Neotoma cinerea. By Felisa A. Smith
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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 37° latitude.


*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 saxatilis* Osgood, 1900:33. Type locality from “slide of large granite boulders [=boulders] at head of Lake Bennett,” British Columbia.

**CONTEXT AND CONTENT.** Order Rodentia, Family Muridae, Subfamily Sigmodontinae, Genus *Neotoma*, Subgenus *Neotoma*. Thirteen subspecies are currently recognized (Carlton, 1960; Hall, 1981):

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

* N. c. alticola* Hooper, 1940:409. Type locality from “Parker Creek [=Shieldes 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. drummondii* (Richardson, 1826:317), see above.

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

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

* N. c. macronot* Kelso, 1949:417. Type locality from “E side confluence Green and White rivers, 4700 ft., 1 mile SE Ouray, Un- itah County, Utah.”

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

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

* N. c. palla* 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 furled 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 prominent than in other species of woodrats (August, 1978; Finley, 1958; Goldman, 1910; Hoffman, 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; Carlton, 1960; Dixon, 1919; Finley, 1958; Goldman, 1910, 1917; Hooper, 1940; Kelso, 1949, 1952; Merriam, 1946). Sphenopalatine vacuities may be present or absent (Allen, 1894; Dixon, 1919; Hooper, 1940; Merriam, 1893, 1894a, 1894b). M1 has a deep antemolarine re-entrant angle; M3 has an anterior closed triangle and two confluent posterior loops (Hall, 1981). The basculum is relatively thin and has an elongate cartilaginous spine (Burt and Barkalow, 1942; Carlton, 1980; Hoffman, 1986; Hooper 1966; 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 solo, differentially-shelled basculum, and longer and more heavily-furred tail (Hoffmeister, 1986; Jones and Hillreh, 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 slightly washed with buff to a dark brownish-black or tawny shade; the underparts may vary from white to pinkish or buff (Allen, 1893; 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 midventral line (Hall, 1981; Howell, 1926), and many populations are white-throated (Hoffmeister, 1986). *N. cinerea* have rooted molars that tend to hypsodonty, resembling

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**Fig. 1.** Captive adult *Neotoma cinerea oreolestes*. 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 oreolutes (NSB #39004) from the upper Tesque 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. alitica; c, N. c. arizonae; d, N. c. cinerea; e, N. c. cinnamomea; f, N. c. drummondii; g, N. c. fusca; h, N. c. lucida; i, N. c. macrodont; j, N. c. occidentalis; k, N. c. oreolutes; l, N. c. pallar; m, N. c. rupicola.

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; Grimmell, 1913; Hoffmeister, 1986; Hooper, 1940). In the Pleistocene the range extended as far south as northern Mexico but was constricted to the north (Harris, 1964a, 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, 1963; 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
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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. parvotoma minuta) dates from the late Miocene at 6.6 ± 10° 3 million years ago or earlier (Dinkin, 1963; Hibbard, 1967; Korth, 1994). Although it is not known when N. cinerata 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 differentiated on the basis of molar dentition by the Rancholabrean at 3.0 ± 10° 3 million years ago (Zakrzewski, 1993). N. cinerata may be derived from the extant species N. amplidonta, dated by biostratigraphy to the Livionatean (1.9 ± 3 to 3.0 ± 10° 3 million years ago; Zakrzewski, 1993). Fossil evidence of N. cinerata 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, 1984a, 1984b, 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. cinerata occurred in southern New Mexico and southwestern Texas, and ranged as far south as northern Mexico (Harris, 1984a, 1985; Van Devender and Bradley, 1990). As climate and vegetation changed during the transition between the Pleistocene and Holocene, N. cinerata retreated to its modern distributional limits. Fossil records have been reported from sites as far south as Dry, Muskox, and U-Bar Caves in New Mexico and Lower Slough Cave in western Texas (Harris, 1984a, 1984b, 1985; Logan, 1981; Van Devender and Bradley, 1990). An early record of woodrat, N. findleyi, was identified by Harris (1984a, 1984b) from Dry Cave and dated at about 3.0 ± 10° 3 million years ago. He suggested that it represented a population of N. cinerata 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, Teonomia splcnsa, Sinclair (1905:148) from Potter Creek Cave, Shasta County, California. Later examination suggested that the specimen actually represented N. cinerata occidentalis (Dixon, 1919; Hooper, 1946; Kellogg, 1912).

