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Neotoma cinerea.

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Neotoma cinerea (Ord, 1815)

Bushy-tailed Woodrat

Mus cinereus Ord, 1815:292. Type locality near Great Falls, Cascade Country, Montana. Based on the "ash-colored rat of Rocky Mountains of Lewis and Clark."

Neotoma cinerea Say and Ord, 1825:346. First use of current name combination.

Myoxus drummondii Richardson, 1828:517. Type locality near Jasper House, Rocky Mountains, British Columbia, at 57° latitude.

Neotoma occidentalis Baird, 1855:335. Type locality from Shoalwater [=Willapa] Bay, Pacific County, Washington.

Neotoma arizonae Merriam, 1893:110. Type locality from "Keams Canyon, Apache [=Navajo] County, Arizona."

Neotoma orolestes Merriam, 1894*a*:128. Type locality from "Saguache Valley, 20 miles west of Saguache," Saguache County, Colorado.

Neotoma rupicola Allen, 1894:323. Type locality from "Corral Draw, southeastern base of Black Hills, 3700 feet altitude," Pine River Indian Reservation, Black Hills, South Dakota."

Neotoma grangeri Allen, 1894:324. Type locality from "Custer, Black Hills," Custer County, South Dakota.

Neotoma cinnamomea Allen, 1895:331. Type locality from Kinney Ranch, Bitter Creek, Sweetwater County, Wyoming.

Neotoma saxamans Osgood, 1900:33. Type locality from "slide of large granite bowlders [=boulders] at head of Lake Bennett," British Columbia.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Sigmodontinae, Genus *Neotoma*, Subgenus Teonoma. Thirteen subspecies are currently recognized (Carleton, 1980; Hall, 1981):

N. c. acraea (Elliot, 1904*a*:247). Type locality from "Hot Springs, Long Canon, Mount Whitney, Inyo County, California. Altitude 8,000 feet." Was misprinted *acraia* in original description (Elliot, 1904*b*).

N. c. alticola Hooper, 1940:409. Type locality from "Parker Creek [=Shields Creek on U.S. Forest Service map, edition of 1932], 5500′ altitude, Warner Mountains, Modoc County, California."

N. c. arizonae Merriam, 1893:110, see above.

N. c. cinerea (Ord, 1815:292), see above.

N. c. cinnamomea Allen, 1895:331, see above.

N. c. drummondi (Richardson, 1828:517), see above.

N. c. fusca True, 1894:354. Type locality from Fort Umpqua, Douglas Country, Oregon (*apicalis* Elliot is a synonym).

N. c. lucida Goldman, 1917:111. Type locality from Charleston Peak, Charleston Mountains, Clark County, Nevada.

N. c. macrodon Kelson, 1949:417. Type locality from "E side confluence Green and White rivers, 4700 ft., 1 mile SE Ouray, Unitah Country, Utah."

N. c. occidentalis Baird, 1855:335, see above (*columbiana* Elliot and *saxamans* Osgood are synonyms).

N. c. orolestes Merriam, 1894*a*:128, see above (*grangeri* Allen is a synonym).

N. c. pulla Hooper, 1940:411. Type locality from "Kohnenberger's Ranch, 3200 feet altitude, South Fork Mountain, Trinity County, California."

N. c. rupicola Allen, 1894:323, see above.

DIAGNOSIS. *Neotoma cinerea* differs from all other species of woodrats in its larger body size, bushy squirrel-like tail, and in having a hind foot sole fully furred from the heel to posterior tubercle (Baird, 1855; Dixon, 1919; Finley, 1958; Goldman, 1910—Fig. 1). The mystacial and superciliary vibrissae of *N. cinerea* are longer than in other species of woodrats and may reach 100 mm (Howell, 1926). The ears are relatively large. Adults have well developed mid-ventral scent glands, which are more pronounced than in other species of woodrats (August, 1978; Finley, 1958; Goldman, 1910; Hoffmeister, 1986; Howe, 1977; Howell, 1926; Wiley, 1980), and produce a persistent musky odor (Dixon, 1919). Overall, the pelage is much longer, denser and softer than in other species. The skull is long and angular (Fig. 2), with a long, narrow rostrum. Other cranial features include prominent temporal ridges, a narrowly constricted and channeled frontal region, long and narrow incisive foramina, and a narrow interorbital region that appears channeled dorsally (Allen, 1894; Carleton, 1980; Dixon, 1919; Finley, 1958; Goldman, 1910, 1917; Hooper, 1940; Kelson, 1949, 1952; Merriam, 1894*b*). Sphenopalatine vacuities may be present or absent (Allen, 1894; Dixon, 1919; Hooper, 1940; Merriam, 1893, 1894*a*, 1894*b*). M1 has a deep anterointernal re-entrant angle; M3 has an anterior closed triangle and two confluent posterior loops (Hall, 1981). The baculum is relatively thin and has an elongate cartilaginous spine (Burt and Barkalow, 1942; Carleton, 1980; Hoffmeister, 1986; Hooper 1960; Howell, 1926). In the southern part of its range where it is smaller, *N. cinerea* may be confused with the semi-bushy-tailed *N. stephensi*. However, even here the larger size of *N. cinerea* serves to distinguish the two, as does the larger (>36 mm) hind foot, more heavily-furred sole, differentially-shaped baculum, and longer and more heavily-furred tail (Hoffmeister, 1986; Jones and Hildreth, 1989).

GENERAL CHARACTERS. The common name "bushy-tailed woodrat" is derived from the long heavily-furred tail (Fig. 1), which is generally sharply bicolored with white below and sooty hairs above. Hairs on the tail are ca. 30 mm in length (Dixon, 1919). Dorsally, coat color varies from a pale gray lightly washed with buff to a dark brownish-black or tawny shade; the underparts may vary from white to pinkish or buff (Allen, 1895; Dixon, 1919; Finley, 1958; Goldman, 1910, 1917; Hoffmeister, 1986; Hooper, 1940; Howell, 1926). Substantial geographic variation is found in pelage color, however, with cooler and more humid climates associated with darker coloration, and paler pelages associated with lower, semiarid habitats (Finley, 1958; Goldman, 1910; Hooper, 1940). In several subspecies of bushy-tailed woodrat the hair is entirely white along the midvental line (Hall, 1981; Howell, 1926), and many populations are white-throated (Hoffmeister, 1986). *N. cinerea* have rooted molars that tend to hypsodonty, resembling

FIG. 1. Captive adult *Neotoma cinerea orolestes*. Courtesy of J. H. Brown.

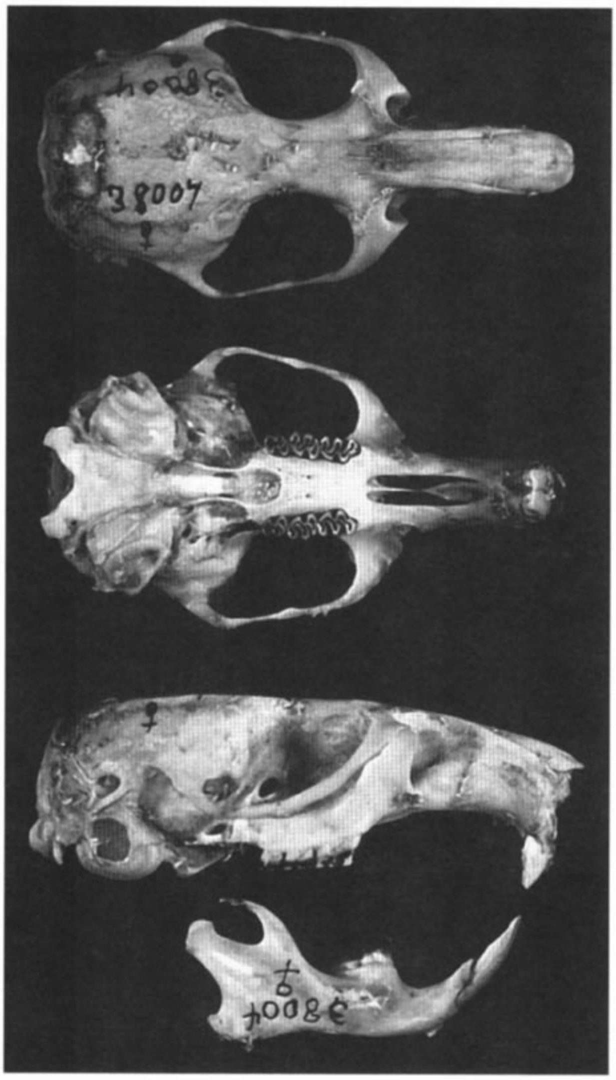

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult female *Neotoma cinerea orolestes* (MSB #38004) from the upper Tesuque Trail, Santa Fe County, New Mexico. Greatest length of cranium is 48.0 mm.

