

*Sylvilagus aquaticus*. By Joseph A. Chapman and George A. Feldhamer

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*Sylvilagus aquaticus* (Bachman, 1837)

Swamp Rabbit

*Lepus aquaticus* Bachman, 1837:319. Type locality western Alabama.

*Lepus telmalemonus* Elliot, 1899:285. Type from Washita River, near Dougherty, Murray County, Oklahoma.

*Sylvilagus aquaticus* Nelson, 1909:270. First use of current 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 two recognized subspecies of *S. aquaticus* (Hall, 1951:166-167; Hall and Kelson, 1959:269) as follows:

*S. a. aquaticus* (Bachman, 1837:319), see above (*telmalemonus* Elliot a synonym).

*S. a. littoralis* Nelson, 1909:273. Type locality Houma, Louisiana.

**DIAGNOSIS.** A larger rabbit than the eastern cottontail (*S. floridanus*) and the marsh rabbit (*S. palustris*) (Fig. 1). Ears medium-sized in relation to body size. Head and dorsum dark, rusty-brown to black in color. The ventral surface, throat, and tail are white. Cinnamon-colored eye-ring is prominent.

Vibrissae generally are black. The skull is large and robust, with a wide rostrum. Width of the rostrum over the anterior maxillary cheekteeth is greater than the interorbital width. Auditory bullae are smaller than the foramen magnum; anterior extension of each bulla is fused to braincase. Anterior face of first upper molariform tooth has three re-entrant angles. Re-entrant angle of second upper molariform tooth is crenate. The ridge of enamel separating each molariform tooth into sections is crenulated (Hall and Kelson, 1959; Golley, 1962; Lowery 1974). The skull is illustrated in Fig. 2.

**GENERAL CHARACTERISTICS.** Descriptions are given in Hall (1951), Hall and Kelson (1959), Golley (1962) and Lowery (1974). Unlike other *Sylvilagus*, in which females are slightly larger than males, there apparently is no sexual dimorphism in *S. aquaticus*. The dental formula is  $i\ 2/1, c\ 0/0, p\ 3/2, m\ 3/3$ , total 28.

Means followed by ranges of external measurements (in mm) for adults, sexes combined, are: total length, 501 (452 to 552); length of tail, 59 (50 to 74); length of hind foot, 101 (90 to 113); length of ear, 70 (60 to 80) (Lowery, 1974). Average weights (g) of 144 male and 180 female swamp rabbits from Alabama were 2059 and 2035, respectively, with no significant difference between sexes (Hill, 1967). Holten and Toll (1960) reported weights for 191 swamp rabbits from Missouri whose age was determined using the epiphyseal closure criterion. Average and extreme weights were as follows: adult males, 2235 (1816 to 2554); adult females, 2161 (1646 to 2668); juvenile males, 2022 (1589 to 2526); and juvenile females, 1954 (880 to 2384). The average weight of seven adults in Louisiana was 1698 (Lowery, 1974). The mean weights of adult swamp rabbits in Indiana were: males, 2254, and females, 2217. Juveniles averaged 1776 (2072 to 2464) (Terrel, 1972). A latitudinal size gradient probably exists for this species (Terrel, 1972). Additional data were presented by Harrison and Hickie (1931), Lowe (1958), Davis (1960), Holten and Toll (1960) and Kirkpatrick (1961).

Cranial measurements (in mm) of 37 adult *S. aquaticus*, sexes combined, from Georgia were: basilar length, 68.1 (60.9 to 72.3); zygomatic breadth, 40.5 (37.1 to 42.4); width of postorbital constriction, 20.5 (18.1 to 29.2); length of nasals, 37.4 (32.5 to 40.8); width of nasals, 15.6 (13.6 to 18.6); length of maxillary toothrow, 17.0 (12.2 to 18.2); diameter of external auditory meatus, 4.6 (4.1 to 5.4); breadth of brain case, 26.7 (24.8 to 27.9); length of palatal bridge, 17.0 (12.2 to 18.2) (Lowe, 1958). Additional data were given in Lowery (1974).

