

Sylvilagus audubonii. By Joseph A. Chapman and Gale R. Willner

Published 21 September 1978 by the American Society of Mammalogists

Sylvilagus audubonii (Baird, 1857)

Desert or Audubon's Cottontail

- Lepus audubonii* Baird, 1858:608. Type locality San Francisco, California.
Lepus baileyi Merriam, 1897:148. Type locality Spring Creek, E side of Big Horn Basin, Wyoming.
Lepus laticinctus Elliot, 1903:254. Type locality Oro Grande, Mohave Desert, San Bernardino Co., California.
Sylvilagus audubonii Nelson, 1909:214. First use of name combination.

CONTEXT AND CONTENT. Order Lagomorpha, Family Leporidae, Genus *Sylvilagus*, Subgenus *Sylvilagus*. There are about 14 recognized species of the genus *Sylvilagus*. There are 12 recognized living subspecies of *S. audubonii* (Hall, 1951:164-166; Hall and Kelson, 1959:265-268) as follows:

- S. a. audubonii* (Baird, 1858:608), see above.
S. a. arizonae (J. A. Allen, 1877:332). Type locality Beals Spring, 50 mi. W Fort Whipple, Arizona (*laticinctus* Elliot, *major* Mearns, and *rufipes* Elliot are synonyms).
S. a. minor (Mearns, 1896:557). Type locality El Paso, Texas.
S. a. baileyi (Merriam, 1897:148), see above.
S. a. confinis (J. A. Allen, 1898:146). Type locality Playa Maria, Baja, California.
S. a. sanctidiegi (Miller, 1899:387). Type locality, Mexican Boundary Monument no. 258, (Pacific Ocean) San Diego Co., California.
S. a. goldmani (Nelson, 1904:107). Type locality Culiacán, Sinaloa.
S. a. parvulus (J. A. Allen, 1904:34). Type locality Apam, Hidalgo.
S. a. cedrophilus Nelson, 1907:83. Type locality Cactus Flat, 20 mi. N Cliff, New Mexico.
S. a. neomexicanus Nelson, 1907:83. Type locality Fort Sumner, New Mexico.
S. a. vallicola Nelson, 1907:82. Type locality San Emigdio Ranch, Kern Co., California.
S. a. warreni Nelson, 1907:83. Type locality Coventry, Colorado.

DIAGNOSIS. Size is relatively large for the genus. Hind legs are long; the feet are slender and do not possess the dense, long pelage of some other members of the genus. Ears are long, pointed, and sparsely haired on the inner concave surface. Vibrissae are generally black. The tail is large, dark above and white underneath. Cranial features are: long rostrum; prominent and upturned supraorbital processes; broad postorbital extensions of the supraorbital processes; general palatine foramina may be constricted posteriorly; palatal bridge medium in length; auditory bullae much inflated. Dental features are: molariform teeth relatively large; anterior surface of first upper molariform tooth having three re-entrant angles; lateral diameters of posterior halves of the second to the fourth lower molariform teeth about 80% of the lateral diameters of the anterior halves; ridge of enamel separating the molariform teeth into anterior and posterior sections strongly crenulated along the median two-thirds (modified from Orr, 1940; Hall, 1951). The skull is illustrated in Figure 1.

GENERAL CHARACTERISTICS. Descriptions are in Nelson (1909:214-237), Orr (1940:110-126), and Hall and Kelson (1959:265). Females are about 2% larger than males (Orr, 1940:20). The dental formula is $i\ 2/1, p\ 3/2, m\ 3/3$, total 28.

Some average external measurements (in mm) for *S. a. audubonii* adult males are: total length, 385.4 (372 to 397); length of tail, 56.0 (45 to 60); length of hind foot, 88.6 (83 to 94); length of ear from notch, 70.5 (70 to 71). Corresponding measurements in females are: 385.4 (375 to 400); 51.3 (39 to 56); 90.1 (81 to 93); 72.8 (72 to 75). Weight of adult males averaged 841.0 (755.7 to 907.5) g and adult females averaged 988.5 (883 to 1250) g (Orr, 1940).