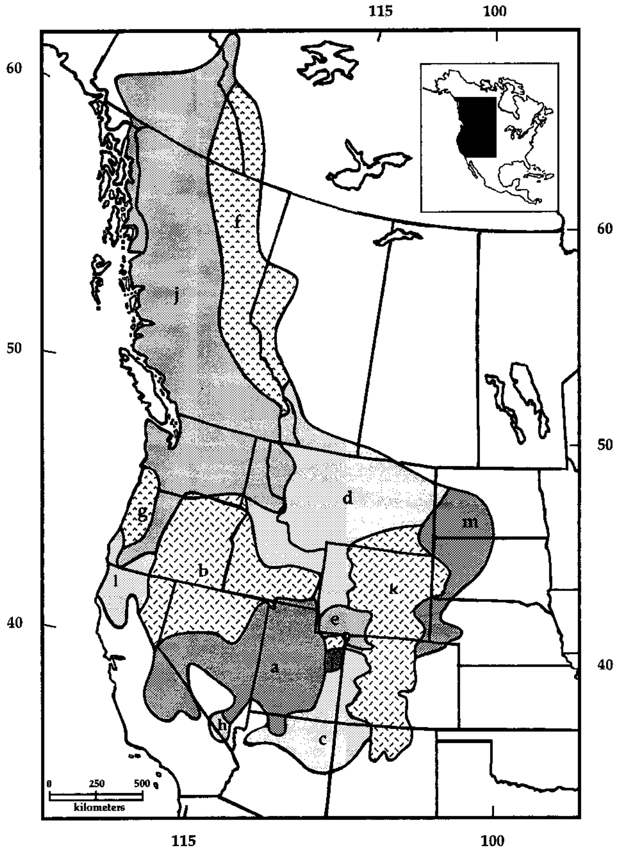

FIG. 3. Geographic distribution of *Neotoma cinerea* (redrawn from Hall, 1981): a, *N. c. acraea*; b, *N. c. alticola*; c, *N. c. arizonae*; d, *N. c. cinerea*; e, *N. c. cinnamomea*; f, *N. c. drummondi*; g, *N. c. fusca*; h, *N. c. lucida*; i, *N. c. macrodon*; j, *N. c. occidentalis*; k, *N. c. orolestes*; l, *N. c. pulla*; m, *N. c. rupicola*.

those of microtines although somewhat less complex (Carleton, 1980; Say and Ord, 1825).

Males are larger than females in all morphological characteristics. In Alberta, adult body mass averaged 419 g for males (*n* = 17; range 379–456) versus 302 g for females (*n* = 42; range 234–359—Hickling, 1987). Extensive geographic size variation occurs in both sexes with measurements differing by >50% between the northern and southern distributional limits (Brown, 1968; Brown and Lee, 1969; Hooper, 1940; Smith et al., 1995). Adult males in the northern portions of the range can exceed 500–600 grams in mass (Escherich, 1981). Average body length (excluding tail) and mass ± 1 *SD* (range in parentheses) for *N. c. arizonae* in Moffat County, Colorado, are (pers. obs.), for females (*n* = 34), 191.5 ± 10.7 mm (173–210 mm), 193.5 ± 27.1 g (140–230 g); for males (*n* = 14), 197.8 ± 13.2 mm (177–213 mm), 231 ± 43.3 g (170–330 g). Similar data for *N. c. alticola* from Sagehen Creek, Nevada, are (pers. obs.), for females (*n* = 25), 206 ± 13 mm (187–233 mm), 265 ± 48 g (173–348 g); for males (*n* = 16), 218 ± 16 mm (186–247 mm), 331 ± 81 g (174–444 g). Means ± 1 *SD* (in mm) and range of animals from the southern part of range in Keams Canyon to near Woodruff, Arizona (Hoffmeister, 1986), are, males (*n* = 8), total length 359 ± 29.4 (326–398), length of tail 148.6 ± 14.4 (130–168), length of body 210.4 ± 16.9 (184–230), length of hindfoot 39.8 ± 1.4 (38–42), greatest length of skull 48.5 ± 2.0 (45.4–51.5), condylobasal length 47.6 ± 1.21 (46.2–49.1), basilar length 40.7 ± 1.9 (37.2–43.5), zygomatic breadth 25.5 ± 0.86 (24.5–26.4), interorbital breadth 5.8 ± 0.32 (5.4–6.2), length of nasal 18.8 ± 0.82 (17.3–20), length of the incisive foramen 11.0 ± 0.36 (10.5–11.5), length of alveolar maxillary toothrow 9.7 ± 0.33 (9.35–10.35), breadth of rostrum 8.0 ± 0.21 (7.75–8.2); females (*n* = 9), total length 329.3 ± 15.9 (302–345), length of tail 142.6 ± 11.9 (127–165), length of body 186.7 ± 12.05 (175–207), length of hindfoot 38.3 ± 2.9 (34–42), greatest length of skull 45.4 ± 1.7 (43–48), condylobasal length 43.5 ± 1.4 (41.4–45.7), basilar length 38.0 ± 1.4 (36.4–40.7), zygomatic breadth 23.7 ± 1.3 (21.5–25.3), interorbital breadth 5.6 ± 0.19 (5.3–5.8), length of nasal 17.8 ± 0.77 (16.6–18.8), length of the incisive foramen 10.3 ± 0.35 (9.9–10.9), length of alveolar maxillary toothrow 9.1 ± 0.48 (8.6–10), breadth of rostrum 7.45 ± 0.36 (7.05–8.15).

DISTRIBUTION. *Neotoma cinerea* occurs in mountainous terrain from southern Yukon and the westernmost Northwest Territories, south through British Columbia and western Alberta, to northern California, Arizona and New Mexico, and as far east as the western portion of the Dakotas (Fig. 3)—a range of 31 degrees of latitude. Currently, the southernmost distribution includes the Sierra Nevada of California, the Kaibab Plateau north of the Colorado River in northeastern Arizona, and the Jemez, San Juan and Sangre de Cristo mountains of New Mexico (Dixon, 1919; Findley et al., 1975; Grinnell, 1913; Hoffmeister, 1986; Hooper, 1940). In the Pleistocene the range extended as far south as northern Mexico but was constricted to the north (Harris, 1984*a*, 1985, 1993). Several specimens were taken from the foothills of the Mackenzie Mountains, Northwest Territories (Martell and Jasper, 1974) and in the southern half of the Yukon Territory, and southeastern Alaska (Manville and Young, 1965; Youngman, 1975). *N. cinerea* has a wide altitudinal distribution as well, ranging from near sea level in Washington state to slightly above timberline at 3600 m in the White Mountains and Sierra Nevada of California (Dixon, 1919; Grayson and Livingston, 1989; Hall, 1946; Hooper, 1940). Individuals have been captured above timberline at ca. 4300 m in the

White Mountains of California (Grayson and Livingston, 1989). These animals were occupying human structures; however, natural habitats may be too marginal and patchily distributed to permit long-term survival at such elevations (Grayson and Livingston, 1989).

