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DISTRIBUTION AND HABITAT AFFINITY OF THE SWAMP RABBIT (*SYLVILAGUS AQUATICUS*: LAGOMORPHA: LEPORIDAE) ON THE EDWARDS PLATEAU OF TEXAS

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The historical distribution of *Sylvilagus aquaticus* is primarily in east Texas, with a western boundary that extends from Cooke, Wise, and Palo Pinto counties in north-central Texas south to Brown County, just north of the Edwards Plateau, thence to Travis and Bexar counties, juxtaposed to the Balcones Escarpment in central Texas, thence south to Aransas County in the southern coastal plains (McCarley, 1959; Davis, 1966; Schmidly, 1983; Dalquest and Horner, 1984; Garner et al., 1990; Davis and Schmidly, 1994). In central Texas, Allen (1895) first reported the species in riverbed drift piles and old fallen trees of the San Antonio and Medina rivers south of the Balcones Escarpment. Later, the species was found east of the escarpment in riparian habitat on the Colorado River in Travis County (Davis, 1966). Although riparian communities of the Colorado and Medina rivers extend westward and northward onto the Edwards Plateau, no specimens or observations of swamp rabbits have been reported for the Edwards Plateau.

The swamp rabbit inhabits swamps and marshes of bottomland forests and shrub-dominated wetlands, where fallen and hollow trees, brush piles, and dense herbaceous vegetation meet year-round habitat requirements of food and cover for the species (Blair, 1936; Lowe, 1958; Hunt, 1959; Terrel, 1972; Chapman and Feldhamer, 1981; Allen, 1985; Kjolhaug et al., 1987). In eastern Texas, *S. aquaticus* inhabits four vegetational areas of the state. In the east Texas Pineywoods, swamp rabbits are common in dense thickets of shrubs, trees, and vines of hardwood bottomland drainage systems and are usually the most common lagomorph in second-growth timber (Taylor and Lay, 1944; Schmidly, 1983). On the Gulf Prairies and Marshes, this lagomorph is common in thick, marsh vegetation and briar bushes of marshes and canals (McCarley, 1959; Schmidly, 1983). They prefer meadows of tall grass, interspersed with scrub oaks, in the ecotone between bottomlands and prairie in the Post Oak Savannah (Schmidly, 1983). In the Blackland Prairies region, the species is virtually restricted to floodplain corridors of rivers and creeks (Hunt, 1959; Schmidly, 1983).

We initiated a study in 1991 to answer three questions. What is the current distribution of swamp rabbits along mesic, riverine, corridor habitats of the Edwards Plateau? What are the characteristics of habitats used by swamp rabbits? Are criteria of the habitat suitability model (sensu Allen, 1985) applicable to riparian habitats inhabited by swamp rabbits along rivers of the Edwards Plateau at the westernmost boundary of the species?

STUDY AREA

The westernmost boundary of the study area was the Nueces River. The continental north-south line for moisture sufficient/deficient regions proposed by Thornthwaite (1948) divides the Edwards Plateau into two regions. The eastern one-half is dry, subhumid, mesothermal with 99.8 to 114 cm of annual precipitation; whereas, the western one-half is semiarid, mesothermal with 85.5 to 99.8 cm of annual moisture. Based on available climatic, floral (Diamond et al., 1987), and topographic (Hatch et al., 1990) information, we assumed the area west of the Nueces River was too arid to support the continuity of mature riparian forests necessary for suitable swamp rabbit habitat. Whereas swamp rabbits need permanent water in their habitat (Terrel, 1972; Allen, 1985), we focused our fieldwork in riparian forests of river systems of the eastern Edwards Plateau.

The composition of the riparian flora of rivers of the eastern Edwards Plateau contrasts with upland vegetation. For example, the floral composition and distribution of the riparian community along the Guadalupe River contrast with the upland shrub-forest of the Edwards Plateau. There is a severe elevational and horizontal compression of the riparian community with a loss of mesic-adapted species on thinner, xeric, upslope soils. Plants with an Austroriparian affinity occur primarily in the streamside riparian forest; several species reach the western boundary of their distribution in this riverine zone (Ford and Van Auken, 1982).

METHODS

From September 1991 to June 1995, a reconnaissance of major river systems of the eastern Edwards Plateau was conducted at highway crossings and on public and private lands to locate sites with potential swamp rabbit habitat. We surveyed riparian plant communities of the Edwards Plateau (Diamond et al., 1987) for habitat similar to that described in the habitat suitability model for swamp rabbits (Allen, 1985). We searched sites identified as potential habitat for swamp rabbits and for fecal droppings. Swamp rabbits, unlike their congeners *S. floridanus* (eastern cottontail rabbit) and *S. audubonii* (desert cottontail rabbit), mark territories by depositing large, discoidal fecal droppings on elevated objects such as tree stumps, fallen logs, rocks and similar perches. This behavior is a useful field indicator that has been used to corroborate the presence of the species and quality of the habitat (Lowe, 1958; Hunt, 1959; Terrel, 1972; Kort and Fredrickson, 1977; Whitaker, 1980; Dailey et al., 1993). Since fecal pellets of the eastern and desert cottontail rabbits and white-tailed deer (*Odocoileus virginianus*) could be mistaken for those of the swamp rabbit, we became proficient in the recognition of known fecal samples from each species at the beginning of the fieldwork. If we found no signs of rabbits on the initial visit to a site, we searched the site a minimum of two additional times. In addition, potential suitable habitat was identified using 1:20,000 or 1:40,000 ASCS (Agricultural Stabilization and Conservation Service) black-and-white aerial photographs taken during 1984 to 1990.

At all sites, the continuity of suitable habitat was characterized and ranked. Sites with a continuous breadth (about 8 km) of upstream and downstream suitable habitat were assigned a rank of 1. Sites with fragmented habitats and patches < 5 km in breadth were given a rank of 0.5. A rank of 0 designated areas with small, isolated patches of unsuitable habitat. The width of the riparian zone at each site was determined by measuring the distance from the edge of the stream to the outermost edge of the riparian community. Width values were obtained for only one side of the stream at a site; however, the symmetry of the plant community on both sides of the stream was noted. If a floodline was present, the width of the riparian zone with adequate cover for rabbits above the floodline was also measured.