**DISTRIBUTION.** The species is found along the Gulf coast of North America in Alabama, Louisiana, and Mississippi and in portions of Texas, Oklahoma, Kansas, Missouri, Illinois, Indiana, Tennessee, Georgia, and South Carolina (Fig. 3) (Hall, 1951; Hall and Kelson, 1959). Swamp rabbits occur primarily in swamps, river bottoms and lowland areas throughout their range.

**FOSSIL RECORD.** Olson (1940) described the swamp rabbit on the basis of several molariform teeth from a late Pleistocene deposit in Missouri. Although identification of Pleistocene *Sylvilagus* to species depends on unusually good material (W. W. Dalquest, pers. comm.), Olson stated that "The fossil teeth may be referred with confidence to *Sylvilagus aquaticus*."

**FORM AND FUNCTION.** The most common method for determining age in swamp rabbits and other lagomorphs is by eye-lens weight. Martinson et al. (1961) reported that all juveniles had eye-lens weights of less than 205 mg and all adults had eye-lens weights greater than 212 mg. These findings were verified by comparing the closure of the distal epiphyses of the radius and ulna. Martinson et al. (1961) used x-ray photos to measure the closure. In early stages of growth, the cartilage plates appear as wide black bands and the margins of the epiphysis and the diaphysis of the bones are flared. As the rabbits mature, the plates become narrower, gradually losing their identity completely as fusion of the epiphysis and diaphysis reaches completion at 11 to 12 months.



FIGURE 1. Photograph of *Sylvilagus aquaticus* (Courtesy of Louisiana Department of Wildlife and Fisheries).