FOSSIL RECORD. The earliest form recognized as *Neotoma* (*N.* [*Paraneotoma*] *minutus*) dates from the late Miocene at 6.6×10^6 years ago or earlier (Dalquest, 1983; Hibbard, 1967; Korth, 1994). Although it is not known when *N. cinerea* diverged from the ancestral stock, the well-differentiated morphology and extensive geographic variation exhibited by this species suggests it may well have been relatively early. Most, if not all, species of woodrat were clearly differentiated on the basis of molar dentition by the Rancholabrean at 3.0×10^5 years ago (Zakrzewski, 1993). *N. cinerea* may be derived from the extinct species *N. amplidonta*, dated by biostratigraphy to the Irvingtonian (1.9×10^6 to 3.0×10^5 years ago; Zakrzewski, 1993). Fossil evidence of *N. cinerea* is relatively abundant; this is at least partially because of the large numbers of paleomiddens that have been preserved within the southwestern United States (Harris, 1984*a*, 1984*b*, 1985; Webb and Betancourt, 1990). Late Rancholabrean fossils are reported from Wyoming, Idaho, Colorado, New Mexico, and California, with all northern records within the present-day range (Kurtén and Anderson, 1980). During the Pleistocene, *N. cinerea* occurred in southern New Mexico and southwestern Texas, and ranged as far south as northern Mexico (Harris, 1984*a*, 1993; Van Devender and Bradley, 1990). As climate and vegetation changed during the transition between the Pleistocene and Holocene, *N. cinerea* retreated to its modern distributional limits. Fossil remains have been reported from sites as far south as Dry, Muskox, and U-Bar Caves in New Mexico and Lower Sloth Cave in western Texas (Harris, 1984*a*, 1984*b*, 1985, 1993; Logan, 1981; Van Devender and Bradley, 1990). An extinct species of woodrat, *N. findleyi*, was identified by Harris (1984*a*, 1984*b*) from Dry Cave and dated at about 3.0×10^4 years ago. He suggested that it represented a population of *N. cinerea* isolated in the highlands of southeastern New Mexico during the mid Wisconsin; other authors disagree (Zakrzewski, 1993). Other fossil records include what was originally described as an extinct form, *Teonoma spelaca*, Sinclair (1905:148) from Potter Creek Cave, Shasta County, California. Later examination suggested that the specimen actually represented *N. cinerea occidentalis* (Dixon, 1919; Hooper, 1940; Kellogg, 1912).

FORM AND FUNCTION. Adult bushy-tailed woodrats have a thickened dermal area midventrally that contains enlarged, highly specialized, glandular sebaceous masses (August, 1978; Escherich, 1981; Finley, 1958; Goldman, 1910; Hickling, 1987; Hoffmeister, 1986; Howe, 1977; Howell, 1926). As in other species of *Neotoma*, the feature is most pronounced in males, and there does not seem to be marked glandular action in females or subadults (Escherich, 1981; Howell, 1926; Wiley, 1980). The scent gland secretions apparently are used to mark territorial boundaries and may facilitate mating (August, 1978; Escherich, 1981; Hickling, 1987; Howe, 1977; Wiley, 1980). Stomach morphology is relatively specialized, reflecting the bulky fibrous diet (Carleton, 1980; Justice and Smith, 1992). The stomach wall can be as thick as 4 mm and is heavily striated with tough muscle and glandular folds (Howell, 1926). The pyloric horn also is well muscled. The cecum is large and well developed with a constricted and differentiated neck (Carleton, 1980; Howell, 1926), permitting efficient microbial fermentation of plant structural components (Justice and Smith, 1992; Smith, 1995). This ability is common to all species of woodrats examined (Justice and Smith, 1991; Smith, 1995). Based on morphological changes in woodrat dentition, Zakrzewski (1993) speculated that a dietary shift towards consumption of harsher vegetation may have resulted from environmental changes during the late Tertiary. Howell (1926) provided detailed myological, osteological, digestive, and urogenital comparisons for several different species of *Neotoma*, including *N. cinerea*.

In *N. cinerea* the glans penis is slender and constricted distally (Burt and Barkalow, 1942; Carleton, 1980; Finley, 1958; Goldman, 1910; Hall, 1981; Hoffmeister, 1986; Hooper, 1960; Howell, 1926). Hooper (1960:11) described the glans as a "delicate, elongate, awl-shaped structure. . . its length 4 times its greatest diameter and 1/4 the hind foot length." The baculum is relatively thin and has an elongate cartilaginous spine of about equal length (Hoffmeister, 1986; Hooper, 1960); in cross section the basal portion of the baculum has a slight concavity in both the dorsal and ventral surface (Burt and Barkalow, 1942). It averages about 5.5 mm in length, 0.9 mm in dorsoventral diameter, and 1.5 mm in lateral diameter (Burt and Barkalow, 1942). The length of the baculum and cartilage tip taken together approximate the length of the glans (about 11 mm—Hooper, 1960). Dimensions vary somewhat with body size and age, but the general shape does not (Burt and Barkalow, 1942; Howell, 1926).

Generally two or three molts occur during the first year followed by a single, annual molt (Dixon, 1919; Finley, 1958). Typically, molts begin on the abdomen and spread laterally up the body. The annual molt is more irregular than the juvenile ones, however, and there may be no clearly recognizable molt line (Finley, 1958). Juvenile pelage is characterized by fuzzy gray fur and the lack of an obviously bushy tail (Allen, 1894, 1895; Dixon, 1919; Elliot, 1898; Finley, 1958; Goldman, 1917; Merriam, 1893). Whitish hairs may persist on the end of the tail until the third molt; this may serve as a diagnostic feature separating first from second year adults (Finley, 1958). In Colorado, the annual molt can occur between June and November, with the majority of animals undergoing molt by early summer. The largest number of bushy-tailed woodrats in postjuvenal molts was reported during July and August (Finley, 1958). In California, annual molts reportedly take place in September and early October (Dixon, 1919).

Although bushy-tailed woodrats often live in relatively arid environments, they are not particularly efficient at water conservation (Boice, 1969; Lee, 1963; Olsen, 1976; Schmidt-Nielsen and Schmidt-Nielsen, 1952). Large amounts of urine are voided daily, requiring consumption of succulent or moist vegetation to maintain water balance (Lee, 1963; Olsen, 1976; Schmidt-Nielsen and Schmidt-Nielsen, 1952). The senses of smell and hearing have been described as highly developed; the long vibrissae facilitate movement in the dark crevices commonly inhabited (Finley, 1958).

ONTOGENY AND REPRODUCTION. The timing and onset of reproduction is heavily influenced by body mass, climate, and/or the presence of sufficient food resources (Hickling, 1987; Hickling et al., 1991). Bushy-tailed woodrats first breed as yearlings, and females are seasonally polyestrous (Egoscue, 1962; Escherich, 1981; Finley, 1958; Hickling, 1987; Hickling et al., 1991; Moses and Millar, 1992; Moses et al., 1995; Warren, 1926). The number of litters depends on the habitat and local environmental conditions. Energetic studies suggest that nutritional needs of pregnant and/or lactating females are considerably higher than those of non-breeding females, averaging 24–93% more, respectively (Hickling et al., 1991). Endogenous fat reserves may be used to supplement daily foraging during reproduction (Hickling, 1987). Food supplementation leads to earlier breeding, an increased number of litters per season, and increased litter size at weaning (Hickling, 1987). Prebreeding body mass is strongly correlated with the sex ratio of the litter, with larger mothers producing litters with more males (Moses et al., 1995). Most populations probably have one to two litters annually (Dixon, 1919; Finley, 1958; Hickling, 1987; Martin, 1973). In Canada, 30–62% of females had multiple litters (mean 1.46 litters/female; $n = 36$; Hickling, 1987). However, up to three litters per year were reported in the Sierra Nevada Mountains of California, with a mean of 2.5 litters/female ($n = 11$; Escherich, 1981).

The mating system has been described as harem polygyny (Escherich, 1981; Hickling, 1987), or alternatively as promiscuous with territories of males overlapping that of multiple females (Topping and Millar, 1996*a*). Occasionally, in small patches of habitat monogamous pairs form; these tend to be transient and generally do not last into successive breeding seasons (Hickling, 1987). Females exhibit asynchronous estrus cycles which may last from 5 to 7 days (Egoscue, 1962; Escherich, 1981). The gestation period is ca. 30 days, but may vary from 27 to 32 (Egoscue, 1962; Escherich, 1981; Hickling, 1987). Kiltie (1982) calculated it as 29 days (± 0.9 *SD*, $n = 7$). Postpartum estrus may occur (Egoscue, 1962; Hickling et al., 1991). Based on embryo counts, live trapping, and laboratory-reared animals, the modal litter size is approximately 3.5, with a range of 3–5 (Dixon, 1919; Egoscue, 1962; Hall, 1946; Hickling, 1987; Horvath, 1966; Warren, 1926). However, animals with six embryos have been reported (Finley, 1958; Warren, 1926).

In Colorado, pregnant or lactating females were trapped from May through August (Finley, 1958). Similar dates were reported from Canada (Hickling, 1987; Hickling et al., 1991; Horvath, 1966; Topping and Millar, 1996*a*, 1996*b*) and California (Dixon, 1919; Elliot, 1898; Escherich, 1981). Sites at lower elevations tend to exhibit earlier breeding and a longer overall reproductive season (Dixon, 1919; Finley, 1958; Warren, 1926). Date of parturition is correlated with body mass, with larger animals breeding sooner; this may reflect greater endogenous fat reserves (Hickling et al., 1991).