The woody and herbaceous vegetation of the riparian zone were sampled and characterized using randomly placed 50 m^2 (5 m x 10 m) quadrats at all sites. A species richness value was obtained by listing all plant species in each quadrat. We used dominant woody species at each site to identify the floral series level (Diamond et al., 1987). Frequencies (%) of plant species at a site were calculated by dividing the number of sites with occurrence by the number of total sampling sites. A value for canopy cover was derived by ocular estimation of canopy cover (Allen, 1985). The total canopy cover for each site was calculated by adding the mean area coverage (%) values for trees, shrubs, herbaceous vegetation, and ground debris. Multilayer canopies had values > 100%. Herbaceous vegetation at each site was

sampled seasonally by four 0.25 m^2 quadrats placed at the corners of the 50 m^2 quadrat. A species list of herbaceous vegetation was developed for each site. We included identifiable dead or dormant annuals in the species list. In each 0.25 m^2 quadrat, the percent area coverage of dominant herbaceous plants and the amount of bare ground were estimated. The presence and percent ground cover by green herbaceous vegetation during winter were recorded. Land use practices on areas next to sampling sites were characterized as to tillage, grazing intensity by livestock, and land development. At sites grazed by livestock, the height of ground cover was randomly measured at 10 sites.

Escape cover in the 50 m^2 quadrat at each site was classified into five categories: vines, rock piles and crevices, drift debris, dense grasses and sedges, and brush and deadfalls. The frequency (%) of each escape cover type was calculated for each site. Vines were classified in cover classes based on growth form.

Statistical analyses were performed with the StatView 4.01 statistical analysis package. Variables measured in integers were analyzed using the Mann-Whitney U test to determine the probabilities of differences in the distribution of measurements between sites with swamp rabbits present or absent. Variables ranked into two categories (swamp rabbits present or absent) were tested for goodness of fit (Zar, 1984) using contingency tables and G^2 probabilities (log likelihood ratios). Habitat continuity data ranked into three categories had χ^2 probabilities determined for the likelihood of differences among sites with swamp rabbits present or absent.

RESULTS

Intensive searches for swamp rabbits or their sign were conducted at 54 sites in 22 counties of the eastern Edwards Plateau. Fourteen new Edwards Plateau and three peripheral county records for *S. aquaticus* in Bandera, Blanco, Bosque, Burnet, Caldwell, Comal, Gillespie, Guadalupe, Hays, Kendall, Kerr, Lampasas, Llano, Medina, Mills, San Saba, and Williamson counties were documented at 39 sites along the Blanco, Bosque, Colorado, Guadalupe, Lampasas, Little Blanco, Llano, Medina, Pedernales, San Gabriel, San Marcos, and San Saba river systems (Fig. 1). Several sightings of swamp rabbits and fecal records on Johnson Creek (3 km S Mountain Home), a tributary of the Guadalupe River in Kerr County, extend the distribution of the species about 125 km north and west of Bexar and Travis counties. This is the westernmost distributional record for the species in North America (Hall, 1981). No signs of swamp rabbits were found on the Colorado River in Brown, Coleman, and McCulloch counties below Stacy Reservoir; Frio River in Real and Uvalde counties; Llano River in Kimble and Mason counties; Nueces River in Edwards, Kinney, and Uvalde counties; or Sabinal River in Bandera and Uvalde counties.

Swamp rabbits inhabited three series-level plant communities along rivers of the eastern Edwards Plateau. The frequency (%) of occurrence by this lagomorph at sites in these communities was Sugarberry-Elm (77%), Bald Cypress-Sycamore (31%) and Pecan-Sugarberry (15%). The westernmost extent of the distribution of swamp rabbits along rivers of the Edwards Plateau corresponded with the upstream distances and continuity of these communities. The dominant trees in these communities were sycamore, Texas sugarberry, pecan, cedar elm, and black willow. The dominant understory shrubs were possumhaw, roughleaf dogwood, waxleaf ligustrum, and false indigobush (Table 1).

The Sugarberry-Elm community provided the best habitat for swamp rabbits. The species inhabited a thick understory of brush, deadfalls, and briars in a Sugarberry-Elm community on Walnut Creek, a tributary of the Colorado River in Travis County. However, swamp rabbits were found at only three isolated sites in a Sugarberry-Elm community along the Colorado River between Travis and San Saba counties. Two sites, Sandy Creek near Lake L B J in Llano County and the convergence of Penny and Hamilton creeks in Burnet County, were at the confluence of creeks where the river was permanently flooded by water impoundments (Joe Wallace, Texas Game Warden, pers. comm.). The other site was at Colorado Bend State Park. Swamp rabbits inhabited a diverse Sugarberry-Elm community on the Lampasas River, a tributary of the Brazos River, near the northeast corner of Burnet County. Steep slopes along the river limited livestock grazing in the riparian zone, and consequently, a lush growth of vines and understory brush combined with boulders and drift piles provided an excellent, yet narrow habitat for swamp