Cranial measurements in millimeters of adult males of *S. a. audubonii* are: basilar length 53.0 (52.0 to 54.1); zygomatic breadth, 34.7 (33.9 to 35.2); postorbital constriction, 11.8 (11.0 to 12.6); length of nasal, 29.4 (28.2 to 30.4); width of nasals, 14.0 (13.2 to 15.4); length of molar series, 13.1 (12.1 to 12.6); diameter of external auditory meatus, 4.4 (4.2 to 4.5); breadth of braincase, 22.6 (21.6 to 23.6); length of palatal bridge, 5.5 (5.1 to 5.9). Corresponding measurements in females are: 53.2 (51.9 to 54.5); 35.2 (34.0 to 36.7); 12.2 (11.2 to 12.8); 29.4 (27.7 to 31.0); 14.1 (12.7 to 15.9); 13.1 (12.2 to 14.3); 4.4 (3.9 to 4.7); 22.4 (21.6 to 23.2); 5.6 (5.0 to 6.1). See Orr, 1940.

DISTRIBUTION. The species ranges from near the Canadian border in Montana south to central México and as far west as the Pacific coast (figure 2). The species is typically an inhabitant of arid regions. *S. audubonii* ranges in elevation (Orr, 1940) from below sea level in Death Valley, California, to at least 1829 m (6000 ft.). According to Findley (1969), this cottontail occurs in woodlands, grasslands, and deserts at all lower elevations in the Southwest.

FOSSIL RECORDS. The fossil history of *S. audubonii* is well documented from Pleistocene deposits. Hay (1927) and Dice (1925) referred specimens from the Rancho La Brea deposits to the subspecies *S. audubonii pix*, which is now extinct. Specimens of *Sylvilagus* from the Pleistocene Slaton local fauna of Texas also are believed to be *S. audubonii* (Dalquest, 1967).

FORM AND FUNCTION. There are four pairs of mammae: one pair pectoral, two pairs abdominal, and one pair inguinal (Dice, 1926).

Seasonal physiological responses of *S. audubonii* were studied by Hinds (1973) near Tucson, Arizona. A shift upward of the thermoneutral zone occurs from winter to summer and basal metabolism decreases by 18% during the same period. There is no relationship between the percent of metabolic heat production dissipated by evaporative heat loss and season of the year; it equals 100% at an ambient temperature of 41.4° C. Body temperature is 38.3° C when ambient temperatures are below 30° C and is not affected by season of the year. Body temperature equals ambient temperature of 41.9° C in summer and a predicted 42.9° C during the winter. According to Hinds (1973:708) "*Sylvilagus audubonii* survives in the desert by taking advantage of every possibility to minimize the heat load and water expenditure." A relatively high evaporative cooling capacity and high lethal body temperature of 44.8° C provide a safety factor for desert cottontails if avoidance is not possible.

ONTOGENY AND REPRODUCTION. The breeding season in California extends for seven months from December through June (Orr, 1940); however, Ingles (1941) found breeding the year around. The breeding season in Arizona lasts eight to nine months from January until August or September (Sowls, 1957; Stout, 1970). In Texas, the breeding season does not begin until late February or early March (Chapman and Morgan, 1974).

Ingles (1941) found the nests of five female *S. audubonii*, three of which contained young. The nests were pear-shaped excavations in the ground, 150 to 250 mm deep, with a 150 mm diameter near the bottom. In all the nests, the axis of the excavation was inclined to the north. The cavity was first lined with a thick layer of fine grass and weeds, then filled with rabbit fur, within which the young were found. The type of site selected for a nest or burrow may vary with habitat (Fitch, 1947).