Woodrats, including *N. cinerea*, are nearly naked when born and have splayed incisors, facilitating attachment to their mother's nipples (Bleich and Schwartz, 1974; Donat, 1933; Escherich, 1981; Feldman, 1935; Horvath, 1966). Neonatal birth mass averages 15 ± 0.2 g for males ($n = 12$), and 14.4 ± 0.2 g for females ($n = 10$; Hickling, 1987). By the 15th day, the juvenile pelage has grown in, the eyes are open, and the young begin trying solid food (Escherich, 1981; Hickling, 1987; Horvath 1966). The lactation period generally lasts about 23–25 days (Hickling, 1987; Hickling et al., 1991) but can continue for 30 days or more (Escherich, 1981). In Alberta, body mass at weaning averaged 103 g for males (range 94–109; $n = 10$), and 92 g for females (range 84–102; $n = 10$; Hickling, 1987). In California, average mass at weaning was 100 g (Dixon, 1919). Growth curves are roughly sigmoidal, and typically young reach an asymptote at around 140 days (Escherich, 1981; Martin, 1973). Most, if not all, bushy-tailed woodrats do not reach sexual maturity until they are yearlings (Egoscue, 1962; Escherich, 1981; Finley, 1958; Hickling, 1987; Moses and Millar, 1992; Warren, 1926). Dispersal generally occurs shortly after weaning. Bushy-tailed woodrats tend to exhibit female-based philopatry with daughters establishing nest sites near their mothers (Hickling, 1987; Moses and Millar, 1992). In Alberta, 71–76% of females remain on or adjacent to their natal territories, compared to 17–29% of males (Hickling, 1987; Moses and Millar, 1992). Generally, males tend to disperse greater distances in search of suitable habitat and den sites (Escherich, 1981; Hickling, 1987). An interesting exception is found in a report of a newly-weaned female in the Sierra Nevada that traveled 3.2 km in less than 28 days; apparently this represents the longest recorded distance by any woodrat. The farthest dispersal distance reported for a yearling male was 2.2 km in 10 days (Escherich, 1981).

Neotoma cinerea is physiologically capable of living three or more years but only rarely achieves this in the field (Escherich, 1981; Finley, 1958). Annual adult survivorship in the wild ranges from 30–50% in the Sierra Nevada Mountains of California (Escherich, 1981). In the Kananaskis Valley, Alberta, annual survivorship ranges from 31–34% for individuals ($n = 51$; Hickling, 1987).

ECOLOGY. Bushy-tailed woodrats are almost obligatorily saxicolous. They typically inhabit boulder outcrops, vertical crevices, clefts or caves in cliffs, or talus slopes (Brown, 1968; Dixon, 1919; Findley et al., 1975; Finley, 1958; Goldman, 1910; Grayson and Livingston, 1989; Hoffmeister, 1986; Moses and Millar, 1992) and are excellent climbers (Finley, 1990; Goldman, 1910). Topography and shelter are important determinants of the suitability of habitat for bushy-tailed woodrats, and the number of den sites may limit population density (Escherich, 1981; Finley, 1958; Hickling, 1987; Moses and Millar, 1992). Although ostensibly found over a wide geographic range, the distribution of *N. cinerea* is actually relatively patchy because favored den sites are numerous only in rugged mountainous or canyon country (Finley, 1958). Bushy-tailed woodrats also frequently inhabit isolated man-made structures such as mine tunnels, cabins or accessible buildings, and even pueblo cliff dwellings (Brown, 1968; Findley et al., 1975; Finley, 1958; Grayson and Livingston, 1989; Hoffmeister, 1986). Although only abandoned human structures normally are inhabited, this is not always the case. In Mesa Verde, for example, prehistoric woodrat middens were found blackened by smoke from Indian fires, suggesting the animals had co-existed with the ancient Anazai (Cary, 1911).

Neotoma cinerea is unable to tolerate high ambient temperatures (Brown, 1968; Brown and Lee, 1969; Finley, 1958; Lee, 1963; Smith et al., 1995). This has been attributed to the relatively thick pelage and insulation, which allows occupation of habitats with severe winters but becomes a liability during warmer conditions (Brown, 1968; Smith et al., 1995). The bushy tail of *N. cinerea* may serve "as a warm wrap" to reduce heat loss during periods of cold ambient temperature (Finley, 1990). Dens also are important in thermoregulation, providing protection against thermal extremes as well as predators (Brown, 1968; Brown and Lee, 1969). When constructed within a rock crevice, den microlimate fluctuates only a few degrees daily, as compared to daily fluctuations of 15–20°C outside (Brown, 1968). Dens constructed within other shelters (e.g., buildings, mine shafts, etc.) provide less consistent thermal protection and experience wider ranges of ambient temperature (Brown, 1968).

Only rarely do *N. cinerea* construct free-standing houses (Cary, 1911; Dixon, 1919; Finley, 1958, 1990). Instead, they gather sticks and other dry vegetation which are stuffed into rocky crevices to form a shelter (Escherich, 1981; Finley, 1958; Hickling, 1987; Goldman, 1910). Within the den or shelter are one or more cup- or dome-shaped nests made of shredded fibrous vegetation such as juniper, sagebrush, or dry grass. Up to four nests per den have been recorded (Finley, 1958). Several middens, or debris piles, are also produced at the periphery of the den. These typically contain fecal pellets, plant fragments, sticks, bones and other refuse, and sometimes unusual items such as Indian artifacts, livestock dung, or owl pellets. Over time, especially with sequential use by generations of bushy-tailed woodrats, the middens may become quite large. Some have been recorded reaching depths of several meters and occupying the entire back surface of large caves (Finley, 1958; pers. obs.). Within the arid southwest, middens indurated with desiccated woodrat urine ("amberat") have been preserved for tens of thousands of years, and provide a rich source of fossil materials (Betancourt et al., 1990). Studies using radiocarbon-dated plant and animal macrofossils from woodrat paleomiddens have yielded remarkable insights into past climate and vegetation distributions as well as the microevolution of woodrats (e.g., Betancourt et al., 1990; Cole, 1985; Smith et al., 1995; Van Devender, 1987; Van Devender and Bradley, 1990; Wells 1966, 1976; Wells and Berger, 1967; Wells and Jorgensen, 1964).

Dens generally contain large quantities of hoarded plant materials (Escherich, 1981; Finley, 1958; Hickling, 1987). One food cache in Alberta, for example, contained approximately 50 kg of vegetation (Salt and Clarke, 1979). Large caches are relatively uncommon during summer, but food caching behavior intensifies during late August and September (Escherich, 1981; Finley, 1958; Hickling, 1987). Vegetation may be dried or cured by woodrats before storage by spreading it out on rocks (Dixon, 1919; Escherich, 1981; Finley, 1958); items may then be stuffed into vertical crevices. In Colorado, a cache made up of ca. 35 l of dried hackberry cuttings filled up all the diagonal crevices near the den (Finley, 1958). Dried mushrooms are often stored (Finley, 1958).

Neotoma cinerea is the most boreal species within the genus (Dixon, 1919; Escherich, 1981; Finley, 1958, 1990). It occurs in a wide variety of biotic communities but over much of the range is associated with douglas fir, spruce, aspen, or ponderosa pine forests (Brown, 1968; Dixon 1919; Escherich, 1981; Findley et al., 1975; Finley, 1958; Hickling, 1987; Hoffmeister, 1986). Rock shelters may be more important than plant communities in determining the suitability of habitat (Finley, 1958). To the south, *N. c. arizonae* often inhabit pinon-juniper woodlands along the base of sandstone cliffs and rock outcrops (Finley et al., 1975; Finley, 1958; Hoffmeister, 1986). Shrub cover is important (Finley, 1958). Typically, bushy-tailed woodrats are found to timberline and only patchily and periodically distributed above (Grayson and Livingston, 1989).