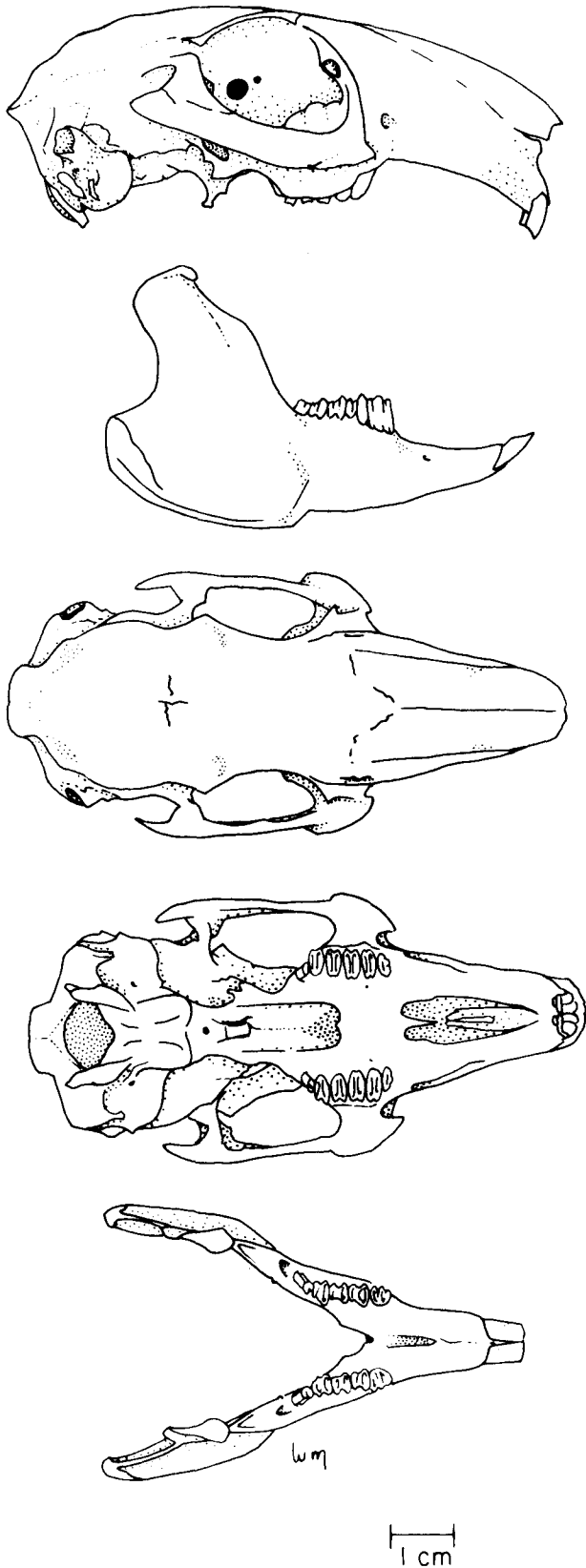


FIGURE 2. Skull of a male *Sylvilagus aquaticus* from Rockefeller Refuge, Cameron Parish, Louisiana (AEL 911). Top, lateral view of cranium and mandible; middle, dorsal view of cranium; bottom, ventral view of cranium and dorsal view of mandible. Drawn by Wilma Martin.

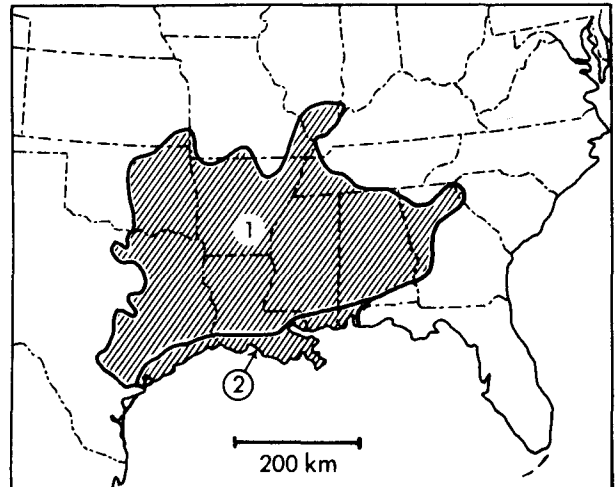


FIGURE 3. Distribution of *Sylvilagus aquaticus* and subspecies in the southeastern United States: 1. *S. a. aquaticus*; 2. *S. a. littoralis* (adapted from Hall, 1951; Hall and Kelson, 1959).

**ONTOGENY AND REPRODUCTION.** Conaway et al. (1960) studied embryo resorption in relation to flooding and subsequent crowding. They found marked increases in the total litter resorption rate when the rabbits were crowded—probably the result of adrenal stress syndrome.

The swamp rabbit is a postpartum synchronous breeder with estrus lasting generally less than an hour (Sorensen et al., 1968). The gestation period varies from 35 to 40 days, with 36 to 37 days being most common (Hunt, 1959; Holler et al., 1963; Sorensen et al., 1968). Juvenile swamp rabbits are capable of breeding at an age of 23 to 30 weeks (Sorensen et al., 1968). However, there are few reports of juveniles actually breeding (Hunt, 1959).

Martinson et al. (1961) examined the uteri of 23 adult and 55 juvenile swamp rabbits. They found that all but one of the adult uteri showed placental scars, while no uteri of juveniles showed scars. Further, the reproductive tracts of the adults were larger and more "strap like" than those of most of the juveniles. Juvenile males may breed in the calendar year of their birth (December); however, this is at the beginning of the breeding season following the one in which they are born (Toll et al., 1960). Yearling females breed in captivity at the same time as adults when densities are low. However, when densities are high, some yearling females breed up to a month later than adults (Sorensen et al., 1968).