Ingles (1941) gave the following approximate measurements for neonates: total length, 90 mm; tail, 10 mm; hind foot, 18 mm; and ear, 15 mm. Hair is sparse on the young and they lack the white spot on the forehead present in the eastern cottontail (*S. floridanus*). When the hair in the nest is touched, the young rabbit lunges upward and utters a "gupp" sound, which may be a call response prior to nursing. Ingles (1941) found that the female nurses the young by crouching over the nest. On one occasion,

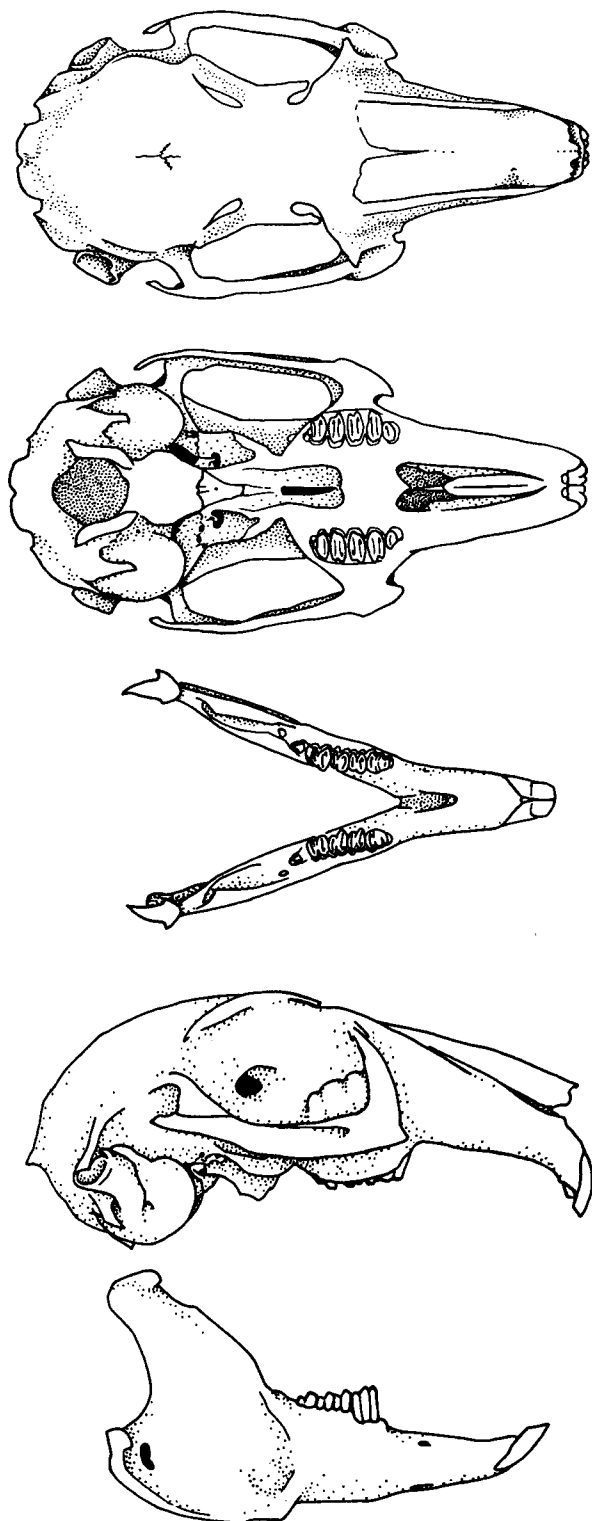


FIGURE 1. Skull of *Sylvilagus audubonii cedrophilus*. From top to bottom, dorsal and ventral view of cranium, dorsal view of dentary bone, lateral view of cranium, and lateral view of dentary. Drawn from an adult female (USNM 160741) collected at Socorro, New Mexico, on 20 August 1909.

the young cottontails were fed between the hours 1300 and 1400 after 31.5 hours had elapsed since the previous feeding. Later, the young were fed at hour 2000 following 30 hours without a feeding.

By postnatal day 10 the young have both eyes open (Ingles, 1941). They leave the nest between days 10 and 14 and remain near the nest for up to three weeks.

