters of 3 ( $n = 5$ ),  $7.8 \pm 0.1$  g for litters of 4 ( $n = 3$ ), and  $6.3 \pm 0.1$  g for litters of 5 ( $n = 2$ ). All young of litters of 1–3 survived to weaning, but only 75% of those in litters of 4 and only 50% of males and 34% of females in litters of 5 survived to weaning. However, average age at weaning was a positive linear function of litter size ( $r^2 = 0.986$ ,  $P = 0.007$ ), with singletons weaned at  $16.0 \pm 0.4$  days, and litters of 5 weaned at  $41.8 \pm 0.3$  days. Conversely, average growth rate ( $\text{g/day}$ ) was a negative linear function of litter size ( $r^2 = 0.804$ ,  $P = 0.039$ ), with singletons growing  $1.58 \text{ g/day}$ , and individuals in litters of 5 growing only  $0.698 \text{ g/day}$  (Cameron 1973).

Wild-caught pregnant *N. l. intermedia* in California ( $n = 14$ ) gave birth to an average of 2.7 (range, 2–4) young in captivity. Average ( $\pm SD$ ) mass at birth was  $9.5 \pm 1.5$  g for females ( $n = 10$ ) and  $9.6 \pm 0.9$  g for males ( $n = 8$ ); by 101 days, females ( $n = 9$ ) averaged  $105.7 \pm 20.0$  g, and males ( $n = 12$ ) averaged  $127.6 \pm 32.0$  g. The latter values were 70.3% and 67.1% of the adult values, respectively (Schwartz and Bleich 1975).

**ECOLOGY.** *Neotoma lepida* usually occurs in habitats with succulent vegetation, but usually is not found in cultivated areas (Cortés-Calva and Alvarez-Castañeda 1997). Occupied habitats include salt marshes (Borell 1935), mule fat (*Baccharis glutinosa*) scrub in a riparian zone (O'Farrell et al. 1994), sagebrush (*Artemisia*—Bleich and Schwartz 1975; Feldhamer 1979), chapparal (Horton and Wright 1944; Schwilk and Keeley 1998), juniper (*Juniperus osteosperma*)—sagebrush (Stones and Hayward 1968), creosote bush (*Larrea divaricata*) scrub (Bradley and Mauer 1973; Cameron and Rainey 1972; Thompson 1982), Joshua tree woodland (*Yucca brevifolia*, *J. californica*, *Eriogonum fasciculatum*), scrub oak woodland (*Quercus turbinella*, *Cercocarpus betuloides*), piñon—juniper woodland (*Pinus monophylla*, *J. californica*, *Y. schidigera*), and a cholla cactus garden (*Opuntia bigelovii*—Cameron and Rainey 1972). In southwestern Utah, *N. lepida* was captured in piñon (*P. edulis* or *P. monophylla*)—juniper (*J. osteosperma*), sagebrush (*A. filifolia* and *A. tridentata*), shadscale (*Atriplex canescens*), blackbrush (*Coleogyne ramosissima*), and creosote bush (*L. tridentata*) communities, but was most abundant in the latter (Honeycutt et al. 1981). In a year-long study on a 2.7-ha trapping grid in a heterogeneous habitat in western Nevada, *N. lepida* was captured only in July–November and only in shadscale (*Atriplex confertifolia*) scrub (O'Farrell 1980). In southern Nevada, *N. lepida* may attain "its upper distributional limit in the upper part of the juniper–piñon community [ $<2,560$  m] and only rarely extends into the fir–pine community" (Deacon et al. 1964:404). In microhabitats within a coastal sage scrub community in California, rates of capture ( $n/100$  trap-nights) of desert woodrats in spring were: 1.8 in clearings  $\geq 4$  m<sup>2</sup>, 4.2 under shrub canopy  $\geq 1$  m tall, 6.5 adjacent to or on boulders  $\geq 1$  m<sup>2</sup>, and 1.1 within patches of fallen dead brush  $\geq 1$  m<sup>2</sup> (Price and Kramer 1984).

The critical feature of the habitat is physical characteristics that afford protection from predators (Brown et al. 1972). These may be alcoves, crevices, rockpiles, and fissures in rimrocks (Llewellyn 1981; Thompson 1982; Verts and Carraway 1998). In a coastal region of California, 89.9% of 99 individuals captured were on transects "having more large rocks ( $>25$  mm diameter)" than others (Fellers 1994:131). In some regions, *N. lepida* relies on joints of cholla cactus that litter the desert floor for protection from predation in addition to using the plant for food, water, and construction of houses (Brown et al. 1972).

On an area in the Mohave Desert, California, where blackbrush, Mohave yucca (*Y. schidigera*), and buckhorn cholla (*O. acanthocarpa*) were the predominant species, 63.5% of 98 woodrat houses were constructed with Mohave yucca as the primary structural support, 34.4% with buckhorn cholla, and 2.1% with pencil cholla (*O. ramosissima*). The principal materials used in the construction of houses were the same as those forming their structural support. Although houses built of Mohave yucca were nearly twice as abundant, mean ( $\pm CI$ ) occupancy rate of those houses by *N. lepida* was about half ( $7 \pm 2.3\%$ ,  $n = 61$ ) that of houses of buckhorn cholla ( $13 \pm 4.7\%$ ,  $n = 35$ ) and pencil cholla ( $13\%$ ,  $n = 2$ ). Also, mean ( $\pm SD$ ) survival was significantly higher ( $P < 0.05$ ) for individuals occupying houses of cholla ( $4.1 \pm 1.8$  months) than of yucca ( $2.5 \pm 1.4$  months—Smith 1995a). Plant residues in middens associated with houses when subjected to radio-carbon dating are useful in the reconstruction of prehistorical plant communities (King 1976).