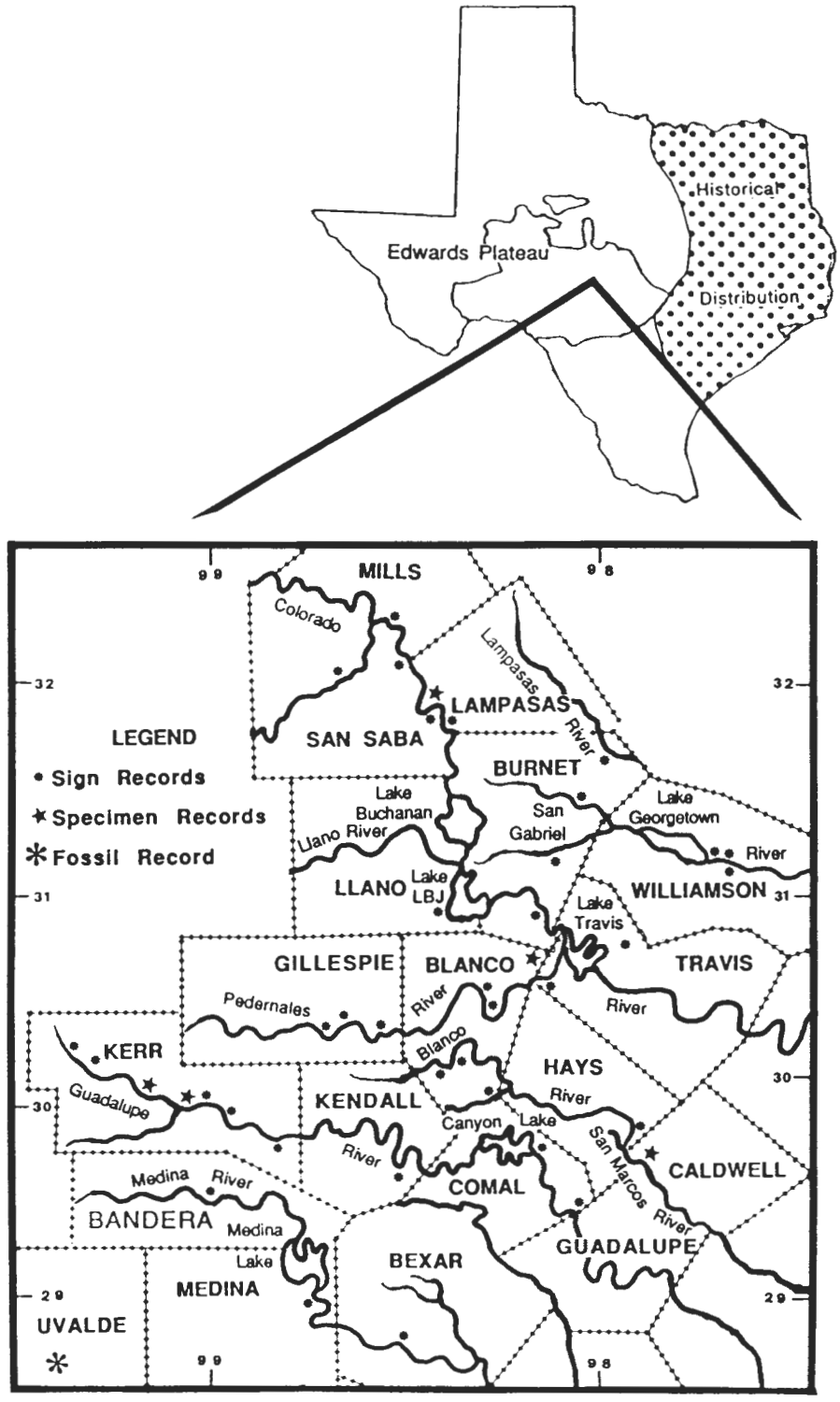

Figure 1. The distribution of *Sylvilagus aquaticus* on the eastern Edwards Plateau compared to the historical distribution in Texas.

rabbits. The Sugarberry-Elm community (and swamp rabbits) continued west along the San Gabriel River to about 16 km east of Burnet, Burnet County. Here, on small creeks, the Sugarberry-Elm community integrated with plateau live oak, cedar elm and Ashe juniper trees. The Sugarberry-Elm community occurred along the Guadalupe River from the Blackland Prairie south of the Edwards Plateau into Kerr County where it became patchy near Kerrville.

The Bald Cypress-Sycamore community was the only riparian community present on some rivers. In expansive river valleys with a multiple-community riparian forest along the river, the Bald Cypress-Sycamore community occupied the immediate streamside. Either a Sugarberry-Elm or Pecan-Sugarberry community or both occurred on upslopes to this community. A Bald Cypress-Sycamore community occurred only along the San Gabriel River in Williamson County, but in Burnet County the upper watershed riparian forests became patchy and swamp rabbits were absent. A substantial Bald Cypress-Sycamore community (and swamp rabbits) extended along the Guadalupe River from the Blackland Prairie south of the Balcones Escarpment west to Kerr County at the river's headwaters. A Bald Cypress-Sycamore community extended west along the Medina River to its headwaters in Bandera County. However, habitat suitable for swamp rabbit was disjunct with swamp rabbits occurring at only one site west of Medina Lake in Bandera County.

Swamp rabbits inhabited only one site with a lush Pecan-Sugarberry community on the San Saba River in San Saba County; however, this community was patchy, with unsuitable habitat south of U. S. Highway 190. This lagomorph inhabited the ecotone between the riparian and upland community series. Fecal materials were found consistently in ecotones near the riparian zone. Here, swamp rabbits were sympatric with eastern cottontails, a species common on xeric upslopes of ectones. The species did not inhabit the Sycamore-Willow series along the upper Nueces River in Edwards and Real counties. This community occurs on gravely soils of flood-scoured streambeds of the Edwards Plateau and consists of small trees, representing growth since the last catastrophic flood, and a poorly developed shrub layer of disturbance-type species. No sign of *S. aquaticus* was found in the Plateau Live Oak-Netleaf Hackberry community, the dominant riparian community in xeric streambeds of the Sabinal, Frio, and Nueces rivers.

The width of the riparian zone at sites inhabited by swamp rabbits ranged from 16 to 220 m ($\bar{X}$ = 61.6 m, SE = 0.31). The width of the riparian zone at sites with swamp rabbits absent ranged from 0 to 175 m ($\bar{X}$ = 54.7 m, SE = 13.9). Swamp rabbit habitat did not occur above floodline at two of 39 sites with swamp rabbits present and seven of 15 sites with the species absent. The maximum width of swamp rabbit habitat above floodline at sites with swamp rabbits present was 120 m ($\bar{X}$ = 27.3 m, SE = 4.2). The width of swamp rabbit habitat above floodline at sites with this lagomorph absent ranged from 0 to 100 m ($\bar{X}$ = 22.1 m, SE = 8.81).