The breeding season of the swamp rabbit varies slightly throughout its range. In northern Alabama, breeding usually starts in mid-February or occasionally late January, slightly before the breeding season of the eastern cottontail. Usually, the first litters are born in mid-March and the last litters in August. In southern Alabama, the breeding season probably starts earlier, coincident with that in Louisiana (Hill, 1967). The breeding season in Missouri begins in early to mid-February, with the peak of reproductive activity lasting until mid-June (Toll et al., 1960; Sorensen et al., 1968). In Louisiana, breeding has been reported in all months except October (Svihla, 1929). In Georgia, pregnant females were collected in September (Lowe, 1958). Hunt (1959) suggested that swamp rabbits breed year-round in Texas. The breeding season is longest in the south-central United States and becomes progressively shorter with increasing latitude throughout their range (Hunt, 1959).

The mean litter size also varies by region. In southern Louisiana, it is 3.7 (Svihla, 1929), although sample size in this study was only three litters; in east-central Texas, 2.8 (Hunt, 1959); and in Missouri, 2.8 (Toll et al., 1960).

First litters are smaller than second litters. In Alabama, first litters averaged 2.8 and second litters 3.2 (Hill, 1967), whereas in Missouri first litters averaged 2.7 and second litters 4.1 (Sorensen et al., 1968). The range of litter sizes varies from 1 to 6, with 3 being the most common (Sorensen et al., 1968).

Yearling females may produce larger litters than older females. Sorensen et al. (1968) reported that nulliparous yearlings produced litter sizes of 3.3 young and adults produced 2.3 young. However, sample sizes were small and the differences were not statistically significant. For second litters, the corresponding lit-

ter sizes were 5.0 and 3.7, and for third litters, 3.0 and 2.5. Sorensen et al. (1968) reported that captive yearling females produced an average of 3.5 litters per year, whereas older females averaged 2.8. Again, however, the differences were not statistically significant.

In confined swamp rabbit populations in Missouri, the number of litters per female per year varied from 1 to 3 (Holler et al., 1963). In another pen study, the number of litters varied from 2 to 5 (Sorensen et al., 1968). Sorensen et al. (1968) found that 27% of the females had two litters, 46% had three, 19% had four, and 9% had five.

Sorensen et al. (1968) reported a sex ratio of 51.9 females to 48.1 males in 106 week-old swamp rabbits. Hill (1967) reported 54% females in a sample of 438 swamp rabbits shot during the hunting season on Wheeler National Wildlife Refuge, Alabama. Hunt (1959) reported 57.3% females in a sample collected in east-central Texas.

Sorensen et al. (1968:527) noted that neonates "... had fur up to about 5 mm long which was dark on the back, sides, and throat but white on the abdomen and chin; the top of the head was tan mixed with black." They reported the average weight of neonates was 61.4 g. Holler et al. (1963) found the average weight of neonates from one litter in Missouri ( $n = 6$ ) was 53.5 g. The eyes of newborn swamp rabbits open between days 5 and 8; young leave the nest between days 12 and 15 (Sorensen et al., 1968). Young born early in the spring reach adult size in December, at about month 10. Young born later in the summer apparently do not attain adult weight until the following spring (Sorensen et al., 1968). The average life span was estimated to be 1.8 years (Terrel, 1972).

**ECOLOGY.** The swamp rabbit is a subtropical species whose distribution extends northward from the Gulf of Mexico to Knox County, Indiana (Terrel, 1972). The northern limit of the species does not extend beyond the southern swamp forest community-type at about the 24°C temperature iso-line. The swamp rabbit is never found far from water, usually being restricted to floodplains, bottomlands, and areas adjacent to tributaries of large rivers or streams and cypress swamps (Svihla, 1929; Cockerum, 1949; Lowe, 1958; Hunt, 1959; Terrel, 1972).

The habitat of the swamp rabbit differs from that of the eastern cottontail. Terrel (1972) found that swamp rabbits were twice as common as eastern cottontails in mature forests and six times as common in logged tracts 15 years old. Svihla (1929) found the forms and runways of swamp rabbits in tangled marsh vegetation and brier bushes. Harrison and Hickie (1931) noted that *S. aquaticus* was closely confined to canebrake (*Arundinaria gigantea*) communities in Indiana, which by 1930 had been greatly reduced in size.