*Neotoma lepida* tends to be a dietary specialist as its feeding is concentrated on relatively few species of plants within a community (Meserve 1974; Vaughan 1982); nevertheless, over its geographic range a wide variety of plants are consumed. For example, on Isla Danzante in the Gulf of California, 79.5% of the diet of *N. l. latirostra* in summer and 63.8% in winter was leaves of ironwood (*Olneya tesota*—Vaughan and Schwartz 1980). Cholla cactus (*Opuntia cholla*) and leaves of a few shrubs also were consumed in small amounts. During a year that ironwood lost its leaves, woodrats shifted their diet to its seeds. They also clipped 43% of the branches of frijolillo (*Desmanthus fruticosus*), but based on fecal samples did not consume much of it (0.9% of the diet in summer and 1.6% in winter—Vaughan and Schwartz 1980). A different plant species (either shrub live oak [*Q. turbinella*], catclaw [*Acacia greggii*], or creosote bush [*L. divaricata*]) was the predominant item in stomachs and food caches of woodrats in 3 communities in Joshua Tree National Monument, California (Cameron and Rainey 1972). In a coastal sage community in California, the primary food (68–91% of the diet) consisted of white sage (*Salvia apiana*); all

parts of the plant were eaten (Meserve 1974). In Utah, desert woodrats fed on juniper (*J. utahensis*) foliage and berries; both were abundant in food caches that also included leaves of Brigham tea (*Ephedra nevadensis*), buckwheat (*Erigonum*), prince's-plume (*Stanleya pinnata*), and sagebrush (*Artemisia tridentata*); seeds of milk-vetch (*Astragalus cibarius*); and flowers of globe mallow (*Sphaeralcea coccinea*—Stones and Hayward 1968). In Idaho, *N. lepida* ate shadscale (*Atriplex confertifolia*) and fleshy parts of prickly pear cactus (*Opuntia*—Johnson 1961). Desert woodrats can consume plants containing large amounts of oxalic acid and resinous and aromatic substances (Meserve 1974). Although particularly sensitive to water deprivation, in desert regions of southern California, desert woodrats can obtain adequate water by consuming either *O. occidentalis* (MacMillen 1964) or possibly *L. divaricata* (Lee 1963). In areas where succulent vegetation is not available, *N. lepida* can increase water-conserving abilities through acclimation. This may explain its broad distribution in comparison with some congeners (Stallone 1979).

Other factors also affect the diet of *N. lepida* as in the Mohave Desert, California, it consumed 60% turbinella oak (*Q. turbinella*), 25% juniper (*J. californica*), and 15% Mohave yucca (*Y. schidigera*) in areas unoccupied by *N. fuscipes*, but 45% oak, 40% juniper, and 13% yucca where the 2 species were syntopic. The behavioral dominance of *N. fuscipes*, as revealed by paired encounters of captive individuals of the 2 species, was believed responsible for the shift in diet by *N. lepida* (Cameron 1971).

In some regions (e.g., parts of the Mohave Desert, California), 70–95% of the dry-season (November–early December) diet consists of creosote bush. Leaves of this shrub are coated with phenolic resins (10–25% of dry mass), with immature leaves having the highest levels. Feeding trials with creosote bush leaves, leaves from which phenolic resins were extracted, and laboratory chow laced with the phenolic resins indicated that desert woodrats fed selectively to minimize resin intake (Meyer and Karasov 1989), but the resin did not reduce digestibility of foods as hypothesized earlier (Rhoades and Cates 1976). Resins in creosote bush, and possibly tannins, flavonoids, turpines, oxylates, and alkaloids in other plants, can reduce food intake to the point of starvation or prevent adequate water balance; thus, populations of desert woodrats tend to be regulated by defensive chemistry of the plants they consume (Karasov 1989; Meyer and Karasov 1989).

In captivity, desert woodrats lost body mass when a half-ration of laboratory chow was supplemented with goldenbush (*Aplopappus* [= *Ericameria*]), snakeweed (*Gutierrezia*), or Joshua tree (*Y. brevifolia*), but they maintained or gained mass when supplemented with four-o'clock (*Mirabilis bigelovii*), tickseed (*Coreopsis bigelovii*), Mojave-aster (*Machaeranthera* [= *Xylorhiza*] *toritifolia*), or creosote bush (*L. divaricata*). Flowers, leaves, and stems of the latter group of species were eaten in that order (Chess and Chew 1971).