FORM AND FUNCTION. Adult bushy-tailed woodrats have a thickened cremasteral area medially that contains enlarged, highly specialized, glandular sebaceous masses (August, 1978; Escherich, 1901; Finley, 1958; Goldmann, 1910; Hickling, 1967; Hoffmeister, 1900; Howell, 1926). As the uppermost part of the feature is most pronounced in males, and there does not seem to be marked glandular action in females or subadults (Escherich, 1911; Howell, 1926; Wiley, 1980). The scent gland secretions apparently are used to mark territorial boundaries and may facilitate mating (August, 1978; Escherich, 1961; Hickling, 1967; 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 hardier vegetation may have resulted from environmental changes during the late Tertiary. Howell (1926) provided detailed myological, osteological, digestive, and urinogenital analysis for several different species of Neotoma, including N. cinerata.

In N. cinerata the glans penis is slender and constricted distally (Burt and Barkalow, 1942; Carleton, 1980; Finley, 1958; Goldmann, 1910; Hall, 1981; Hoffmeister, 1986; Hooper, 1966; Howell, 1900; Hilgard, 1901) described the penis as a "shapeless 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 spire of about equal length (Hoffmeister, 1986; Hooper, 1966); in cross section the basal portion of the baculum has a slight convexity in both the dorsal and ventral surface (Burt and Barkalow, 1942). It averages about 5.5 mm in length, 0.9 mm in diameter, and dorsovertebral 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, 1966). Dimensions vary somewhat with body size and age, but the general shape does not (Burt and Barkalow, 1942; Finn, 1958).