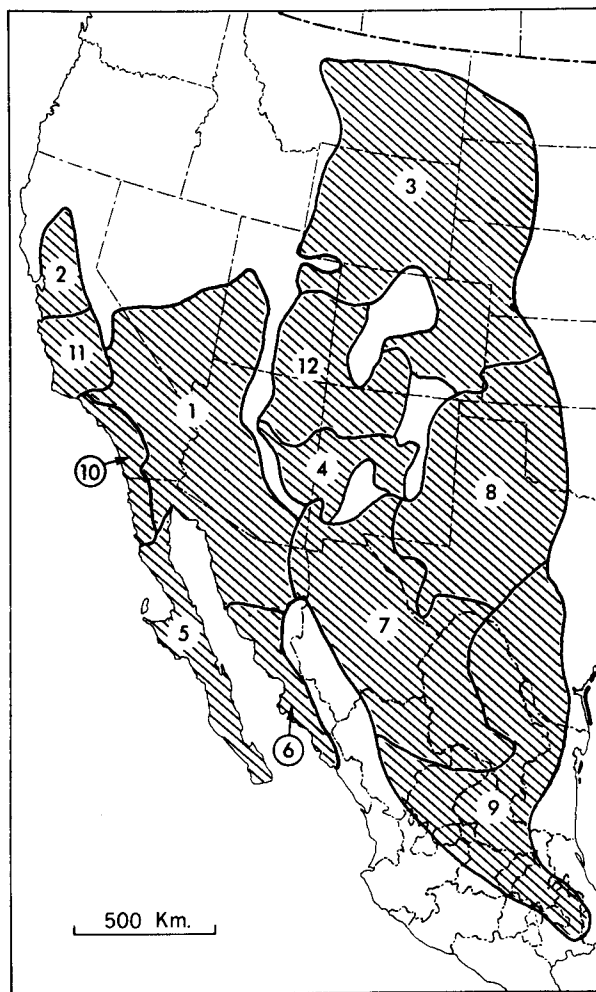


FIGURE 2. Distribution of *Sylvilagus audubonii* and its subspecies in North America: 1, *S. a. arizonae*; 2, *S. a. audubonii*; 3, *S. a. baileyi*; 4, *S. a. cedrophilus*; 5, *S. a. confinis*; 6, *S. a. goldmani*; 7, *S. a. minor*; 8, *S. a. neomexicanus*; 9, *S. a. parvulus*; 10, *S. a. sanctidiegi*; 11, *S. a. vallicola*; 12, *S. a. warreni* (adapted from Hall and Kelson, 1959).

The desert cottontail appears to be less fecund than some other members of the genus. Mean litter sizes reported for Arizona are 2.9 (Sowls, 1957) and 2.7 (Stout, 1970). The mean size for first litters in Texas is 2.6 (Chapman and Morgan, 1974). In California, Orr (1940) reported a mean litter size of 3.6.

In Texas, the mean ovulation rate for rabbits pregnant with their first litters was 3.30, indicating that 6% of the ova failed to implant; 16% of the embryos were resorbed (Chapman and Morgan, 1974). Stout (1970) found that 40% of the *S. audubonii* examined from Arizona contained visibly resorbing embryos.

Apparently, sexual maturity is attained as early as day 80 (Stout, 1970). The gestation period is 28 days (Dice, 1929).

Assuming that *S. audubonii* is a post-partum breeder, as are other members of the genus, these rabbits could produce a large number of litters each year. However, Sowls (1957) estimated that five was a reasonable average for litters actually produced in Arizona.

ECOLOGY. The species is found throughout lower elevations and deserts of the Southwest and the intermountain region, hence its vernacular name "desert cottontail." In California, the species occurs in heavy brush and willows along rivers where Dice (1926) noted some burrows of this cottontail. Dice further reported *S. audubonii* living under old buildings, around lumber piles and brush piles, and in fields where weeds made a thick mat a meter or so high. In winter, these rabbits remain hidden in thickets during the day, but in late spring they may be seen moving about at any time (Ingles, 1941).