In a creosote bush community in southern Nevada, *N. lepida* composed 1.6% of 1,207 rodents captured and 4.5% of biomass of rodents (Bradley and Mauer 1973). On a 16,215-ha area burned during a wildfire in California, relative density of *N. lepida* was greatest near the center of the population in chapparal habitats, but greatest near the edge in coastal sage–scrub habitats (Schwilk and Keeley 1998). An estimate of June–July density in a coastal sage community in California was ca. 30/ha; no animal was captured  $>7$  m from rocks (Bleich and Schwartz 1975). Also, in California, density of a *N. lepida* population on a 3.1-ha grid in coastal sage scrub declined from 19 to 2 from July to December, remained stable till March, increased to 11 by May, and then declined to 4 by September. Eight of 17 new individuals captured in April–July were transients; of 44 individuals captured, only 21 became resident, and those residents remained an average of only 3.5 months (M'Closkey 1972). In the San Gabriel Mountains, California, densities ( $n/ha$ ) in January–December on a 2.7-ha grid, as calculated by the Lincoln Index, were 1.4, 1.7, 1.9, 4.4, 3.4, 3.2, 4.9, 3.7, 3.8, 3.9, 2.6, and 2.6 during 1958. Average persistence of 133 individuals marked on the grid was 4.1 months (MacMillen 1964). In another California study, rates of capture ( $n/100$  trap-nights) were 0 in areas vegetated by gray rabbitbrush (*Chrysothamnus nauseosus*) and creosote bush, 0.2 in those dominated by gray rabbitbrush, and 0.1–2.5 in those dominated by creosote bush (Hafner 1977). In southern California, rate of capture (percent trap success) of *N. lepida* declined from 21.7 in spring 1975, when precipitation was near the long-time average, to 2.4 in spring 1976, when cumulative precipitation

was 16.04% below average (Spevak 1983). Sex ratio in a sample ( $n = 80$ , age not reported) from California was 1.1:1 in favor of males (Schwilk and Keeley 1998).

Insular races of *N. lepida* off Baja California are usually larger than their presumed mainland counterparts because of a combination of an absence of predators and the advantage larger size imparts for the ability to extract "more energy and nutrients" from plants in their diet through enhanced digestion of fiber by hindgut fermentation (Smith 1992, 1995b:304). Competition with other herbivores for food resources was rejected as a possible selective pressure because some races of insular woodrats tend to be dietary specialists (Smith 1992). In captivity, smaller individuals of *N. l. lepida* and *N. l. intermedia* reduced fiber in the diet by discarding high-fiber particles (Justice and Smith 1992).

Mammalian associates of *N. lepida* include *Ammospermophilus insularis*, *A. leucurus*, *Canis latrans*, *Chaetodipus arenarius*, *C. fallax*, *C. rudinoris*, *Dipodomys agilis*, *D. merriami*, *D. microps*, *D. ordii*, *D. panamintinus*, *D. stephensi*, *D. venustus*, *Felis silvestris*, *Lynx rufus*, *Mephitis mephitis*, *Microdipodops megacephalus*, *Microtus californicus*, *M. montanus*, *Mus musculus*, *N. cinerea*, *N. fuscipes*, *Notiosorex crawfordi*, *Onychomys leucogaster*, *O. torridus*, *Peromyscus boylii*, *P. californicus*, *P. crinitus*, *P. eremicus*, *P. eva*, *P. fraterculus*, *P. maniculatus*, *P. merriami*, *P. truei*, *Perognathus californicus*, *P. formosus*, *P. longimembris*, *P. parvus*, *Rattus rattus*, *Reithrodontomys megalotis*, *Spermophilus beecheyi*, *S. canus*, *Sylvilagus auduboni*, *S. nuttalli*, *Tamias dorsalis*, *T. minimus*, *Taxidea taxus*, *Thomomys talpoides*, *Urocyon cinereoargenteus*, and *Vulpes velox* (Bradley and Mauer 1973; Deacon et al. 1964; Egoscue 1957; Feldhamer 1979; Fellers 1994; Fisher 1941; Honeycutt et al. 1981; McClenaghan and Taylor 1993; O'Farrell 1980; O'Farrell et al. 1994; Riddle et al. 2000; Rutledge et al. 1979; Ryckman et al. 1965; Stones and Hayward 1968). Lizards associate with desert woodrats and their nests include *Sceloporus graciosus*, *S. magister*, *Uta stansburiana*, and *Xantusia vigilis* (Egoscue 1957; Wood 1944). California quail (*Lophortyx californicus*) nest inside stick houses of *N. lepida* in Baja California Sur (Ryckman and Ryckman 1960).

Predators of *N. lepida* include *C. latrans*, *V. velox*, *Buteo jamaicensis*, and *Bubo virginianus* (Egoscue 1957; Vaughan 1954; White et al. 1995), and possibly *T. taxus* (Egoscue 1957). Desert woodrats also consume conspecifics and other rodents caught in traps (Vaughan 1954).