Swamp rabbits use holes in the ground or in trees as form sites (Hunt, 1959). They also use elevated objects as defecation sites (Terrel, 1972). Such sites may be important habitat requirements. Lowe (1958) reported that the tops of vegetation-covered stumps, low crotches of trees, logs, Japanese honeysuckle tangles, cane patches, and open grassy places in floodplains were common form sites.

Home ranges of swamp rabbits vary in size. Using trapping data and the "trap squares" calculation method, Toll et al. (1960) reported average home ranges for seven adult females to be 2.4 ha (5.9 acres). The home range of seven adult males was 1.9 ha (4.6 acres). Using the "minimum area" method, home ranges of females and males, respectively, were 0.8 ha (2.1 acres) and 0.7 ha (1.8 acres). Maximum home ranges were calculated to be 2.2 ha (5.5 acres) for females and 3.2 ha (7.9 acres) for males as determined by "chasing" with dogs. Lowe (1958) reported the average maximum home range for seven swamp rabbits, sexes combined, was 7.6 ha (18.9 acres).

The density of a swamp rabbit population in the fall in the canebrake area of Indiana was estimated to be 1 per 2.4 ha. The population was composed of 50 to 55% juveniles (Harrison and Hickie, 1931).

Unlike many other species of *Sylvilagus*, few predators have been recorded for swamp rabbits. Lowe (1958) reported that swamp rabbits are occasionally caught by domestic dogs; American alligators (*Alligator mississippiensis*) feed on *S. aquaticus* (Svihla, 1929). However, the most important causes of mortality appear to be hunting by man (Terrel, 1972) and high water which undulates marshes for prolonged periods of time (Svihla, 1929).

A variety of parasites have been reported from swamp rabbits (Price, 1928; Chandler, 1929; Ward, 1934; Smith, 1940; Erickson, 1947; Lumsden and Zischke, 1962). Internal parasites include: trematodes, *Haustorium texensis*, *H. tricolor*; cestodes,

*Cittotaenia ctenoides*, *C. variabilis*, *Multiceps serialis*, and *Railletina stilesiella*; and nematodes, *Graphidium strigosum*, *Nematodirus leporis*, *Obeliscoides cuniculi*, *Parasalarus ambiguus*, *Trichostrongylus calcaratus*, and *Trichuris leporis*. Ward (1934) and Harkema (1938) reported the parasitic mite, *Haemaphysalis leporis-palustris*.

Swamp rabbits feed on a variety of plants (Svihla, 1929; Smith, 1940; Calhoun, 1941; Toll et al., 1960). Terrel (1972) reported that plants eaten in order of preference were (1) *Bignonia capreolata*, (2) sedges, (3) *Rhus radicans*, (4) grasses, (5) *Smilax* sp., and (6) tree seedlings. Toll et al. (1960) found that plants were eaten according to their abundance. In their study, the main food item was swamp grass, *Carex lupulina*. Other plants which were heavily browsed included blackberry, *Rubus* sp., hazelnut, *Corylus* sp., deciduous holly, *Ilex decidua*, and spicebrush, *Lindera benzoin*. Blair and Langlais (1960) reported that under certain conditions swamp rabbits may damage bald cypress seedlings (*Taxodium distichum*) by clipping.

**BEHAVIOR.** Social organization of captive swamp rabbits was studied extensively by Marsden and Holler (1964). They identified two basic behavior patterns: (1) a linear dominance hierarchy among males and mutual toleration among females; and (2) organization into two breeding groups (Marsden and Holler, 1964). The male dominance hierarchy had five apparent functions, the first being that it prevented fighting among reproductively active males. Alpha males dominate males below them, with emphasis on the immediate subordinates; subordinate animals attempt to minimize contacts with higher-ranking males. The number of dominance displays was directly correlated with the social status of the male. Male movement and proximity to females were directly correlated with social status. The top two males were responsible for most of the male-female interactions and the  $\alpha$ -male was responsible for most copulations (Marsden and Holler, 1964). Holler and Sorensen (1969) suggested that male swamp rabbits with dominant status maintain their status from year to year.