In pinyon-juniper woodlands, shrubs are the primary cover for desert cottontails (Kundacli and Reynolds, 1972); 170 to 220

downed trees or shrubs per hectare provided the best habitat. Uprooting, piling, and burning all the pinyon-juniper trees in an area of New Mexico was found to depress the population of cottontails (Kundaali and Reynolds, 1972).

The species mostly inhabits the Lower Sonoran Life-Zone in California (Orr, 1940). Plant species associated with this rabbit in Butte County, California, were willow (*Salix* sp.), buttonwillow (*Cephalanthus occidentalis*), and wild grape (*Vitis californica*). In the Berkeley Hills, the species was most often associated with arroyo willow (*S. lasiolepis*). In Fresno County, it was seen at the edges of brushland (*Adenostoma fasciculatum*) and on hillsides interspersed with *Eriodictyon* and *Eriogonum* sp. Occasionally, the species is found where there is little or no vegetative cover (Orr, 1940). In southern Nevada, these cottontails were commonly associated with arrow-weed (*Pluchea sericea*), screw-bean mesquite (*Prosopis pubescens*), and catclaw (*Acacia greggii*) (Orr, 1940).

Cattle grazing affects the abundance of desert cottontails, which are most common in pastures under moderate-summer and moderate-winter grazing pressures (Flinders and Hansen, 1975).

Home range size of desert cottontails in California was found to be equal to the size of the blackberry clumps they inhabited (Ingles, 1941). This finding was also reported for the brush rabbit, *S. bachmani*, in western Oregon (Chapman, 1971). The home range of males may be as much as 15 acres (6.1 ha), whereas that of females may be less than 1 acre (0.4 ha) (Ingles, 1941). Ingles reported that in his study area the species rarely used holes, relying on thick brambles for cover. Little difference in the size of home ranges was found for males and females on the San Joaquin Experimental Range; the size was 8 or 9 acres (3.2 to 3.6 ha) for both sexes (Fitch, 1947). Young individuals have smaller foraging ranges than do adults (Fitch, 1947).

Homing ability was reported by Fitch (1947). Three rabbits displaced distances of from 4400 ft. (1341 m) to 3150 ft. (960 m) returned to their original home ranges. However, 10 others established themselves at the release sites. Fitch (1947) observed shifting of home ranges, which he believed resulted from changes in critically needed food or succulence.

On the San Joaquin Experimental Range, the following number of cottontails on 80 acres (32.4 ha) was reported: 1939, 153; 1940, 53; and 1941, 95 (Fitch, 1947). The following densities per hectare were calculated: 1939, 4.7; 1940, 1.6; and 1941, 2.9. A density of 6.6 desert cottontails per acre (16.3 per ha) was reported by Flinders and Hansen (1973) for northeastern Colorado.

Seasonal availability of food plants was the most important influence of feeding cottontails according to Fitch (1947).

Orr (1940) also reported seasonal variation in desert cottontail diets, consisting of various unidentified grasses, foxtail grass (*Hordeum murinum*), galingale (*Cyperus* sp.), sedge (*Carex* sp.), rush (*Juncus* sp.), willow, valley oak (*Quercus lobata*), miner's lettuce (*Montia perfoliata*), blackberry (*Rubus vitifolius*), California wild rose (*Rosa californica*), hoarhound (*Marrubium vulgare*), *Baccharis douglasii*, and California mugwort (*Artemisia vulgaris*). Cottontails living in fields depended almost entirely on grasses for food (Orr, 1940).