Ectoparasites of *N. lepida* include bot fly larvae (Diptera: *Cuterebra*—Baird and Graham 1973; Egoscue 1957; MacMillen 1964; Stones and Hayward 1968). Mites and chiggers (Acarina) include: *Acomatacarus linsdalei*, *A. micheneri*, *Androlaelaps casalis*, *A. fahrenholzi*, *Androlaelaps*, *Brevisterna utahensis*, *Dermanyssus becki*, *D. gallinae*, *Echinonyssus bisetosus*, *E. hilli*, *E. incomptus*, *E. neotomae*, *E. utahensis*, *Eubrachylaelps circularis*, *E. hollisteri*, *Euschoengastia ambocalis*, *E. californica*, *E. criceticola*, *E. fasolla*, *E. frondifera*, *E. lacerta*, *E. lanceolata*, *E. marginalis*, *E. obessa*, *E. radfordi*, *E. utahensis*, *Eutrombicula batatas*, *Haemogamasus ambulans*, *H. casalis* (?), *H. pontiger*, *H. utahensis*, *Hexidionis jessiemae*, *H. navajoae*, *Leeuwenhoekia americana*, *Liponyssoides becki*, *Microtrombicula nasalis*, *M. wrenni*, *Neotrombicula californica*, *Odontacarus arizonensis*, *O. cognatus*, *O. chiapanensis*, *O. kromani*, *O. linsdalei*, *Parasitus*, *Pseudoschoengastia*, *Trombicula allredi*, *T. belkini*, *T. microti*, *T. panamensis*, *T. potosina*, *T. sargenti*, *T. sola*, and *Whartonia whartoni* (Allred 1957; Allred and Goates 1964; Bennett and Loomis 1980; Brennan 1966; Brennan and Beck 1955; Goff and Loomis 1973; Hansen 1964; Loomis 1963; Loomis and Bunnell 1962; Loomis and Somerby 1966; Lucas and Loomis 1968; Radford 1950; Webb and Loomis 1970; Whitaker and Wilson 1974; Wrenn and Loomis 1973; Wrenn and Somerby 1974). Desert woodrats are also infested with ticks (Acarina): *Dermacentor parumapertus*, *D. andersoni*, and *Ornithodoros hermsi* (Egoscue 1957; Hansen 1964); lice (Anoplura): *Neohaematopinus neotomae* and *N. inornatus* (Hansen 1964; Ryckman and Lee 1958); and fleas (Siphonaptera): *Aetheca* (= *Monopsyllus wagneri*, *Anomiopsyllus amphibolus*, *A. falsicalifornicus*, *A. nudatus*, *Atyphloceras echis longipalpus*, *A. felix* [sic; ? = *Ctenocephalides felis*]), *Delotelis mohavensis*, *Echnidnophaga gallinacea*, *Eumolpianus eumolpi*, *Malaraeus sinomus*, *M. telchinus*, *Megarthroglossus smiti*, *Meringis dipodomys*, *Opisodasys*, *Orchopeus leucopus*, *O. sexdentatus agilis*, *Phalacropsylla oregonensis*, *Rhadinopsylla heiseri*, *Stenistomera alpina*, *S. macrodactyla*, and *Traubella neotomae* (Angustson 1941; Barnes et al.

1977; Casebeer 1965; Egoscue 1957, 1976; Good 1942; Hansen 1964; Hubbard 1968; Lewis et al. 1988; Parker and Howell 1959; Prince et al. 1976).

Endoparasites include acanthocephalans (Acanthocephala): *Moniliformis clarki* (McKeever 1963); and roundworms (Nematoda): *Nematodirus tortuosus* (Tucker 1942). Adults of the lymphatic-dwelling filarial nematodes *Brugia pahangi* and *B. malayi* were recovered from various tissues of some captive desert woodrats after inoculation with the infective stages, but no microfilariae (larvae) were found in the blood (Ash and Riley 1970a, 1970b). Protozoan hemoparasites thought to be either *Plasmodium* or *Babesia* were found in the erythrocytes of *N. lepida* that exhibit cachexia in Utah (Frandsen and Grundmann 1961). Piroplasms of *B. microti* were found in *N. lepida* in southern California (Van Peenen and Duncan 1968).

Arthropod consorts in houses in Utah include 11 families in 3 orders of Arachnoidea and 34 families in 12 orders of Insecta (Beck et al. 1953). A year-long collection at 98 houses occupied by *N. lepida* contained an average of 20.6 fleas/house; species and numbers (in parentheses) of each were: *Aetheca wagneri* (17), *Aetheca* (2), *Anomiopsyllus amphibolus* (1,726), *Atyphloceras echis* (27), *Epitedia stanfordi* (57), *Malareus euphorbi* (2), *Megarthroglossus smiti* (182), *Meringis parkeri* (1), *Orchopeus leucopus* (7), *O. sexdentatus agilis* (3), and *Thrassis gladiolus caducus* (2). Fleas were rare or absent in houses in June–September (Howell 1955). In a similar study nearby, 111 active houses contained an average of 7.8 fleas/house; species and numbers (in parentheses) of each were: *Aetheca wagneri* (3), *Anomiopsyllus amphibolus* (697), *Megarthroglossus smiti* (111), *Meringis parkeri* (21), *Thrassis aridis campestris* (4), and *T. bacchi* (5). Most were found in October–December; none was found mid-April–mid-September (Howell 1957). *Aetheca euphorbi* and *M. wagneri*, both common parasites of *Peromyscus*, and *T. bacchi* were considered accidental in woodrat houses (Howell 1955, 1957). *Anomiopsyllus amphibolus*, the most common species found in *N. lepida* houses, is rarely found on the animals (Howell 1955). One specimen of *Epitedia wemmanni* was collected in autumn from a house (Beck et al. 1953), and 1 larva of a ground squirrel flea (*Oropsylla bacchi gladiolus*) also was taken from a nest (Kucera 1990). In Oregon, Hubbard (1968) collected 28 male and 33 female *Orchopeus sexdentatus agilis*, 1 male *Foxella ignota reclusa*, and 1 each male and female *Aetheca wagneri* from a desert woodrat house in the attic of an abandoned house. Some species of fleas found on desert woodrats and in their houses are implicated in the transmission of *Yersinia pestis*, the causative agent of plague (Beck et al. 1953). *N. lepida* tested positive for the disease and may be involved in periodic epizootics (Eskey and Haas 1940; Hampton 1940).