Significantly more plant species occurred at sites with swamp rabbits present than sites with swamp rabbits absent (χ^2 = 18.7, d. f. = 1, $p < 0.001$). Seventy-seven plant species were identified at sites with swamp rabbits present. The mean number of plant species for sites with swamp rabbits present was 17.7 (SE = 0.7), whereas sites with the species absent had a mean of 11.7 (SE = 1.2). Six of 13 common plants at sites with swamp rabbits absent had an affinity with upland plant communities. Vines were an important component of swamp rabbit habitat. Saw greenbriar was the most common vine associated with swamp rabbit habitat, occurring at 82% of sites with this lagomorph present. Other common vines associated with swamp rabbit habitat were dewberry, grapevine, poison ivy and Carolina snailseed (Table 1).

Forbs and tall grasses composed a canopy of herbaceous vegetation at a height about 1 m. Important forbs and grasses of this canopy layer in suitable habitat were giant ragweed, frostweed, common goldenrod, switchgrass, Johnsongrass, and Indiangrass (Table 1). During winter significantly more green herbaceous vegetation occurred at sites with swamp rabbits present (95%) than sites with this lagomorph absent (40%) (G^2= 18.6, d. f. = 1, $p < 0.001$). Excessive grazing in the riparian zone was common at several sites. There was a substantial, but insignificant, difference in the amount and height of vegetation (G^2 = 3.1, d. f. = 1, $p = 0.08$) at sites with swamp rabbits present compared to sites

Table 1. Percent frequency of woody vegetation, understory shrubs and vines, and herbaceous ground vegetation at sites with Sylvilagus aquaticus *along rivers of the eastern Edwards Plateau, 1993.*

TAXON	COMMON NAME	FREQUENCY
Canopy Woody Species		
Acer negundo	Box Elder	54
Carya illinoensis	Pecan	77
Celtis laevigata	Texas Sugarberry	79
Celtis reticulata	Net-leaf Hackberry	44
Diospyros texana	Mexican Persimmon	38
Fraxinus pennsylvanica	Green Ash	41
Fraxinus velutina	Arizona Ash	18
Juglans nigra	Little Walnut	28
Juglans microcarpa	River Walnut	10
Juniperus ashei	Ashe Juniper	44
Maclura pomifera	Osage Orange, Bois d'Arc	31
Melia azedarach	Chinaberry	51
Morus rubra	Red Mulberry	18
Platanus occidentalis	Sycamore	82
Populus deltoides	Eastern Cottonwood	10
Quercus buckleyi	Texas Oak	15
Quercus macrocarpa	Bur Oak	13
Quercus shumardii	Shumard Oak	13
Quercus fusiformis	Plateau Live Oak	56
Salix nigra	Black Willow	67
Sambucus canadensis	American Elderberry	10
Taxodium distichum	Baldcypress	33
Ulmus americana	American Elm	36
Ulmus crassifolia	Cedar Elm	74
Understory Shrubs and Vines		
Amorpha fruticosa	False Indigobush	21
Ampelopsis arborea	Peppervine	15
Baccharis neglecta	Roosevelt Weed	26
Bumelia lanuginosa	Wooly Bumelia	18
Cocculus carolinus	Carolina Snailseed	31
Cornus drummondii	Rough-leaf Dogwood	56
Ilex decidua	Possumhaw	56
Ligustrum lucidum	Wax-leaf Ligustrum, Privet	23
Lonicera japonica	Japonese Honeysuckle	18
Parthenocissus quinquefolia	Virginia Creeper	28
Ptelea trifoliata	Waferash	13
Rhamnus caroliniana	Carolina Buckthorn	13
Rubus trivialis	Dewberry	77
Smilax bona-nox	Greenbriar	82
Toxicodendron radicans	Poison Ivy	38
Vitis mustangensis	Mustang Grape	54

without this species. Although herbaceous vegetation was reduced by livestock grazing at 92% of sites with swamp rabbits present compared to 73% of sites with swamp rabbits absent, the amount of reduction was substantially greater at sites with the species absent.

Woody vegetation canopy cover and closure at sites with swamp rabbits present were compared to sites with no swamp rabbits (Table 2). An incomplete canopy closure was characteristic of most sites. This openness in the canopy enhanced development of a dense under-

Table 1. continued.

TAXON	COMMON NAME	FREQUENCY
Herbaceous Ground Vegetation		
Ambrosia trifida	Giant Ragweed	77
Arundo donax	Giant Reed	10
Carex spp	Sedges	41
Chasmanthium latifolium	Creek Oats	21
Cynodon dactylon	Bermudagrass	56
Elymus canadensis	Canada Wild Rye	10
Panicum virgatum	Switchgrass	72
Ricinus communis	Castorbean	10
Schizachyrium scoparium	Little Bluestem	31
Solidago altissima	Tall Goldenrod	38
Sorghastrum nutans	Indiangrass	36
Sorghum halepense	Johnsongrass	67
Typha latifolia	Cattail	10
Verbesina virginica	Frostweed	38
Vernonia baldwinii	Western Ironweed	23
Xanthium spinosum	Spiny Cocklebur	49

story of shrubs and ground vegetation. Although only one canopy cover type (debris ground cover) was significantly different in a comparison of sites with swamp rabbits present versus sites with the species absent, there was a highly significant difference in total canopy cover between sites where this lagomorph was present or absent. Habitats with swamp rabbits present had denser foliage and a more complex stratification of canopy layers.

Vine tangles, brush and deadfalls, and drift debris were identified as the most important types of escape cover for swamp rabbits (Table 3). The amounts of all escape cover types except dense grass at sites with swamp rabbits present were significantly greater than the amounts at sites with the species absent. Drift debris and brush piles or fallen tree tops occurred at 87% of sites with swamp rabbits present and only 64% of sites with the species absent. Rock piles and crevices provided escape cover at 33% of sites with swamp rabbits present.