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 in 1981 there may be no dateable (1982) calculable 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, 1988; 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 postjuvenile 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 climates, they are not particularly efficient at water conservation (Boise, 1969; Lee, 1963; Olsen, 1976; Schmidt-Nielsen and Benedict, 1989; Van Devender and Bradley, 1990). Many species of woodroids, including N. findleyi, are reported to be capable of up to 54 days 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 the presence of sufficient food resources (Hickling, 1967; Hickling et al., 1991). Bushy-tailed woodrats first breed as yearlings, and females are seasonally polyestrous (Egoscue, 1962; Escherich, 1961; Finley, 1958; Hickling, 1967; Hickling et al., 1991; Moses and Millar, 1992; Moss et al., 1992; Warren, 1926). The number of litters per season is related to 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 are used to supplement daily foraging during reproduction (Hickling, 1967). Food supplementation leads to a decrease in the 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 (Moss et al., 1992). Most populations probably have one to two litters annually (Dixon, 1919; Finley, 1958; Hickling, 1967; 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 2.6 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 (Toppling and Millar, 1996a). Occasionally, in small patches of habitat monogamous pairs form; these tend to be transient and generally do not last into successive breeding seasons (Hickling, 1967). 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, 1967; Hickling et al., 1982). Calculated from birth, the duration is 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). However, females 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, 1996a, 1996b) and California (Dixon, 1919; Elliot, 1895; Escherich, 1901). Sites at lower elevations tend to exist along streams and a longer reproductive period (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 meiopos, 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 begins to grow 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 (Gesoeasu, 1962; Escherich, 1981; Finley, 1958; Hickling, 1987; Moses and Millar, 1992; Warren, 1962). Dispersal generally occurs shortly after weaning. Bushy-tailed woodrats tend to exhibit female-based philopatry with daughters also dispersing to sites near their natal territories (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 (Bleich, 1977; Dixon, 1981; Hickling, 1987). An interesting exception is that females 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 30–30% 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, cliffs, or talus slopes (Brown, 1968; Dixon, 1919; 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 puehlo cliff dwellings (Brown, 1968; Finley 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). N. cinerea may serve "as a warm wrap" to reduce heat loss during periods of cold ambient temperature (Finley, 1990). Den sites 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 microclimate fluctuates only a few degrees daily, as compared to daily fluctuations of 15–20°C outside (Brown, 1968). Bushy-tailed woodrats construct dens in crevices in rock walls (e.g., buildings, mine shafts, etc.) to provide 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 grasses 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 illusive vegetation such as jackrabbit, sagebrush, or rabbitbrush. Up to four nests in Colorado 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 ("amheras") 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 rock wall palaeodens have yielded remarkable insights into past climate and vegetation distributions (Cary, 1911; Finley, 1958; Goldsmith, 1986; Moseley, 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)."
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dens), pines (Pinus flexilis and P. ponderosa, 9/4/2s dens), and juniper (Juniperus monosperma, J. scopulorum and J. utahensis, 9/4/2s 1988). Food items more commonly found for N. c. eremicus in Colorado included juniper (J. monosperma, J. scopulorum and J. utahensis, 9/1/11 dens), mountain mahogany (Cercopis cerodulis, 9/4/11 dens), saltbrush (Artemisia canescens, A. confertifolia and A. nattallii, 9/1/11 dens), pinon (Pinus, 6/1/11 dens), prickly pear (Opuntia, 9/4/11 dens), rabbitbrush (C. greenei, C. vacciniflora, C. nauseosa, and C. parryi, 6/1/11 dens), and Russian thistle (Salsola kali, 3/1/11 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, Abriria (Sambucus racemosa), elderberry (Sambucus nigra), 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 (Parshus 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, 1996). Like other small, hard-fruit foraging herbivores they have an enlarged cecum, which houses symbiotic microorganisms capable of fermenting cellulose and hemielucose (Justice and Smith, 1992; Smith, 1995). This dietary strategy requires consumption of large quantities of plant material. Energy balance data for a captive N. c. eremicus digested about 35% of the total fiber in the diet (about 70% of the available fiber) and obtained about 21% of its digestive energy solely from microbial fermentation of plant fibers (Smith, 1995). N. c. eremicus 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. c. eremicus 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 common housefly, and the stable fly, and the horsefly (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 Aplodontiophthalmus (a small elongate mite found on the hair of wood rats, and evidently the most abundant), Miayotrombicula cynos, Echinonyssus neotamiae, Neotrombicula cavicola, N. microti, Euschoengastia orogenensis, E. guaniyeri, E. lucetia, E. finleyi, E. cristicala, E. peromysci, E. pomerantzi, Androlepidae rubalid, Hologomus neatiae, Radoftoma neotamiae, Acomastura mchineri, Leenawenka americana, Trombicula alfredi, T. autumnalis, T. finleyi, T. harperi, T. microti, and T. potozima (Cudmore, 1986; Finley, 1958).