In year-long studies at 2 locations in Utah, the tick *Ornithodoros hermsi* occurred in 46 (34.1%) of 135 *N. lepida* houses at 1,418–1,463 m and 34 (34.7%) of 98 houses at 1,570–1,600 m. Averages of 2.82 and 2.23 nymphal and adult ticks/house were collected at the 2 sites, respectively. Peak numbers of ticks (all stages combined) occurred in August–September at the 2 sites, respectively (Beck and Allred 1955).

In Toole Co., Utah, 1,935 mites (Acarina) of 31 species (25 families) were found in 98 houses (Howell et al. 1957). Taxa followed by an asterisk (\*) were believed to be permanent residents of desert woodrat houses (Allred and Roscoe 1957). These were (parasitic mites): *Androlaelaps fahrenholzi*, *A. megaventralis*, *Brevisterna utahensis*, *Echinonyssus occidentalis*, *Echinonyssus*, *Eubrachylaelps circularis*, *Haemogamasus ambulans*, *H. oudemansi*, *Ornithonyssus bacoti*\*, *Trombicula*, and undescribed species in the families Pterygosomidae\* and Pyemotidae\*; (predatory mites, families only): Anystidae, Bdellidae\*, Caeculidae, Cheyletidae\*, Cunaxidae, Erythraeidae, Nanorchestidae\*, Pachygnathidae, Phytoseiidae\*, Raphignathidae\*, Smaridiidae, Trombidiidae, and Tydeidae\*; and (scavenger mites, families only): Camisiidae, Carabodidae\*, Eremaeidae\*, Glycyphagidae, Hypochthoniidae\*, and Palaeacaridae\*. In Jaub Co., Utah, 80 km south of the previous study, 16,442 mites of 53 species (36 families) were collected from 118 houses (Allred and Roscoe 1957). Additional taxa of mites collected were (parasitic mites): *Dermanyssus*, *Echinonyssus geomysidis*, *E. incomptus*, *E. bisetosus*\*, *Euschongastida*, *Ischyropoda*, *Myobia*, and Listrophoridae; (predatory mites): Paratydeidae, and Teneriffidae; (scavenger mites): Acaridae, Belbidae, Chortoglyphidae, Cymbaeremaeidae, Glycyphagidae, and Liacaridae; and (miscellaneous mites): Phytoseiidae and Tetranychidae. The para-

sitic mites *Echinonyssus occidentalis*, *Haemogamassus ambulans*, and *H. oudemansi*, and the scavenger mites in the family Hypochtoniidae were not found in the latter study. In 1953, an average of 134 mites/house (range, 1–1,036) occurred in 35 houses of *N. lepida* that included 25 families of mites unique to houses of *N. lepida*, 5 unique to houses of *N. cinerea*, and 13 in houses of both species (Allred and Beck 1953).

Cone-nosed bugs (*Triatoma* and *Paratriatoma*, Hemiptera: Triatominae: Reduviidae) occasionally are found in woodrat houses (Egoscue 1957; Lent and Wygodzinsky 1979; Wood 1978). In California, 4.1–37.5% of *Triatoma protracta* found in houses occupied by *Neotoma* (including, but not restricted to, *N. lepida*) were infected with *Trypanosoma cruzi*, the infective agent of Chagas' disease (Wood 1941). The trypanosome subsequently was isolated from *N. lepida* (Wood 1952). One (0.15%) of 68 *Triatoma peninsularis* from a house and pooled feces of *Triatoma rubida* from another house constructed by *N. lepida* in Baja California, Mexico, tested positive for *Trypanosoma cruzi* (Ryckman et al. 1965). *N. lepida* hosts another reduviid, *P. hirsuta*, that apparently is not infected naturally with *T. cruzi*, but can be infected experimentally and the organism transmitted to woodrats through ingestion of *P. hirsuta* viscera (Ryckman et al. 1965).

Five strains of a new species of *Brucella* (*B. neotomae*) were isolated from *N. lepida*; none produced significant pathological changes when injected into juvenile desert woodrats and only "minimal" pathological changes in laboratory mammals (Stoerner and Lackman 1957:950). *B. neotomae* also was found in fleas (*Orchopeus sexdentatus*) on *N. lepida* in Utah (Thorpe et al. 1967).

*Coxiella burnetii*, the rickettsial agent responsible for Q-fever in humans, produced mild infections when injected intraperitoneally in *N. lepida* (Sidwell and Gebhardt 1963). The organism was isolated in only 3 of 537 *N. lepida* collected in western Utah in 1954–1962, but complement-fixing antibodies to Q-fever were found in sera of 32 of 361 of the same specimens (Sidwell et al. 1964).