There was a significant difference in swamp rabbit presence based on habitat continuity ranks ($\chi^2 = 33.5$, d. f.= 2, $p < 0.0001$). Swamp rabbits inhabited all sites (32) with a continuity rank of 1.0. The species occurred at only seven of 17 sites with a continuity rank of 0.5. Neither swamp rabbits or their signs were found at sites with a continuity rank of 0.

Table 2. Mean canopy cover and closure (%) for sites with Sylvilagus aquaticus *present or absent along rivers of the eastern Edwards Plateau, 1992-1993.*

	Present (n = 39)		Absent (n = 15)		
Parameter	$\bar{X}$	$s_{\bar{X}}$	$\bar{X}$	$s_{\bar{X}}$	χ^{2*}
Tree Canopy Cover	50.2	5.2	31.4	6.8	P=0.086
Shrub Canopy Cover	18.3	3.9	13.5	3.7	P=0.862
Herb. Canopy Cover	45.3	5.8	25.3	7.3	P=0.084
Debris Ground Cover	10.3	1.7	4.5	1.6	P=0.052
Total % Canopy Cover	124.9	4.4	74.7	9.6	P<0.001

*degrees of freedom = 1

Table 3. Percent frequency of escape cover types at sites with Sylvilagus aquaticus *present or absent along rivers of the eastern Edwards Plateau, 1993.*

Parameter	Present	Absent	G^2
Vine Tangles	97	13	p<0.001
Brush/ Deadfalls	87	27	p<0.001
Dense Grass/ Sedges	74	67	p=0.576
Drift Debris	64	20	p=0.003
Rocks/ Crevices	33	7	p=0.028

DISCUSSION

Past Distribution

Holocene fossil remains of swamp rabbits from Levels 5 and 6 of Kinkaid Shelter (Uvalde County, late Rancholabrean) have been dated between about 8,000 to 6,000 yBP (Tamers et al., 1964). Specimens from Holocene Strata IIa and IIb of Eagle Cave and the Upper Zone of Centipede Cave (Val Verde County) with dates between about 5,000 to 400 yBP were assigned to *S. aquaticus* by discriminate analysis; however, because of an inherent 8% error in the analysis, Hulbert (1984) concluded that the species was a doubtful member of the fauna . Fossil remains from several sites of small mammals (*Sorex vagrans*, *Blarina brevicauda*, *Zapus hudsonius*, *Synaptomys cooperi*, *Microtus pennsylvanicus*, *Lepus townsendii*) with present distributions far north and east of central Texas indicate a moist and cool environment existed during the late Pleistocene-early Holocene in central Texas (Lundelius, 1967; Dalquest et al., 1969; Semken, 1983; Hulbert, 1984; Winkler, 1990; Wilkens, 1992; Hafner, 1993). Hafner (1993) considered the presence of *Zapus hudsonius* in Schulze Cave (Edwards County) as confirmation that an eastern grassland mammalian assemblage influenced the Wisconsinan fauna of central Texas.

The Kinkaid Shelter site is located about 45 km west of swamp rabbit records on the Medina River (Medina County). Our findings, when combined with the fossil evidence, suggest that swamp rabbits have probably inhabited the eastern Edwards Plateau for several thousand years. Thus, the occurrence of swamp rabbits along riparian corridors of the eastern Edwards Plateau is not considered a recent biological event, but rather, the result of intensive collecting effort. Residents of Kerr County reported that swamp rabbits were more common in river bottoms from 1930 to 1950 (Al Kanz, pers. comm.; Frank Syfan, pers. comm.). However, it is interesting that Lacey and Bailey collected mammals along the Guadalupe River (Bailey near Ingram, one of our collection sites) in Kerr County in the late 1800s, but neither reported collecting swamp rabbits (Allen, 1895; Bailey, 1905). The fragmented distribution of the species and large tracts of inaccessible private land limited our ability to document all possible occurrences of the species on the eastern Edwards Plateau.

Primary Habitat

Community diversity.-- Species richness is a characteristic of suitable swamp rabbit habitat. The significant difference in the mean number of plant species at sites with swamp rabbits present compared to sites with swamp rabbits absent indicates that riparian community complexity benefits swamp rabbits. Ford and Van Auken (1982) reported that the greatest total density, total dominance, and species richness for plants occurred at the water's edge along Edwards Plateau rivers. In a comparison of woody plants of uplands and creek bottoms with associated Quaternary deposits of the southern Edwards Plateau, Van Auken et al. (1979) found 49% of the species had a riparian affinity, 14% occurred only on uplands, and 37% were common to both habitats. Creek bottoms had three times greater densities of woody plant species than the adjacent Buda formation of uplands. Periodic flooding may be important in maintaining the diversity of plant communities inhabited by swamp rabbits. Floods improve the habitat for swamp rabbits in riparian communities by depositing topsoil, piling up flood debris, stimulating forb growth and thinning the forest. Bald Cypress-Sycamore forests of the eastern Edwards Plateau require disturbance for growth of seedlings and maintenance of floral diversity and interspersion (Van Auken, 1993).

Canopy.-- Shrubs are a source of food and an important structural component of habitat used for escape cover by swamp rabbits (Allen, 1985). The mean percent shrub crown canopy closure for all sites in this study was well below the optimum (50%) reported for the suitability model. Sites with swamp rabbits present had a higher mean shrub canopy closure. Only six of 54 sites had ≥ 50% shrub crown canopy closure value; values ranged from 50% to 98%. Swamp rabbits inhabited five of these sites. Compared to its importance in the habitat suitability model for the eastern United States, shrub canopy closure apparently is not as an important component of swamp rabbit habitat on the eastern Edwards Plateau.

In the habitat suitability model (Allen, 1985), tree canopy closure ranges from 25% to 60%. Tree canopy closure values for Edwards Plateau sites with swamp rabbits present fit the model. This optimum level of tree canopy closure occurs in riparian communities because trees grow in narrow strips, and the edge is near

any point within the forest. Even sites with swamp rabbits absent had values slightly below the optimum suitability value.