Marsden and Holler (1964) reported synchronized estrous behavior in unbred females on a 12-day cycle. A series of behaviors preceded estrus: (1) female chasing or threatening the male, (2) the male dash, (3) the jump sequence, and (4) copulation, preceded by chasing of the female.

Sorensen et al. (1972) studied parental behavior in confined swamp rabbit populations. Most nests were found against or under fences, bases of trees, boards, or similar structures. Some nests were built a few days before parturition, but others were apparently built the same night. Females regularly built dummy nests. Only half as many dummy as active nests were found, however. Young were sometimes scattered at birth. One female lined her nest with fur just prior to giving birth, then began nursing immediately following birth. Most nursing occurred at dawn and dusk. Young continued to nurse after leaving the nest (Sorensen et al., 1968). Young from other nests were readily adopted. Males showed no interest in the young.

Goodpaster and Hoffmeister (1952) indicated that nests of *S. aquaticus* differed from those of the eastern cottontail. They discovered one nest which was built on top of the ground, in a heavy weed patch, with stalks of dead weeds pulled around an inner lining of fur. Nests are about 4 to 7 cm deep, 15 cm wide, and 18 cm high and have side entrances (Lowe, 1958; Holler et al., 1963).

Sorensen et al. (1972) used a simple technique to determine which female swamp rabbit had young in a given nest. Before nest building occurred, females were live-trapped and their abdomens were dyed. They were then released. Because females line active nests with abdominal fur shortly before parturition (they do not line dummy nests), a quick check of active nests indicated which female they belonged to. Data such as average litter size or average numbers of litters can easily be determined using this method.

Unlike many congeners, swamp rabbits are territorial. They are vocal and the males demonstrate "chinning"—a pheromone marking display most noted in the European rabbit (*Oryctolagus cuniculus*) (Marsden and Holler, 1964).

Holler and Marsden (1970) studied the onset of evening activity in swamp rabbits. They found that the activity of individual swamp rabbits was delayed as sunset became progressively later in the spring. The delay was greatest for females and lower ranking males. The time and onset of evening activity was variable, but occurred well before sunset in late spring and summer. In late winter and early spring, the onset of evening activity was during the twilight period.

Live-trapped swamp rabbits tend to be more difficult to handle than other cottontails. Unlike eastern cottontails, swamp rabbits strike out with their hindfeet even if their eyes are covered. Lowe (1958) suggested that to prevent scratching, one should grasp the hindfeet with one hand, then slide the other hand forward until it is around the front legs and head. If held stretched between the two hands, the rabbit should remain quiet.

Swamp rabbits use various maneuvers to confuse pursuers. One behavior is to climb onto a log or similar object, walk along its length, then backtrack and jump to the side, traveling at right angles to the former course. Following this behavior, the rabbit may travel only a short distance, then watch its backtrail (Terrel, 1972).

Swamp rabbits are excellent swimmers and will use this capability to avoid danger. Lowe (1958) observed a swamp rabbit backtrack upstream along the water's edge and then go into the water and float away downstream. Hunt (1959) observed another swamp rabbit, chased by a dog, swim under a bank where it remained with only its eyes and nose above water.

Coprophagy has been reported for the swamp rabbit (Hamilton, 1955; Layne, 1958; Toll et al., 1960). Coprophagy occurs mainly during the daytime and not at night when the rabbits are feeding.

**REMARKS.** Nothing has been reported concerning the genetics of swamp rabbits. This is one of the least studied species of *Sylvilagus*. It is interesting to note that the major studies dealing with the swamp rabbit have been done in peripheral areas of its range. The geographic range appears to be diminishing. In optimal habitat in Louisiana, we have observed this species in apparent densities far greater than those reported for most other *Sylvilagus* species.

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