Bushy-tailed woodrats appear to have a broad and flexible diet when viewed over their entire range, but regional specialization occurs with animals feeding on items that are locally abundant and accessible (Dixon, 1919; Escherich, 1981; Finley, 1958, 1990). They are primarily folivorous, although bark, seeds, fruits and other items also are consumed (Dixon, 1919; Finley, 1958, 1990; Goldman, 1910; Howell, 1926). Food items collected vary with habitat and subspecies (Dixon, 1919; Finley, 1958). Based on analysis of the food caches within 58 dens, *N. c. orolestes* prefers mesophytic shrubs, aspen and conifers, whereas *N. c. arizonae* prefers xerophitic shrubs and conifers (Finley, 1958). Common food items collected by *N. c. orolestes* in Colorado included aspen (*Populus tremuloides*, found in 13/42 dens), Douglas fir (*Pseudotsuga menziesii*, 12/42 dens), choke-cherry (*Prunus virginiana*, 8/42 dens), rabbitbrush (*Chrysothamnus greenei*, *C. viscidiflorus*, *C. nauseosus* and *C. parryi*, 14/42 dens), mountain lover (*Pachystima myrsinites*, 6/42 dens), snowberry (*Symphoricarpos*, 14/42 dens), squaw currant (*Ribes cereum*, 16/42 dens), goldenrod (*Solidago*, 6/42 dens), wild rose (*Rosa*, 14/42 dens), Engelmann spruce (*Picea engelmanni*, also *P. pungens* and *P. aristata* to some extent, 4/42 dens), pines (*Pinus flexilis* and *P. ponderosa*, 9/42 dens), and juniper (*Juniperus monosperma*, *J. scopulorum* and *J. utahensis*, 9/42 dens—Finley, 1958). Food items reported for *N. c. arizonae* in Colorado included juniper (*J. monosperma*, *J. scopulorum* and *J. utahensis*, 9/11 dens), mountain-mahogany (*Cercocarpus ledifolius*, 4/11 dens), saltbrush (*Atriplex canescens*, *A. confertifolia* and *A. nuttallii*, 9/11 dens), pinon (*Pinus*, 6/11 dens), prickly pear (*Opuntia*, 6/11 dens), rabbitbrush (*C. greenei*, *C. viscidiflorus*, *C. nauseosus*, and *C. parryi*, 6/11 dens), and Russian thistle (*Salsola kali*, 3/11 dens—Finley, 1958). Vegetation was not consumed in direct proportion to its availability; many of these items were located further than 30 meters from the den site (Finley, 1958). In California, red elderberry (*Sambucus racemosa*), alder (*Alnus tenuifolia*), fir (*Abies*), and various composites were important items (Dixon, 1919). Vegetation noted in food caches in California included aspen, dogwood (*Cornus stolonifera*), mountain alder (*Alnus tenuifolia*), bitter cherry (*Prunus emarginata*), juniper, bitter brush (*Purshia tridentata*), mountain mahogany, and sagebrush (*Artemisia frigida*; Escherich, 1981; Nelson and Smith, 1976).

In addition to obtaining energy from the enzymatically digestible cell contents of plant forage, bushy-tailed woodrats derive substantial benefit from the microbial fermentation of plant structural components (Justice and Smith, 1992; Smith, 1995). Like other small hindgut-fermenting herbivores they have an enlarged cecum, which houses symbiotic microbes capable of fermenting cellulose and hemicellulose (Justice and Smith, 1992; Smith, 1995). This dietary strategy requires consumption of large quantities of plant materials to maintain energy balance. In laboratory trials, *N. cinerea* digested about 35% of the total fiber in the diet (about 70% of the available fiber) and obtained about 21% of its digestible energy solely from microbial fermentation of plant fibers (Smith, 1995). *N. cinerea* probably face seasonal shortages of food (Hickling, 1987), and it has been suggested that their dietary strategy facilitates survival during stressful environmental conditions (Justice and Smith, 1992).

Population density of *N. cinerea* is both seasonally and annually variable (Dixon, 1919; Escherich, 1981; Finley, 1958; Howell, 1926). Even within favorable habitat, the local distribution is often irregular. This seasonal variation has often been remarked upon: "Certain rock slides may be found to be occupied by wood rats, while near-by slides, apparently just as well adapted to their needs, seem altogether neglected by the animals" (Dixon, 1919: 66), and "During favorable seasons individuals may fairly swarm in certain [rock] slides, while there is no sign of them in others apparently as suitable" (Howell, 1926:10).

Because of the large amount of time spent in the nest, bushy-tailed woodrats are particularly susceptible to a wide diversity of ectoparasites. These include ticks, larval chiggers, mites, lice, the cone-nosed bug, warble fly, and fleas (Cudmore, 1986; Finley, 1958; Wood, 1936). Thirty-seven different ectoparasitic and phoretic species were taken from bushy-tailed woodrats in western Oregon (Cudmore, 1986). The most specious taxa were mites (26 species) followed by fleas (five species) and ticks (four species; Cudmore, 1986). Mites reported included *Aplondontopus* (a small elongate mite found on the hair of woodrat tails, and evidently the most abundant), *Miyatrombicula cynos*, *Echinonyssus neotomae*, *Neotrombicula cavicola*, *N. microtii*, *Euschoengastia oregonensis*, *E. guntheri*, *E. lacerta*, *E. finleyi*, *E. criceticola*, *E. peromysci*, *E. pomerantzi*, *Androlaelaps fahrenholzi*, *Haemogamasus reidi*, *Radfordia neotomae*, *Acomatacarus micheneri*, *Leeuwenhoekia americana*, *Trombicula alfredugesi*, *T. autumnalis*, *T. finleyi*, *T. harperi*, *T. microti*, and *T. potosina* (Cudmore, 1986; Finley, 1958). In western Oregon, 40% of animals housed mites of the genus *Aplodontopus*, with an average number of 169 per animal (Cudmore, 1986). Common ticks species were *Ixodes angustus* and *I. I. pacificus* (Cudmore, 1986), but others recorded include *Dermacentor andersoni*, *Ixodes spinipalpis*, and *I. woodi* (Finley, 1958). A single species of lice, *Neohaematopinus inornatus*, has been found on *N. cinerea* (Cudmore, 1986; Finley, 1958). Perhaps the most prominent ectoparasite found on *Neotoma* is the warble (bot) fly larva, *Cuterebra tenebrosa*, which forms large subcutaneous cysts (Finley, 1958). Warbles occur most frequently in the summer months and are usually found on the throat, breast, or on the side of the neck. The most abundant flea found is *Orchopeas sexdentatus*, sometimes called the "woodrat flea" because it is the major species found on all members of the genus (Cudmore, 1986; Finley, 1958; Nelson and Smith, 1976; Wood, 1936). In Oregon, over 93% of *N. cinerea* housed this species, with an average number of eight fleas per host (Cudmore, 1986). However, over 50 different species of fleas are found on bushy-tailed woodrats throughout their range (Cudmore, 1986). Other common flea species include *Stenistomera alpina*, *Atyphloceras multidentatus*, *Catallagia*, *Diamanus montanus*, *Megarthroglossus*, *Phalacropsylla allos*, *Malaraeus*, and *Monopsyllus* (Cudmore, 1986; Finley, 1958; Nelson and Smith, 1976). Additional parasites include *Ornithodorus*, *Brevisterna utahensis*, *Euhaemogamasus ambulans*, *Haemolaelaps geomys*, *H. glasgowi*, and *Hirstionyssus neotomae* (Finley, 1958). A single species of tapeworm, *Andrya* cf. *A. macrocephala*, has been described (Finley, 1958). In addition to ectoparasites found directly on bushy-tailed woodrats, a wide variety of predatory and saprophagus invertebrates are found associated with their dens. These include predatory mites (mostly *Hypoaspis*), oribatid mites, acarid mites, millipeds, *Collembola*, and both larvae and adult Coleoptera, Diptera, and Lepidoptera (Nelson and Smith, 1976).

Neotoma cinerea is susceptible to at least some of the disease carried by parasites. Several species of woodrat flea and ticks are vectors for diseases such as trypanosomes, bubonic plague, or spotted fever (Birdseye, 1912; Nelson and Smith, 1976; Wood, 1936). For example, the majority of a population of bushy-tailed woodrats was extirpated during an epizootic of sylvatic plague from Lava Beds National Monument in northeastern California (Nelson and Smith, 1976).

Common predators on bushy-tailed woodrats include long-tailed weasels (*Mustela frenata*), martens (*Martes americana*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), great horned owls (*Bubo virginianus*), red-tailed hawks (*Buteo jamaicensis*), and goshawks (*Accipiter gentilis*); some species of snakes may also be important (Dixon, 1919; Escherich, 1981; Goldman, 1910). Commensals found within and around the den site include pikas (*Ochotona princeps*), ground squirrels (*Spermophilus*), alpine chipmunks (*Tamias alpinus*), marmots (*Marmota marmox*), and various species of deer mice (*Peromyscus*—Dixon, 1919; Finley, 1990).