Herbaceous vegetation dominates open areas along rivers of the eastern Edwards Plateau. Herbaceous vegetation provides critical escape cover and is the primary source of food for swamp rabbits (Bailey, 1969; Smith, 1982; Allen, 1985). In the habitat suitability model, the optimum coverage for herbaceous canopy is 75%. Although the mean canopy cover (45.3%) for herbaceous vegetation at sites with swamp rabbits present in our study was substantially below the optimum value of the suitability model, this value for herbaceous canopy cover would have an index value of 0.6 in the suitability model (Allen, 1985). However, 14 of 39 (36%) sites with swamp rabbits present had a > 75% herbaceous plant cover. Green vegetation occurred throughout the year at 95% of sites with swamp rabbits present compared to only 40% at sites with swamp rabbits absent.

Ground cover.-- Diversity and interspersion of cover types are an important aspect of swamp rabbit habitat (Chapman et al., 1982). Dense, low-growing tangles of vines provide escape cover for swamp rabbits. In the habitat suitability model, Allen (1985) grouped vines with trees, shrubs, or herbaceous vegetation depending on their physiognomy, but he suggested that vines should be a separate canopy cover type in future habitat studies. Vines were analyzed as a separate cscape cover type in our study. Dense vine tangles of saw greenbriar, dewberry or Japanese honeysuckle provided the most important type of escape cover at 97% of sites with swamp rabbits present.

Ground debris was not included as a separate cover type in the habitat suitability model (Allen, 1985). This cover type was an important cover component of habitat in the eastern Edwards Plateau. Although a small percent of the surface area at sites with swamp rabbits present was ground debris, it covered a larger area at sites with swamp rabbits present than sites with the species absent. However, when identifying types of escape cover at sites with swamp rabbits present, ground debris composed one of three important cover types. Observations and/or collection of swamp rabbits often occurred at drift piles or fallen tree tops.

Disturbance.-- Swamp rabbit habitat is enhanced by disturbance, and areas with intermittent flooding have a higher habitat suitability index (Allen, 1985). Streams of the eastern Edwards Plateau because of topography have substantial periodic flooding after torrential rains. Flooding displaces swamp rabbits from the riparian zone onto upland areas, but as the water recedes, rabbits usually return to previously occupied areas (Conaway et al., 1960). The intensity of land use near streams may determine swamp rabbit survival during floods. Since most suitable habitat for swamp rabbits on the Edwards Plateau occurs in relatively narrow strips, compression of or loss of riparian zones during flooding may cause severe survival problems for swamp rabbits (J. K. Jones, Jr., pers. comm.). Blair (1939) studied the adverse effects of flooding on populations of small, terrestrial mammals inhabiting river floodplains in eastern Oklahoma and found terrestrial species confined to floodplains may be virtually extirpated in parts of their range by severe floods. After such a flood, one swamp rabbit was the only small mammal observed in the floodplain. When swamp rabbits are forced out of suitable habitat by floods, predation probably increases.

Fragmentation of habitat.-- Several factors contributed to fragmentation of habitat for swamp rabbits along rivers of the eastern Edwards Plateau. A thin, sandy substrate on the Pedernales River in Blanco County east of Johnson City at the Robinson Ranch and Pedernales Falls State Park caused an unsuitable edaphic habitat for the plant species of riparian communities. Riverbed physiography caused a natural break in suitable habitat on the Medina River in Bandera County, where flooding had deposited debris up to the Ashe Juniper-Live Oak community. Similarly, the riparian community along the Llano River is very narrow and patchy. The westernmost rivers of the eastern Edwards Plateau, such as the upper Nueces River, have poorly developed riparian zones juxtaposed to a Live Oak-Midgrass Savannah community. These rivers with narrow strips or small isolated patches of riparian habitat next to intensely used land are poor swamp rabbit habitat (Kort and Fredrickson, 1977).

Water impoundments on the rivers cause substantial breaks in the continuity of swamp rabbit habitat along Edwards Plateau rivers. A series of dams impound the Colorado River between Travis County and

San Saba County for a distance of about 222 km. At Lake Georgetown on the San Gabriel River, the water level extnds up to the Ashe Juniper-Live Oak and Live Oak-Midgrass communities for 8 km. Canyon Lake covers 16 km of former riparian habitat on the Guadalupe River, and 24 km of former riparian habitat on the Medina River is inundated by Medina Lake. Neither swamp rabbits nor their signs were found along the shores of these reservoirs.

Conversion of bottomland hardwood forest to agricultural use has been the primary cause of swamp rabbit habitat loss in eastern parts of its range (Terrel, 1972; Schmidly, 1983; Kjolhaug et al., 1987). Since 98% of the Edwards Plateau is rangeland (Hatch et al., 1990), timber harvesting and farming are not major causes of habitat degradation. Farm use of bottomlands near study sites was pecan orchards and hay fields. The major agricultural use of land that is detrimental to the habitat of swamp rabbits is the reduction of available food and ground cover by intense grazing of livestock. Swamp rabbits seem to tolerate a moderate reduction of vegetation, but severe overgrazing results in an unsuitable habitat.

Swamp rabbits inhabited undisturbed lots between houses in subdivisions along Edwards Plateau rivers. The rate of development and density of houses are important factors in the degradation of habitat. However, often the purchase of land for a subdivision usually results in the removal of livestock, fallowing of land, succession of the plant community, and an improvement in the continuity of an otherwise fragmented riparian habitat. The continuity of riparian habitat improves, and depending on the intensity of vegetation management by landowners and density of houses, the subsequent development of the subdivision may not be as detrimental as livestock grazing on the swamp rabbit population.

Swamp rabbits occupied undeveloped riparian habitat at some state parks and natural areas. The intensity of vegetation management seems to determine their presence. Picnic grounds at Blanco State Park on the Blanco River have a closely mowed bermudagrass lawn. Swamp rabbits were not observed in this part of the park. However, swamp rabbits inhabited undeveloped land downstream and upstream from the picnic grounds. Swamp rabbits were observed in tall grass and deadfalls along the hiking trail upstream from the campgrounds at Colorado Bend State Park. Cover was patchy because the vegetation had been severely damaged by foraging feral hogs. This lagomorph also inhabited a Bald Cypress-Sycamore community at Honey Creek State Natural Area.