Four (26.7%) of 15 desert woodrats from 1 of 3 populations sampled in Utah were serologically positive for antibodies to Sin Nombre virus (a hantavirus). Viral RNA was most similar to that in *Peromyscus maniculatus*, suggesting transmission between these species. Viral RNA also was detected  $\geq 2$  months after capture (Dearing et al. 1998).

A massive die-off, cause unknown, of *N. lepida* occurred in 1929 in Nevada, where the species was common a year earlier (Linsdale 1938). A few occurred in the area the following year.

In California, of 20 individuals captured in live traps, 4 were involved in double captures (Evans and Holdenreid 1943). Longevity records of captive animals include 1 of 5 years + 1 month (Egoscue et al. 1970) and 1 of 5 years + 7 months (Rabb 1960).

**BEHAVIOR.** Desert woodrats are active mostly at night to avoid temperature extremes (Nelson and Yousef 1979). However, a few are captured in traps or observed during daylight hours (Deacon et al. 1964; Evans and Holdenreid 1941), and some are taken by hawks, indicating some diurnal activity (Egoscue 1957).

Desert woodrats build conspicuous houses mostly of sticks, joints of cholla cacti, soil, and cattle dung, but may use a variety of debris, including wool, feathers, paper, tin cans, shed antlers, bottle caps, plastic bags, and shotgun shells (Long 1940; Stones and Hayward 1968; Verts and Carraway 1998). In open areas, houses usually are conical if built at the base of a tree, cactus, or shrub, but ovate or spherical if in the branches of a tree (Stones and Hayward 1968; Vaughan 1954). In rocky areas, crevices or fissures may be fortified with as much as several cubic meters of material (Verts and Carraway 1998). Individual woodrats may select different proportions of various materials available for construction of houses (Bonaccorso and Brown 1972). In captivity, woodrats averaged adding >200 units of available material to houses per night; 1 individual added 359 units in 1 night (Bonaccorso and Brown 1972). Desert woodrats commonly insert sticks similar to those used in the construction of houses into open live traps (MacMillen 1964).

Houses usually have 1–6 entrances and 1–8 chambers interconnected by tunnels. One to 3 chambers may be "gourd shaped" and used as nests, and 1 or more other chambers may be used as a food cache (Stones and Hayward 1968:471). Houses constructed by *N. lepida* are relatively simple in comparison with those built by some other species of *Neotoma* (Vaughan 1954). An elaborate house built by *N. lepida* in southern California was 36 cm tall and

94 by 104 cm at the base; it was built of sticks of coastal sage (*Artemisia*) and buckwheat (*Erigonum fasciculatum*) around the base of a prickly pear cactus (Vaughan 1954). It contained a 30-by-48-cm chamber served by two 7.6-cm-diameter tunnels and enclosing 2 cup-shaped grass nests ca. 10 cm in diameter; a 3rd grass nest also was located on the ground ca. 90 cm away from the house. Several other houses constructed by desert woodrats had 1–3 grass nests within ca. 120 cm (Vaughan 1954). Usually only 1 adult is captured at a house at any 1 time, but over time an individual may occupy several different houses (Stones and Hayward 1968). In Utah, densities of houses were 12.1–21.0 houses/ha (Stones and Hayward 1968).

In arenas, lactating females approached and attacked male intruders more than nonlactating females, but did not exhibit a significant difference in response to lactating and nonlactating female intruders or to cohabiting males. Lactating females were less aggressive toward juveniles than toward adults. In home cages, however, lactating resident females usually exhibited dominance over all alien intruders; they attacked 77% of the time when an intruder stuck its head into a house occupied by young. Nonlactating resident females were less frequently dominant, but were more likely to exhibit dominance over female than male intruders. Lactating resident females usually were dominant, but during late lactation were less aggressive toward female intruders even though they retained dominant position (Fleming 1979). When a maternal female was removed from its cage, both male and nonlactating female intruders spent less time in the house containing young than in the other house provided. Alien lactating intruders and juveniles <50 days old, however, spent more time with young than in the other house. Responses of older young were similar to those of adults (Fleming 1979).

Scent marking in *N. lepida* is sexually dimorphic with males exhibiting ventral rubbing more commonly than females and females displaying rolling more commonly than males. The former behavior consists of rubbing on the substrate and other areas an oily, musky-smelling sebum produced by large ventral sebaceous glands. Rolling consists of vigorous digging followed by rolling the hind leg, flank, shoulder, and cheek on the ground. Ventral rubbing is under androgenic control, whereas rolling is partly under estrogenic control (Fleming and Tambosso 1980). Before social encounters, ventral rubbing was performed more frequently in response to odors of conspecifics than to neutral odors or to their own odors; after social encounters, males increased rubbing in cages of females but not in those of males. Males rubbed more in areas soiled by other males, but rolled more in areas soiled by females. Estrogen-primed females rolled more in areas soiled by males than those soiled by other females (Fleming and Tambosso 1980).