BEHAVIOR. Female bushy-tailed woodrats are usually philopatric (Escherich, 1981; Hickling, 1987; Moses and Millar, 1992). Once resident in an area they exhibit "absolute site tenacity," breeding on the same outcrop over successive years (Escherich, 1981; Hickling, 1987; Moses and Millar, 1992). Males are more mobile as yearlings and may travel some distance in dispersing from their natal den (Escherich, 1981; Moses and Millar, 1992). Both sexes are relatively sedentary once a territory is established (Escherich, 1981; Moses and Millar, 1992).

Social organization is variable and is apparently related to the distribution and the size of the available habitat (Hickling, 1987). Several authors have characterized the social system as polygynous with loosely associated "groups" that occupy the same outcrop (Escherich, 1981; Hickling, 1987), others as promiscuous (Topping and Miller, 1996*a*), or as a sort of "cohesive sociality" (Moses and Millar, 1992). Occasionally, groups of bushy-tailed woodrats contain several adult males, although they probably have separate mutually exclusive territories (Hickling, 1987). About 29% of males are nonterritorial transients; these are generally yearlings (Hickling, 1987; Moses and Millar, 1992). The size of the habitat patch is positively correlated with the number of females found within the group, although generally only a single male is found (Escherich, 1981; Hickling, 1987). Solitary breeding females sometimes occupy the smallest patches (Hickling, 1987). In general, the average group within a rocky outcrop contains a single male and two or three females and/or associated juveniles (Moses and Millar, 1992). Despite some spatial cohesiveness, bushy-tailed woodrats are relatively unsocial animals, exhibiting tolerance only towards close relatives (Caldwell et al., 1984; Finley, 1990; Hickling, 1987; Moses and Millar, 1992). In fact, stable cohesive relationships have only been observed between mother and offspring, while interactions between nonrelatives are highly agonistic (Moses and Millar, 1992). Bushy-tailed woodrats do not readily form non-territorial dominance hierarchies that would allow them to coexist with non-relatives (Hickling, 1987).

In Alberta, about 83% of female bushy-tailed woodrats foraged at distances greater than 60 m from the den (Topping and Millar, 1996*b*). Females foraged over greater distances when pregnant or lactating than when non-reproductive ($P < 0.05$, $n = 10$; based on a one-tailed Wilcoxon's signed-rank test of data presented by

Topping and Millar, 1996*b*:table 1). This may be a result of more selective foraging during periods of greater energy requirements. Home range may be much greater than the 50-60 m commonly cited (Finley, 1958, 1990). The mean maximum foraging radius for females in Alberta, was ca. 144 m (n = 10); several individuals had a maximum foraging radius of over 200 meters when pregnant (Topping and Millar, 1996*b*). Males have significantly larger home ranges than females (Hickling, 1987; Moses and Millar, 1992; Topping and Millar, 1996*c*). In Alberta, the average home range of males was 6.12 ha (n = 23; range 1.6–11.2 ha) versus 3.56 ha for females (n = 27; range 0.1–10.4 ha; Topping and Millar, 1996*c*). Territory sizes were ca. 10-20 times larger than those estimated for other species of *Neotoma* (Topping and Millar, 1996*c*) and much greater than previously reported for bushy-tailed woodrats in the southern portion of their range (Finley, 1958, 1990). It is not clear whether the large discrepancy reflects a reduced food supply in Alberta relative to other areas or an underestimation of home range size by previous workers. Bushy-tailed woodrats are generally nocturnal, although some diurnal activity may occur under dense rock or shrub cover (Dixon, 1919; Finley, 1958, 1990).

Olfaction is an important mediator of social behavior in woodrats (Howe, 1977, 1978). The dusky odor imparted by the midventral sebaceous gland is used to indicate territorial boundaries and also is closely associated with male agonistic behavior (August, 1978; Escherich, 1981; Finley, 1958; Goldman, 1910; Hickling, 1987; Hoffmeister, 1986; Howe, 1977; Howell, 1926; Wiley, 1980). Males "tooth chatter" when exposed to scent from another male's gland (Howe, 1977). Scent marking probably also functions as a component of courtship (August, 1978; Finley, 1990; Howe, 1977); female bushy-tailed woodrats are strongly attracted to sebum from the ventral gland of males (August, 1978). Scent marking behaviors are most pronounced in males and there does not seem to be noticeable glandular action in either females or juveniles (Escherich, 1981; Howell, 1926; Wiley, 1980). Scent marking apparently operates both inter- and intraspecifically (Howe, 1977); this may help maintain the genetic integrity of closely related species such as *N. micropus*, *N. albigula* and *N. floridana* that occur in sympatry or parapatry and that have been demonstrated to hybridize in the laboratory (August, 1978). Woodrats also exhibit responses to conspecific urine. The ability to deduce gender using odor stimuli probably reduces the number of agonistic encounters and increases reproductive efficiency (August, 1978).

Neotoma cinerea uses "urinating posts," which appear as white streaks and blotches on rocks and are sometimes taken for bird guano (Dixon, 1919; Emerson and Howard, 1978; Escherich, 1981; Nelson and Smith, 1976). Over the years the encrustations on urinating posts can accumulate to a thickness of several centimeters (Emerson and Howard, 1978). "The urine thus expelled at any one of several particular places by rats over a period of many years accumulates to a thickness of several inches, hardens, and becomes semi-transparent. Not infrequently this hardened residue is taken for a mineral. . . ." (Hall, 1946:535). The "whitewash," as it is sometimes called, is made of microcrystalline encrustations consisting mostly of calcite, particularly calcium oxalates (Emerson and Howard, 1978).

Footstomping is a widespread behavior among woodrat species (Howe, 1978) and is generally seen in agonistic contexts. Rainey (1956) suggested it was an automatic alarm reflex.

GENETICS. *Neotoma cinerea* has a diploid number of 54 and a fundamental number of 60 (Baker and Mascarello, 1969; Carleton, 1980; Koop et al., 1985; Mascarello and Hsu, 1976). Of the autosomal chromosomes, there are 22 pairs of acrocentrics, one medium-sized subtelocentric, and three pairs with small arms. The X is a large submetacentric and the Y is a medium-sized subtelocentric (Baker and Mascarello, 1969; Mascarello and Hsu, 1976). *N. cinerea* and *N. fuscipes* share an absence of the proximal one-third of the acrocentric primitive G-band sequence on chromosome 2 and a translocation and pericentric inversion in chromosome 3 (Koop et al., 1985). Despite their patchy distribution, bushy-tailed woodrats may have relatively high degrees of gene flow. Six populations of *N. cinerea* from isolated mountain ranges averaged a pairwise genetic-distance measure of only 0.0025 (Mewaldt and Jenkins, 1986). *N. cinerea* is reportedly more heterozygous in the Great Basin than in either the Sierra Nevada or Rocky Mountains, suggesting somewhat greater gene flow (Mewaldt and Jenkins, 1986). Little additional information exists on the genetics of this species.

REMARKS. The generic name *Neotoma* is derived from the Greek words *neos* meaning "new," and *tomos* meaning "cut or cutting." The specific name *cinerea* is from the feminized Latin word *cinereus* meaning "ashy" or "ash-colored," in deference to Lewis and Clark's original description of an "ash-colored rat" from the Rocky Mountains (Ord, 1815). Earlier authors placed *N. cinerea* and *N. fuscipes* in separate subgenera (Burt and Barkalow, 1942; Goldman, 1910; Merriam, 1894*a*, 1894*b*), but Carleton (1980) has suggested that *N. fuscipes* and *N. cinerea* share common ancestry. Comparison of ectoparasite communities between *N. cinerea* and *N. fuscipes* also supports this hypothesis (Cudmore, 1986).

Common vernacular names include "trade rat" and "packrat" and result from the particularly well-developed collecting instinct of *N. cinerea*. "It is supposed that when one of these rats carrying an object of its fancy comes to another more attractive object, it drops the first and continues on its way with the second. If the second object be the watch of a camper, who in the morning finds a piece of old bone where the watch lay when the camper went to sleep the evening before, he will think the name trade rat appropriate. . . ." (Hall, 1946:533). The subspecies *N. c. acraia* (Elliot, 1904*a*) actually was named *acraea* from the Greek meaning "dwelling on the hills," but a misprint in the original publication resulted in the subspecific name commonly used (Elliot, 1904*b*). Here, I have resurrected the original spelling.