Recruitment and dispersal are important biological processes of rabbit populations, and when suitable riparian habitats are fragmented on a large portion of a river, the dispersal corridor for recruits is lost (Chapman et al., 1982). Kjolhaug et al. (1987) found rabbits in small areas connected by narrow habitat corridors along Illinois rivers, however smaller, isolated areas located on small tributary streams were unsuitable habitat. Riparian forests of the eastern Edwards Plateau are often discontinuous "islands" of habitat. Eighteen percent of sites with swamp rabbits were classified as patchy, unsuitable habitat, suggesting the species is vulnerable to extirpation in these areas. Swamp rabbits inhabiting riparian corridors along rivers of the eastern Edwards Plateau live in environments that would be classified as marginal to poor habitat when compared to the habitat suitability model of the species. Swamp rabbit populations tend to fluctuate, but with a discontinuous riparian habitat, isolated populations are unlikely to be reestablished once extirpated (Kjolhaug et al., 1987).

Decreasing the fragmentation of plant communities inhabited by swamp rabbits would be the most effective method of managing for swamp rabbits in riparian corridors. In the eastern Edwards Plateau, the best habitat for swamp rabbits often occurs in right-of-ways under highway bridges, vacant lots in minimally developed subdivisions, undeveloped areas of state parks and natural areas and ungrazed riparian areas. Improvement of swamp rabbit habitat along rivers and streams of the eastern Edwards Plateau could be accomplished by expanding the patch size of these habitats by allowing the growth of vines, grasses and forbs, selectively thinning mature forests, excluding livestock grazing (at least until shrub thickets form), controlling feral hog populations, and leaving piles of brush or fallen tree tops for structure. An essential component of swamp rabbit habitat is adequate cover above the floodline. Disturbances to the Sugarberry-Elm and Bald Cypress-

Sycamore community series along rivers of the eastern Edwards Plateau should not be closer than 100 m above the floodline. Habitat corridors to allow dispersal of swamp rabbits could be created around large reservoirs and sections of rivers that naturally have a poorly developed riparian forest by planting or allowing the growth of native species.

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LITERATURE CITED

Allen, A. W. 1985. Habitat suitability index models: swamp rabbit. U. S. Fish Wildl. Serv. Biol. Rep., 82 (10.107). 20 pp.

Allen, J. A. 1895. Descriptions of new American mammals. Bull. Amer. Mus. Nat. Hist., 7 (10): 327-328.

Bailey, J. A. 1969. Exploratory study of nutrition of young cottontails. J. Wildl. Mgmt., 33: 346-353.

Bailey, V. 1905. Biological survey of Texas. N. Amer. Fauna, 25: 1-222.

Blair, W. F. 1939. Some observed effects of stream-valley flooding on mammalian populations in eastern Oklahoma. J. Mamm., 20: 304-306.

Chapman, J. A., and G. A. Feldhamer. 1981. Mamm. Species. 151: 1-4.

Chapman, J. A., J. G. Hockman, and W. R. Edwards. 1982. Cottontails *Sylvilagus floridanus* and allies. Pp 83-123 *in* Wild mammals of North America: biology, management, and economics. (J. A. Chapman and G. A. Feldhamer, eds.). Johns Hopkins Univ. Press, Baltimore. XIII + 1147 pp.

Conaway, C. H., T. S. Baskett, and J. E. Toll. 1960. Embryo resorption in the swamp rabbit. J. Wildl. Mgmt., 24: 197-202.

Dailey, T. V., T. M. Vangilder, and L. W. Burger, Jr. 1993. Swamp rabbit distribution in Missouri. Proc. Southeastern Assoc. Fish Wildl. Agencies, 47: 251-256.

Dalquest, W. W., and N. V. Horner. 1984. Mammals of north-central Texas. Midwestern State Univ. Press, Wichita Falls. 261 pp.

Dalquest, W. W., W. E. Roth, and F. Judd. 1969. The mammal fauna of Schulze Cave, Edwards County, Texas. Bull. Florida State Mus., Biol. Sci., 13: 205-276.

Davis, W. B. 1966. The mammals of Texas. Texas Parks and Wildl. Dept., Bull. 41: 236-244.

Davis, W. B., and D. J. Schmidly. 1994. The mammals of Texas. Texas Parks and Wildl. Press, Austin. x + 338 pp.

Diamond, D. D., D. H. Riskind, and S.L. Orzell. 1987. A framework for plant community classification and conservation in Texas. Texas J. Sci., 39: 203-221.

Ford, A. L., and O. W. Van Auken. 1982. The distribution of woody species in the Guadalupe River floodplain forest in the Edwards Plateau of Texas. Southwestern Nat., 27: 383-392.

Garner, W. H., J. G. Joy, K. D. Huckabee, R. M. Pitts. 1990. Additional records of mammals along the boundary of the Kansan-Texan biotic provinces in north-central Texas. Texas J. Sci., 42: 308-310.

Hafner, D. J. 1993. Reinterpretation of the Wisconsin mammalian fauna and paleoenvironment of the Edwards Plateau Texas. J. Mamm., 74: 162-167.

Hall, E. R. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 1: XV + 1-600 + 90 and 2: VI + 601-1181 + 90.

Hatch, S. L., K. N. Gandhi, and L. E. Brown. 1990. Checklist of the vascular plants of Texas. MP-1655. Texas Agric. Exper. Stn., College Station. 158 pp.

Hulbert, R. C., Jr. 1984. Latest Pleistocene and Holocene leporid faunas from Texas: their composition, distribution and climactic implications. Southwestern Nat., 29: 197-210.

Hunt, T. P. 1959. Breeding habits of the swamp rabbit with notes on its life history. J. Mamm., 40: 82-91.

Kjolhaug, M. S., A. Woolf, and W. D. Klimstra. 1987. Current status and distribution of the swamp rabbit in Illinois. Trans. Illinois Acad. Sci., 80: 299-308.