In captivity, females within 2 weeks after parturition readily adopted young of similar age whose mothers died or were unable to provide sufficient milk (Egoscue 1957); acceptance of young likely is related to suckling response (Bleich and Schwartz 1974). Also, neonates and young *N. lepida* were adopted by postpartum female *N. fuscipes*. However, a 2-day-old *N. fuscipes* placed in a cage with a female *N. lepida* with an 8-day-old litter was adopted initially, but disappeared 3 days later (Bleich and Schwartz 1974).

In test encounters of *N. l. lepida* and *N. fuscipes macrotis* from an area in California where they are sympatric and compete for the primary food source (turbine oak), *N. fuscipes* was always dominant. *N. lepida* usually attempted to hide or flee while uttering low cries, but *N. fuscipes* was not deterred and usually killed the subordinate desert woodrat (Cameron 1971).

In Utah, maximum movements of males averaged 76.8 m, with the longest 147.9 m; 1 individual moved 125.6 m in 1 night. Females moved an average of 41.5 m with the longest movement 195.7 m (Stones and Hayward 1968). In a coastal sage (42.4%) community in California, exclusive boundary-strip home ranges (Stickel 1954) averaged 371 m<sup>2</sup> for males ( $n = 7$ ) and 433 m<sup>2</sup> for females ( $n = 3$ )—Bleich and Schwartz 1975). In the San Gabriel Mountains, California, average ( $\pm SD$ ) home ranges calculated similarly were 1,942  $\pm$  607 m<sup>2</sup> for males ( $n = 6$ ) and 2,064  $\pm$  648 m<sup>2</sup> for females ( $n = 10$ )—MacMillen 1964).

Maximum running speed in laboratory trials ( $n = 10$  individuals) averaged ( $\pm SD$ ) 17.1  $\pm$  1.3 km/h (range, 14.9–19.2 km/h). The fastest individual exceeded running speeds of 131 individuals of 18 species of rodents (Djawan and Garland 1988).

Copulation in *N. lepida* is characterized by the absence of locking and of intravaginal thrusting, ejaculation upon 1 insertion,

and multiple ejaculations. The apparent absence of locking is unique among species of *Neotoma* tested and was attributed to the absence of spines and low diameter:length ratio of the glans penis (Estep and Dewsbury 1976). However, Fleming et al. (1981) observed resistance to withdrawal of the penis including the female dragging the male for a distance in 67% of observed copulations. Also, males achieved multiple intromissions in rapid succession, suggesting that ejaculation may not occur with each intromission. Nevertheless, spermatozoa always were detected in vaginal smears made immediately after single intromissions.

Average ( $\pm SE$ ) number of 10-s intervals during 15-min observation periods in which various behaviors were exhibited at least once by male and female (in parentheses) for 9 pairings of desert woodrats in which the female was in natural estrus were: precopulatory: approach,  $8.8 \pm 2.2$  ( $22.6 \pm 4.4$ ); sniff head,  $34.8 \pm 5.4$  ( $35.2 \pm 5.2$ ); sniff anogenital region,  $19.7 \pm 4.4$  ( $3.1 \pm 2.6$ ); trail,  $14.1 \pm 4.5$  ( $3.0 \pm 1.8$ ); vocalize,  $11.8 \pm 2.8$  ( $6.7 \pm 5.2$ ); trail-vocalize,  $8.8 \pm 2.3$  ( $0.2 \pm 0.2$ ); hop and dart, 0 ( $11.5 \pm 2.4$ ); groom other,  $4.8 \pm 2.1$  ( $1.2 \pm 0.7$ ); foot thump/tail wag,  $8.1 \pm 2.0$  ( $3.8 \pm 3.2$ ); and ear wiggle, 0 ( $9.6 \pm 2.3$ ); copulatory: mount,  $8.1 \pm 1.7$  ( $0.4 \pm 0.3$ ); intromission,  $4.1 \pm 1.0$  (0); and lordosis, 0 ( $8.6 \pm 2.1$ ); agonistic: box,  $38.8 \pm 11.0$  ( $38.8 \pm 11.0$ ); chase,  $7.3 \pm$  [no SE reported] ( $3.1 \pm 2.0$ ); attack,  $1.4 \pm 1.2$  ( $0.9 \pm 0.9$ ); and run away,  $6.3 \pm 2.8$  ( $7.5 \pm 5.5$ ); and self grooming: groom genital,  $17.0 \pm 3.5$  ( $2.9 \pm 1.3$ ) and groom body,  $7.0 \pm 2.5$  ( $3.8 \pm 1.6$ ). The observed copulatory pattern was "qualitatively different" from that reported for most rodents (Fleming et al. 1981:743). Observations and experiments involving ovariectomy with estrogen and progesterone replacement, odors of urine and vaginal secretions, and olfactory bulbectomy indicate that normal sexual behavior in male *N. lepida* requires that the female both emit attractive odors and engage in appetitive precopulatory behavior (Fleming et al. 1981). Females exhibited fewer lordosis responses to male attempts to mount when rasping vocalizations produced by the male were prevented either by temporarily deafening the female or devocalizing the male, but lordosis responses returned when tapes of recordings of male vocalizations were played at the appropriate time (White and Fleming 1987).