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LITERATURE CITED

ALLEN, J. A. 1894. Descriptions of ten new North American mammals, and remarks on others. Bulletin of the American Museum of Natural History, 6:317–332.

———. 1895. Descriptions of new North American mammals. Bulletin of the American Museum of Natural History, 7:327–340.

AUGUST, P. V. 1978. Scent communication in the southern plains wood rat, *Neotoma micropus*. American Midland Naturalist, 99:206–218.

BAIRD, S. F. 1855. Characteristics of some new species of North American Mammalia, collected chiefly in connection with the United States surveys of a railroad route to the Pacific. Proceedings of the Academy of Natural Science, Philadelphia, 7: 333–336.

BAKER, R. J., AND J. T. MASCARELLO. 1969. Karyotypic analyses of the genus *Neotoma* (Cricetidae, Rodentia). Cytogenetics, 8: 187–198.

BETANCOURT, J. L., T. R. VAN DEVENDER, AND P. S. MARTIN. 1990. Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson, 467 pp.

BIRDSEYE, C. 1912. Some common mammals of western Montana in relation to agriculture and spotted fever. United States Department of Agriculture Farmer's Bulletin, 484:3–46.

BLEICH, V. C., AND O. A. SCHWARTZ. 1974. Interspecific and intergeneric maternal care in woodrats (*Neotoma*). Mammalia, 38:381–387.

BOICE, R. 1969. Water intake as a function of ease of access in *Neotoma*. Journal of Mammalogy, 50:605–607.

BROWN, J. H. 1968. Adaptation to environmental temperature in two species of woodrats, *Neotoma cinerea* and *N. albigula*. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 135:1–48.

BROWN, J. H., AND A. K. LEE. 1969. Bergmann's rule and climatic adaptation in woodrats (*Neotoma*). Evolution, 23:329–338.

BURT, W. H., AND F. S. BARKALOW. 1942. A comparative study of the bacula of wood rats (subfamily Neotominae). Journal of Mammalogy, 28:287–297.

CALDWELL, G. S., S. E. GLICKMAN, AND E. R. SMITH. 1984. Seasonal aggression independent of seasonal testosterone in woodrats. Proceedings of the United States National Academy of Science, 81:5255–5257.

CARLETON, M. D. 1980. Phylogenetic relationships in Neotomine-

Peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 157:1–146.

Cary, M. 1911. A biological survey of Colorado. North American Fauna, 33:1–256.

Cole, K. L. 1985. Past rates of change, species richness, and a model of vegetational inertia in the Grand Canyon, Arizona. American Naturalist, 125:289–303.

Cudmore, W. W. 1986. Ectoparasites of *Neotoma cinerea* and *N. fuscipes* from western Oregon. Northwest Science, 60:174–178.

Dalquest, W. W. 1983. Mammals of the Coffee Ranch local fauna Hemphillan of Texas. Pearce-Sellards Series, Texas Memorial Museum, 38:1–41.

Dixon, J. 1919. Notes on the natural history of the bushy-tailed wood rats of California. University of California Publications in Zoology, 21:49–74.

Donat, F. 1933. Notes on the life history and behavior of *Neotoma fuscipes*. Journal of Mammalogy, 14:19–26.

Egoscue, H. J. 1962. The bushy-tailed woodrat: a laboratory colony. Journal of Mammalogy, 43:328–337.

Elliot, D. G. 1898. Lists of species of mammals, principally rodents, obtained by W. W. Price, Dr. S. E. Meek, G. K. Cherrie, and E. S. Thompson in the states of Iowa, Wyoming, Montana, Idaho, Nevada and California with descriptions of new species. Field Columbian Museum, Zoological Series, 1:193–221.

———. 1904*a* ("1903"). Descriptions of twenty-seven apparently new species and subspecies of mammals. Field Columbian Museum, Zoological Series, 3:239–261.

———. 1904*b*. Catalogue of mammals collected by E. Heller in southern California. Field Columbian Museum, Zoological Series, 3:271–321.

Emerson, D. O., and W. E. Howard. 1978. Minerology of woodrat, *Neotoma cinerea*, urine deposits from northeastern California. Journal of Mammalogy, 59:424–425.

Escherich, P. C. 1981. Social biology of the bushy-tailed woodrat, *Neotoma cinerea*. University of California Publications in Zoology, 110:1–132.

Feldman, H. W. 1935. Notes on two species of wood rats in captivity. Journal of Mammalogy, 16:300–303.

Findley, J. S., A. H. Harris, D. E. Wilson, and C. Jones. 1975. Mammals of New Mexico. University of New Mexico Press, Albuquerque, 360 pp.

Finley, R. B., Jr. 1958. The wood rats of Colorado. University of Kansas Publication, Museum of Natural History, 10:213–552.

———. 1990. Woodrat ecology and behavior and the interpretation of paleomiddens. Pp. 28–42, *in* Packrat middens: the last 40,000 years of biotic change (J. L. Betancourt, T. R. Van Devender, and P. S. Martin, eds.). University of Arizona Press, Tucson, 467 pp.

Goldman, E. A. 1910. Revision of the wood rats of the genus *Neotoma*. North America Fauna, 31:1–124.

———. 1917. New mammals from North and Middle America. Proceedings of the Biological Society of Washington, 30:107–116.

Grayson, D. K., and S. D. Livingston. 1989. High-elevational records for *Neotoma cinerea* in the White Mountains, California. Great Basin Naturalist, 49:392–395.

Grinnell, J. 1913. A distributional list of the mammals of California. Proceedings of the California Academy of Science, 3: 265–390.

Hall, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley, 710 pp.

———. 1981. The mammals of North America. John Wiley & Sons, New York, 2:601–1181 + *90*.

Harris, A. H. 1984*a*. *Neotoma* in the late Pleistocene of New Mexico and Chihuahua. Pp. 164–178, *in* Contributions to Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday (H. H. Genoways, and M. R. Dawson, eds.). Special Publications of the Carnegie Museum of Natural History, 8:1–538.

———. 1984*b*. Two new species of late Pleistocene woodrats (Cricetidae: *Neotoma*) from New Mexico. Journal of Mammalogy, 65:560–566.

———. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin, 293 pp.

———. 1993. Quaternary vertebrates of New Mexico. Pp. 179–197, *in* Vertebrate Paleontology in New Mexico (S. G. Lucas, and J. Zidek, eds.). New Mexico Museum of Natural History and Science, Bulletin 2,281 pp.

Hibbard, C. W. 1967. New rodents from the late Cenozoic of Kansas. Papers of the Michigan Academy of Science, Arts, and Letters, 52:115–131.

Hickling, G. J. 1987. Seasonal reproduction and group dynamics of bushy-tailed woodrats, *Neotoma cinerea*. Ph.D. dissertation, University of Western Ontario, 163 pp.

Hickling, G. J., J. S. Millar, and R. A. Moses. 1991. Reproduction and nutrient reserves of bushy-tailed wood rats (*Neotoma cinerea*). Canadian Journal of Zoology, 69:3088–3092.

Hoffmeister, D. F. 1986. Mammals of Arizona. University of Arizona Press, Tucson, 602 pp.

Hooper, E. T. 1940. Geographical variation in bushy-tailed wood rats. University of California Publications in Zoology, 42:407–424.

———. 1960. The glans penis in *Neotoma* (Rodentia) and allied genera. Occasional Papers of the Museum of Zoology, University of Michigan, 618:1–20.

Horvath, O. 1966. Observation of parturition and maternal care of the bushy-tailed wood rat (*Neotoma cinerea occidentalis* Baird). Murrelet, 47:6–8.

Howe, R. J. 1977. Scent-marking behavior in three species of woodrats (*Neotoma*) in captivity. Journal of Mammalogy, 58: 685–688.

——— 1978. Agonistic behavior of three sympatric species of woodrats (*Neotoma mexicana*, *N. albigula*, and *N. stephensi*). Journal of Mammalogy, 59:780–786.

Howell, A. B. 1926. Anatomy of the wood rat. Monographs of the American Society of Mammalogists, 1:1–225.

Jones, C., and N. J. Hildreth. 1989. Neotoma stephensi. Mammalian Species, 328:1–3.

Justice, K. E., and F. A. Smith. 1992. A model of dietary fiber utilization by small mammalian herbivores with empirical results for *Neotoma*. American Naturalist, 139:398–416.