In the Sacramento Valley, California, the following plants are important foods: Johnson grass (*Holcus halepensis*), Bermuda grass (*Cynodon dactylon*), blue grass (*Poa pratensis*), ripgut grass (*Bromus rigidus*), wheat grass (*Agropyron caninum*), morning glory (*Convolvulus* sp.), bull mallow (*Malva borealis*), honey suckle (*Lonicera* sp.), and sow thistle (*Sonchus asper*). In addition, cultivated hollyhock, carrots (pulled), acorns of valley oak and, fruit of almond and peach are eaten (Ingles, 1941).

Hall (1916), Herman and Jankiewicz (1943), Stiles (1896), and Erickson (1947) reported the following internal parasites from *S. audubonii*: cestodes, *Cittotaenia variabilis*, *Raillietina retractilis*, and *Taenia pisiformis*; nematodes, *Dermatoxys veligera*, *Nematodirus leporis*, *Obeliscoides cuniculi*, and *Passalurus ambiguus*. Fitch (1947) also reported two intestinal protozoans (*Trichomonas* and *Chilomastix*). Fleas, *Spilopsyllus* sp. and *Ctenocephaloides felis*, and bots, *Cuterebra* sp. (Hall, 1921; Ingles, 1941; Fitch, 1947) also have been reported.

Mammalian predators include: coyote, *Canis latrans*; gray fox, *Urocyon cinereoargenteus*; badger, *Taxidea taxus*; bobcat, *Lynx rufus*; raccoon, *Procyon lotor*; skunk, *Mephitis mephitis*; mink, *Mustela vison*; and kit fox, *Vulpes macrotis*. Avian predators include: red-tailed hawk, *Buteo borealis*; Cooper's hawk, *Accipiter cooperi*; marsh hawk, *Circus hudsonius*; Swainson's hawk, *B. swainsoni*; golden eagle, *Aquila chrysaetos*; horned owl, *Bubo virginianus*; and barn owl, *Tyto alba*. Reptilian predators include rattlesnakes (*Crotalus confluenti*) and gopher snakes (*Pi-*

tuophis catenifer). Domestic dogs and cats also prey on *S. audubonii*. Records of predation are from Orr (1940); Ingles (1941), and Fitch (1947).

Ingles (1941) believed that this cottontail is short-lived. The greatest age in his study was 19 months and only seven of 29 rabbits lived longer than one year.

BEHAVIOR. The desert cottontail is most active in the early morning and evening (Ingles, 1941). Rabbits sought shelter when it rained, especially if the rain was accompanied by high winds. There was also clear evidence that the rabbits preferred still nights for their activities. They were inactive at temperatures above 80°F (Ingles, 1941).

These cottontails swim with rapid strokes, much as does a dog, and move the legs alternately (Ingles, 1941). They also climb trees and brush piles (Sumner, 1931; Ingles, 1941). The only other member of the genus known to do this is the brush rabbit, *S. bachmani* (Chapman, 1974).

Individuals take advantage of the alarm calls of other species (Orr, 1940; Ingles, 1941): the alarm behavior of sparrows warned cottontails on at least one occasion observed by Ingles, and they react also to the alarm signals of California ground squirrels (*Spermophilus beecheyi*) according to Orr (1940). The tail of *S. audubonii* is used as an alarm signal. When the tail is raised so as to expose the maximum amount of white, the animals run for cover; when the tail points toward the ground showing little white, the rabbits move about leisurely.

Freezing, a rigid posture adopted during times of uncertainty or possible danger, has been reported for *S. audubonii*. However, when an animal is truly alarmed, it dashes toward the nearest brush (Cushing, 1939). Orr (1940) reported that brush-inhabiting cottontails invariably ran for cover when alarmed.

On one occasion, Ingles (1941) heard a desert cottontail squeal while being removed from a trap. Orr (1940) reported that wounded rabbits often emitted a short, high-pitched squeal. One rabbit also attempted to bite while being handled (Ingles, 1941). Orr (1940) reported a thumping of the hind feet as an alarm signal.

Ingles (1941) observed as many as three females foraging together without antagonism. Interaction between males was observed; on one occasion, one male chased another away from a favored station. These rabbits may occasionally fight each other, although Ingles did not observe this.