Kort, P. A., and L. H. Fredrickson. 1977. Swamp rabbit distribution in Missouri. Trans. Missouri Acad. Sci., 10 and 11: 72-77.

Lowe, C. E. 1958. Ecology of the swamp rabbit in Georgia. J. Mamm., 39: 116-127.

Lundelius, E. L., Jr. 1967. Late Pleistocene and Holocene faunal history of central Texas. Pp 287-319 *in* Pleistocene extinctions: the search for a cause (P. S. Martin and H. E. Wright, Jr., eds.). Yale Univ. Press, New Haven. 453 pp.

McCarley, H. 1959. The mammals of eastern Texas. Texas J. Sci., 1: 385-426.

Schmidly, D. J. 1983. Texas mammals east of the Balcones fault zone. Texas A&M Press, College Station. 400 pp.

Semken, H. A., Jr. 1983. Holocene mammalian biogeography and climatic change in the Eastern and Central United States. Pp 182-207 *in* Late-Ouarternary environments of the United States, the Holocene (H. E, Wright, Jr., ed.). Univ. Minnesota Press, Minneapolis. 277 pp.

Smith, M. W. 1982. Effects of selected silvicultural practices on swamp rabbit (*Sylvilagus aquaticus*) habitat. Unpublished M. S. thesis., Mississippi State Univ., State College. 176 pp.

Tamers, M. A., F. J. Pearson, and E. M. Davis. 1964. University of Texas radiocarbon dates II. Radiocarbon, 6: 138-159.

Taylor, W. P., and D. W. Lay. 1944. Ecologic niches occupied by rabbits in eastern Texas. Ecology, 25: 120-121.

Terrel, T. L. 1972. The swamp rabbit (*Sylvilagus aquaticus*) in Indiana. Amer. Midl. Nat., 87: 283-295.

Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. Geog. Rev., 38: 55-94.

Van Auken, O. W. 1993. Size distribution pattern and potential population change of some dominant woody species of the Edwards Plateau region of Texas. Texas J. Sci., 45: 200-210.

Van Auken, O. W., A. L. Ford, and A. Stein. 1979. A comparison of some woody upland and riparian plant communities of the southern Edwards Plateau. Southwestern Nat., 24: 165-180.

Whitaker, J. O., Jr. 1980. The Audubon Society field guide to North American mammals. Alfred A. Knopf Publ., New York. 745 pp.

Wilkins, K. T. 1992. Mammalian paleofaunas of central Texas from the late Wisconsinan glacial period to the latest Holocene. Texas J. Sci. 44: 263-281.

Winkler, A. J. 1990. Small mammals from a Holocene sequence in central Texas and their paleo-enviromental implications. Southwestern Nat., 35: 199-205.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs. 718 pp.

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APPENDIX

Specimens examined or swamp rabbits observed: All collected materials are housed in the Southwest Texas State University Mammal Collection. All counties listed are in Texas. *Bandera*: Medina River, 13 km E Medina; Bexar: Medina River, 16 km S San Antonio; *Blanco*: Little Blanco River, 21 km W Fischer; Cypress Creek, 21 km SE Johnson City; Pedernales River, 5 km NE Johnson City; Pedernales River, 5 km N Johnson City; Blanco River, 5 km S Blanco; Blanco River, 5 km W Blanco; *Bosque*: Bosque River, Valley Mills; *Burnet*: Colorado River, 11 km E Marble Falls; Lampasas River, 40 km NE Burnet; San Gabriel River, 13 km NE Bertram; San Gabriel River, 11 km N Bertram; San Gabriel River, 5 km SE Bertram; Confluence of Penny and Hamilton Creeks, 5 km E Marble Falls; *Caldwell*: San Marcos River, Martindale; *Comal*: Guadalupe River, 3 km N Sattler; York Creek, 13 km E New Braunfels; Honey Creek, Honey Creek State Natural Area; *Gillespie*: Pedernales River, 8 km E Stonewall; Pedernales River, 5 km E Stonewall; Pedernales River, 8 km W Stonewall; *Guadalupe*: San Marcos River, Staples; *Hays*: Blanco River, 5 km N San Marcos; San Marcos River, San Marcos; *Kendall:* Guadalupe River, 21 km NE Boerne; *Kerr*: Guadalupe River, 19 km W Hunt (SWTSU 107); Johnson Creek, Ingram; Johnson Creek, 4 km SE Mountain Home; Guadalupe River, 3 km W Ingram (SWTSU 85); Guadalupe River, 5 km W Ingram; Guadalupe River, 5 km W Center Point; Johnson Creek, 3 km S Mountain Home (SWTSU 92); *Lampasas*: Colorado River, 32 km W Lampasas (SWTSU 102, 103); *Llano*: Sandy Creek, 17 km SE Kingsland; Llano River, Kingsland; *Medina*: Medina River, 8 km N Castroville; *Mills*: Colorado River, 13 km S Goldthwaite; *San Saba*: Colorado River, 21 km SE San Saba; Colorado River, 16 km E San Saba; San Saba River, 8 km W San Saba; *Travis:* Cypress Creek, 40 km SW Austin; Walnut Creel, Austin; *Williamson*: San Gabriel River, 3 km W Georgetown; San Gabriel River, 5 km NW Georgetown, San Gabriel River, 13 km NW Georgetown.

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It was through the efforts of Horn Professor J Knox Jones, as director of Academic Publications, that Texas Tech University initiated several publications series including the Occasional Papers of the Museum. This and future editions in the series are a memorial to his dedication to excellence in academic publications. Professor Jones enjoyed editing scientific publications and served the scientific community as an editor for the Journal of Mammalogy, Evolution, The Texas Journal of Science, Occasional Papers of the Museum, and Special Publications of the Museum. It is with special fondness that we remember Dr. J Knox Jones.

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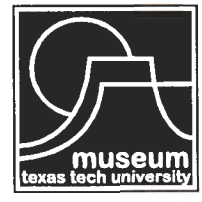

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