Kellogg, L. 1912. Pleistocene rodents of California. University of California Publication Bulletin, Department of Geology, 7: 151–168.

Kelson, K. R. 1949. Two new wood rats from eastern Utah. Journal of the Washington Academy of Science, 30:417–419.

———. 1952. Comments on the taxonomy and geographic distribution of some North American woodrats (genus *Neotoma*). University of Kansas Publications, Museum of Natural History, 5:233–242.

Kiltie, R. A. 1982. Intraspecific variation in the mammalian gestation period. Journal of Mammalogy, 63:646–652.

Koop, B. F., R. J. Baker, and J. T. Mascarello. 1985. Cladistical analysis of chromosomal evolution within the genus *Neotoma*. Occasional Papers of the Museum, Texas Tech University, 96:1–9.

Korth, W. W. 1994. The Tertiary record of rodents in North America. Plenum Press, New York, 319 pp.

Kurtén, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, 442 pp.

Lee, A. K. 1963. The adaptations to arid environments in wood rats of the genus *Neotoma*. University of California Publications in Zoology, 64:57–96.

Logan, L. E. 1981. The mammalian fossils of Muskox Cave, Eddy County, New Mexico. Proceedings of the 8th International Congress of Speleology, 1:159–160.

Manville, R. H., and S. P. Young. 1965. Distribution of Alaskan Mammals. United States Department of the Interior, Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, Circular 211:1–74.

Martell, A. M., and J. N. Jasper. 1974. A northern range extension for the bushy-tailed wood rat, *Neotoma cinerea* (Ord). Canadian Field Naturalist, 88:348.

Martin, R. J. 1973. Growth curves for bushy-tailed woodrats based upon animals raised in the wild. Journal of Mammalogy, 54:517–518.

Mascarello, J. T., and T. C. Hsu. 1976. Chromosomal evolution in woodrats, genus *Neotoma* (Rodentia: Cricetidae). Evolution, 30:152–169.

MERRIAM, C. H. 1893. Two new woodrats from the plateau region of Arizona (*Neotoma pinetorum* and *N. arizonae*) with remarks on the validity of the genus *Teonoma* of Gray. Proceedings of the Biological Society of Washington, 8:109–112.

———. 1894*a*. Abstract of a study of the American wood rats, with descriptions of fourteen new species and subspecies of the genus *Neotoma*. Proceedings of the Biological Society of Washington, 9:117–128.

———. 1894*b*. A new subfamily of murine rodents—the Neotominae—with description of a new genus and species and a synopsis of the known forms. Proceedings of the Academy of Natural Sciences of Philadelphia, 46:225–252.

MEWALDT, W. T., AND S. H. JENKINS. 1986. Genetic variation of woodrats (*Neotoma cinerea*) and deer mice (*Peromyscus maniculatus*) on montane habitat islands in the Great Basin. Great Basin Naturalist, 46:577–580.

MOSES, R. A., AND J. S. MILLAR. 1992. Behavioural asymmetries and cohesive mother-offspring sociality in bushy-tailed wood rats. Canadian Journal of Zoology, 70:597–604.

MOSES, R. A., G. J. HICKLING, AND J. S. MILLAR. 1995. Variation in sex ratios of offspring in wild bushy-tailed woodrats. Journal of Mammalogy, 76:1047–1055.

NELSON, B. C., AND C. R. SMITH. 1976. Ecological effects of a plague epizootic on the activities of rodents inhabiting caves at Lava Beds National Monument, California. Journal of Medical Entomology, 13:51–61.

OLSEN, R. W. 1976. Water: a limiting factor for a population of woodrats. Southwestern Naturalist, 21:391–398.

ORD, G. 1815. Zoology of North America. Guthries' Geography, 2nd American edition, pp. 291–361. [reprint Rhoads, S. N. Philadelphia, 1894]

OSGOOD, W. H. 1900. Mammals of the Yukon region. North American Fauna, 19:21–45.

RAINEY, D. G. 1956. Eastern woodrat, *Neotoma floridana*: life history and ecology. University of Kansas Publications Museum of Natural History, 8:535–646.

RICHARDSON. J. 1828. Short characters of a few quadrupeds procured on Captain Franklin's late expedition. The Zoological Journal, 3:516–520.

SALT, J. R., AND R. CLARKE. 1979. Mammalian fauna of the Kananaskis Lakes, Upper Kananaskis River and Highwood Pass region, Alberta. Alberta Naturalist, 9:22–45.

SAY, T., AND G. ORD. 1825. A new genus of Mammalia proposed, and a description of the species upon which it is founded. Journal of the Academy of Natural Science of Philadelphia, 4: 345–349.

SCHMIDT-NIELSEN, K., AND B. SCHMIDT-NIELSEN. 1952. Water metabolism of desert animals. Physiological Review, 32:135–166.

SINCLAIR, W. J. 1905. A preliminary account of the exploration of Potter Creek Cave, Shasta County, California. Science, 17: 708–712.

SMITH, F. A. 1995. Scaling of digestive efficiency with body size in *Neotoma*. Functional Ecology, 9:299–305.

SMITH, F. A., J. L. BETANCOURT, AND J. H. BROWN. 1995. Evolution of body size in the woodrat over the past 25,000 years of climatic change. Science, 270:2012–2014.

TOPPING, M. G., AND J. S. MILLAR. 1996*a*. Spatial distribution in the bushy-tailed wood rat (*Neotoma cinerea*) and its implications for the mating system. Canadian Journal of Zoology, 74:565–569.

———. 1996*b*. Foraging movements of female bushy-tailed woodrats (*Neotoma cinerea*). Canadian Journal of Zoology, 74: 798–801.

———. 1996*c*. Home range size of bushy-tailed woodrats (*Neotoma cinerea*) in southwestern Alberta. Canadian Field Naturalist, 110:351–353.

TRUE, F. W. 1894. Diagnosis of some undescribed wood rats (genus *Neotoma*) in the National Museum. Preprint, pp. 1–4 of Proceedings of the United States National Museum, 17:353–355.

VAN DEVENDER, T. R. 1987. Holocene vegetation and climate in the Puerto Blanco Mountains, southwestern Arizona. Quaternary Research, 27:51–72.

VAN DEVENDER, T. R., AND G. BRADLEY. 1990. Late Quaternary mammals from the Chihuahuan Desert: paleoecology and latitudinal gradients. Pp. 350–362, *in* Packrat middens: the last 40,000 years of biotic change (J. L. Betancourt, T. R. Van Devender, and P. S. Martin, eds.). University of Arizona Press, Tucson, 467 pp.

WARREN, E. R. 1926. Notes on the breeding of wood rats of the genus *Neotoma*. Journal of Mammalogy, 7:97–101.

WEBB, R. H., AND J. L. BETANCOURT. 1990. The spatial and temporal distribution of radiocarbon ages from packrat middens. Pp. 85–103, *in* Packrat middens: the last 40,000 years of biotic change (J. L. Betancourt, T. R. Van Devender, and P. S. Martin, eds.). University of Arizona Press, Tucson, 467 pp.

WELLS, P. V. 1966. Late Pleistocene vegetation and degree of pluvial climatic change in the Chihuahuan Desert. Science, 153:970–975.

———. 1976. Macrofossil analysis of wood rat (*Neotoma*) middens as a key to the Quaternary vegetational history of arid America. Quaternary Research, 6:223–248.

WELLS, P. V., AND R. BERGER. 1967. Late Pleistocene history of coniferous woodland in the Mohave Desert. Science, 155: 1640–1647.

WELLS, P. V., AND C. D. JORGENSEN. 1964. Pleistocene wood rat middens and climatic change in the Mohave Desert: a record of Juniper woodlands. Science, 143:1171–1174.

WILEY, R. W. 1980. Neotoma floridana. Mammalian Species, 139: 1–7.

WOOD, F. D. 1936. *Trypanosoma neotomae*, sp. nov., in the dusky-footed wood rat and the wood rat flea. University of California Publications in Zoology, 41:133–144.

YOUNGMAN, P. M. 1975. Mammals of the Yukon Territory. National Museum of Natural Sciences Publications in Zoology, 10:1–192.

ZAKRZEWSKI, R. J. 1993. Morphological change in woodrat (Rodentia: Cricetidae) molars. Pp. 392–410, *in* Morphological change in quaternary mammals of North America (R. A. Martin, and A. D. Barnosky, eds.), Cambridge University Press, Cambridge, 414 pp.

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