In open situations, these rabbits frequent burrows during most of their daily periods of inactivity (Orr, 1940). They hide by sitting in forms, small cleared places on the ground. Desert cottontails are more wary in the late morning and early evening than at dawn or dusk (Orr, 1940).

With regard to locomotion, Orr (1940:133) stated: "When running, members of this species take small bounds into the air in order to clear tufts of grass and other obstacles which may be in their way. As open patches of ground are chosen for running, cottontails seldom appear to travel in a straight line. Individuals were observed at times running as far as 100 yards [91 m] in the open, pursuing a somewhat zig-zag course." The speed of a running cottontail was estimated at 15 miles (24.13 km) per hour (Grinnell and Storer, 1924).

Orr (1940:133) reported that: "At dawn or dusk, the white tails of these animals appear to be especially prominent as the rest of the body blends well in color with the landscape. Cottontails seen at such times were frequently undiscernable when viewed from the side at a distance of ten yards [9 m], whereas individuals which were running directly away from the observer were easily followed by the eye to a distance of 70 yards [64 m] because of the white tail. Immediately upon their stopping, however, such rabbits are lost to sight. This may be an adaptation to confuse pursuing enemies. One, upon watching a running cottontail under such circumstances, tends to look only at a conspicuous white tail. When this suddenly disappears, due either to their stopping or veering off their course, the animal seems to vanish completely."

In cottontail territories, low prominences, such as logs and tree stumps, invariably had feces deposited on them (Orr, 1940). These places were believed to be lookout posts used after dark. Desert cottontails are not gregarious. They and jackrabbits have been observed feeding together without animosity. Similar observations have been made with regard to the California ground squirrel.

The type of cover is an important factor in determining feeding sites. In areas of brushy cover adjacent to open grassland, much of the late morning and early evening feeding takes place under the shelter of brush. Habitat, season of the year, fog, rain,

and wind are important factors that affect daily periods of feeding. Maximum numbers of these cottontails always were observed feeding at dawn, if the mornings were not foggy or windy. Wind appeared to interfere greatly with normal feeding. Light intensity was also an important factor determining the distance from shelter a cottontail will venture for food. After dark, cottontails were observed to travel up to 110 yards (100 m) from cover (Orr, 1940).

In open situations, desert cottontails feed by taking a number of successive mouthfuls. The head is then elevated and chewing begins. The terminal portions of plants are generally taken. When feeding on low-growing grass, rabbits appear to extend the body along the ground. The neck is stretched out and the front feet edge forward. When food can no longer be reached, the hind feet are brought forward with a hop. When eating, brush rabbits were frequently seen standing on their hind legs. Rabbits feeding in this manner leave a twig characteristically cut at a 45° angle (Orr, 1940).

GENETICS. The desert cottontail has a diploid chromosome number of 42 (Worthington and Sutton, 1966) with five metacentric pairs, 11 submetacentric pairs, and four acrocentric pairs of autosomes. *Sylvilagus audubonii* differs from *S. nuttallii* in having one exceptionally large pair of acrocentric chromosomes. The Y chromosome is dotlike (Worthington and Sutton, 1966).

Chapman and Morgan (1973) electrophoretically examined the blood of several species and subspecies of cottontails. They studied 18 individuals of *S. audubonii neomexicanus* and reported that the species had a unique serum protein pattern when compared to the serum of four subspecies of *S. floridanus* and *S. transitionalis*. The *S. a. neomexicanus* serum contained 20 serum proteins with several variant protein systems including a polymorphic transferrin. Electrophenograms and schematic drawings were presented for several members of *Sylvilagus* including *S. audubonii*. Johnson (1968) also electrophoretically examined several *Sylvilagus* including one *S. audubonii*.

REMARKS. The desert cottontail has been inadvertently (along with *S. floridanus*) introduced widely into Maryland and probably other regions of the eastern United States. However, there is no evidence that this species has become established as a result of these introductions.

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