In western Oregon, 40% of animals housed mites of the genus Aplodontiophthalmus, with an average number of 169 per animal (Cudmore, 1986). Common ticks species were Isodes angustus and I. I. pacificus (Cudmore, 1986), but others reported include Dermacentor andersoni, Isodes spinapalis, and I. woodsii (Finley, 1958). A single species of lice, Neohaematopinus inornatus, been been recorded nonrelatives (Cudmore, 1986). Of the most prominent ectoparasite found on Neotamiae is the warlike (bot) fly larvae, Caterebra tebelosa, which forms large subcumbentous 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 se-
dentatus, 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. c. eremicus housed this species, with an average number of five fleas per host (Cudmore, 1986). However, over 50 different flea species are found on bushy-tailed woodrats throughout their range (Cudmore, 1986). Other common flea species include Stenotoma alpina, Apllydrocerius multidentatus, Catallagia, Damanus montanus, Megasteglossus, Phalaropraula allos, Malavaraeus, and Monopolyulus (Cudmore, 1986; Finley, 1958; Nelson and Smith, 1976). Additional parasites include Ornitho-
dorus, Brevipalpa utahensis, Euxenagomus ambulans, Hae-
moeola emmeyi, H. glasgowi, and Hystixspus neotamiae (Fin-
ley, 1958). A single species of tapeworm, Andraea c. L. macroce-
phala, has been described (Finley, 1958). In addition to ectoparasites found commonly on bushy-tailed woodrats, a wide variety of predatory and saprophagous invertebrates are found associated with their dens. These include predatory mites (mostly Hya-
opus), orbited mites, acarid mites, millipedes, Collembola, and both larvae and adult Coleoptera, Diptera, and Lepidoptera (Nelson and Smith, 1976). Neotamiae is susceptible to at least some of the disease carried by parasites. Several species of woodrat fleas 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 exterminated during an epidemic of sylvatic plague from Lake Bed National Monument in northeastern California (Nelson and Smith, 1976).

Common predators on bushy-tailed woodrats include long-tailed weasels (Mustela frenata), martens (Martes), 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 (Och-
stona princeps), ground squirrels (Spemophilus), alpine chip-
munks (Tamias alpinus), marmots (Marmota marmos), and various species of deer mice (Peromyscus—Dixon, 1919; Finley, 1990).

Behavior. Female bushy-tailed woodrats are usually philo-
patric (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 (Esch-
erich, 1981; Hickling, 1987), others as promiscuous (Topping and Miller, 1990e), 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 non-
territorial 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, al-
though 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). De-
spite some spatial cohesiveness, bushy-tailed woodrats are rela-
tively unsocial animals, exhibiting tolerance only towards close rela-
tives (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 yearlings and males (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, 1996b). Females foraged over greater distances when pregnant or lactating than when non-productive (P < 0.05, n = 10); based on a one-tailed Wilcoxon's signed-rank test of data presented by
Topping and Millar, 1996: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, 1996b). Males have significantly larger home ranges than females (Hickling, 1987; Moses and Millar, 1992; Topping and Millar, 1996c). 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, 1996c). Territory sizes were ca. 10-20 times larger than those estimated for other species of Neotoma (Topping and Millar, 1996c) 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; Hofmeister, 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 scum 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; Howe, 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. microopus, N. albigena and N. floridana which 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 reproductivity 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; Finley, 1958). Over the years the encrusted urine 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 somewhat transparent. Not infrequently this hardened urine is taken for a mineral...” (Hall, 1946:335). 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 2n = 4 and a fundamental number of 2n = 8 (Baker and Mascarell, 1969; Carleton, 1980; Koop et al., 1985; Mascarell and Hsu, 1976). Of the autosomal chromosomes, there are 22 pairs of acrocentrics, one medium-sized subteloctenic, and three pairs with small arms. The X is a large subteloctenic and the Y is a medium-sized subteloctenic (Baker and Mascarell, 1969; Mascarell and Hsu, 1976). N. cinerea is 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 0.0065 (Meadow and Jenkins, 1996). N. cinerea is reportedly more heterozygous in the Great Basin than in either the Sierra Nevada or Rocky Mountains, suggesting somewhat greater gene flow (Meadow 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 tonos meaning “cut or cutting.” The specific name cinerea is from the feminized Latin word cinereus meaning “seized” 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, 1894a, 1894b), but Carleton (1980) has suggested that N. cinerea and N. fuscipes share common ancestry. Comparison of ecotopic 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, 1946:333). The subspecies N. c. acrura (Elliot, 1904a) actually was named acrura from the Greek meaning “dwelling on the hills,” but a misprint in the original publication resulted in the subspecific name commonly used (Elliot, 1904b). Here, I have resurrected the original spelling.

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