In observed copulations of captives ( $n = 42$ ), intromission was attained after a mean latency of 739 s (range, 145–3,259 s) and lasted an average of 4.9 s (range, 2–8 s). During a 1-h test, males ejaculated an average of 3.3 times (range, 1–7). In 28 of 30 tests in which males copulated  $\geq 3$  times, the interval was greater between the last 2 intromissions than the first 2 (Estep and Dewsbury 1976).

**GENETICS.** *Neotoma lepida* has a diploid number of 52 and a fundamental number of 60–66 (Baker and Mascarello 1969). The X chromosome is a large metacentric. The Y chromosome is small; however, as males are usually heteromorphic, the form of the Y chromosome cannot be "determined by morphology alone" (Baker and Mascarello 1969:169). Polymorphisms occur at both the inter- and intrapopulation levels. Chromosomes 1, 3, and 4 have heterochromatic short-arms. Chromosomes 1 and 3 also are polymorphic in *N. lepida* (Koop et al. 1985). Chromosomes 2 and 6 are not heterochromatic and contain pericentric inversions as in *N. devia* and *N. fuscipes* (Koop et al. 1985; Mascarello and Hsu 1976).

The 2 morphotypes within *N. lepida* possess allozymic differences (Mascarello 1978). The Baja type has Idh-1<sup>82</sup> and, depending on the population, Pgm-1<sup>92</sup> occurs at a frequency (%) of 11–17, Adh<sup>168</sup> at 8, Pep-1<sup>92</sup> at 8–10, and 6-Pgd<sup>72</sup> at 8–28 (Mascarello 1978). The western type has Idh-1<sup>100</sup> and, depending on the population, Pgm-1<sup>92</sup> occurs at a frequency of 3, Adh<sup>168</sup> at 60–98, Pep-1<sup>92</sup> at 29–83, and 6-Pgd<sup>72</sup> at 57–100 (Mascarello 1978). Est-1, Est-2, Fum, Gdh, Got-1, Got-2, Ipo, Lap, Ldh-2, and Sdh were homozygous across all populations, and, except for single individuals at various localities, Idh-2, Mdh-2, and Pep-2 also were homozygous (Mascarello 1978). Further support for distinguishing the 2 morphotypes with similar geographic distributions was provided by mitochondrial DNA restriction fragment length polymorphism data (Riddle et al. 2000).

**CONSERVATION.** *Neotoma l. intermedia* is a subspecies of special concern (State of California 1993). *N. l. abbreviata*, *N. l. insularis*, *N. l. latirostra*, *N. l. marcosensis*, *N. l. nudicauda*, *N. l. perpallida*, and *N. l. vicina* are threatened (= vulnerable category of International Union for the Conservation of Nature; Nor-

ma Oficial Mexicana 2000). Anthropogenic factors (destruction of vegetation and introduction of competitors and predators) believed responsible for the probable extinction of *N. bunkerii* are believed to threaten some of the insular races of *N. lepida* (Smith et al. 1993).

**REMARKS.** The generic name *Neotoma* was derived from the Greek *neos* meaning new and *tomos* meaning cut or cutting (Jaeger 1978). The specific epithet *lepida* was derived from the Latin *lepida* meaning pretty or graceful (Jaeger 1978).

Formerly, races east and south of the Colorado River (*auriculata*, *auripila*, *bensoni*, *devia*, *flava*, *harteri*, *monstrabilis*, and *sanrafaeli*) were considered subspecies of *N. lepida* (Hall 1981), but based on biochemical, chromosomal, cranial, mensural, and penile characters, *devia* was elevated to specific level (Koop et al. 1985; Mascarello 1978) and the remaining 7 races tentatively allocated to *N. devia* (Musser and Carleton 1993). Earlier, Goldman (1937) recognized the Colorado River as a barrier that separated *N. l. devia* from northern and western races. However, based on cranial morphometrics and shape of glans penes, Hoffmeister (1986:413) claimed that *lepida*-like woodrats on opposite sides of the Colorado River were "remarkably close morphologically" in northern Arizona, those east of the river in central Arizona were "inseparable" from those in northern Arizona and eastern California, and those in southwestern Arizona, although usually smaller than those in central and northern Arizona, included intermediates. He retained *devia* as a subspecies, but included *grinnelli* and *monstrabilis* as synonyms thereof. Sequence data from the mitochondrial cytochrome-*b* gene for a small number of desert woodrats from the region were considered "equivocal with regard to this debate" by J. L. Patton and S. T. Alvarez-Castañeda (in litt.).

Mascarello (1978:493) reported that the desert woodrat in northern Baja California was genetically "equidistant from *N. devia* and other *N. lepida*" and "Mensurally, it falls well away from both." Nevertheless, he declined to offer taxonomic conclusions. Analysis of cytochrome-*b* sequence data produced 2 major clades: 1 occurring in coastal California and the Baja California peninsula and the other occurring in northwestern Sonora, Arizona, and desert areas in the southern portions of California, Nevada, and Utah (J. L. Patton and S. T. Alvarez-Castañeda, in litt.). They believe that desert woodrats forming the 2 clades likely are specifically distinct.

Goldman (1910, 1932) considered *N. nevadensis* a synonym of *N. desertorum* (= *N. lepida*). Hall (1946) believed the black *nevadensis* to intergrade with the grayish *lepida*, thus was subspecifically different.

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