

*Sigmodon hispidus*. By Guy N. Cameron and Stephen R. Spencer

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*Sigmodon hispidus* Say and Ord, 1825

Hispid Cotton Rat

- [*Sigmodon*] *hispidus* Say and Ord, 1825:354. Type locality St. Johns River, northeastern Florida.  
*Sigmodon baileyi* Allen, 1903:601. Type locality La Ciénaga de las Vacas, 6,500 ft., Durango.  
*Sigmodon berlandieri* Baird, 1855:333. Type locality Rio Nazas, Coahuila.  
*Sigmodon borucae* Allen, 1897:40. Type locality Boruca, near Rio Diquis, 1,600 ft., about 12 mi. from Pacific Coast, Puntarenas, Costa Rica.  
*Arvicola texiana* Audubon and Bachman, 1853:229. Type locality Brazos River, Texas.  
[*Hesperomys*] *toltecus* Saussure, 1860:98. Type locality mountains of Veracruz (probably near Mirador, Dalquest, 1953:163).  
*Sigmodon zanjonensis* Goodwin, 1932:1. Type locality Zanjon, 9,000 ft., Quezaltenango, Guatemala.

**CONTEXT AND CONTENT.** Order Rodentia, Suborder Myomorpha, Family Muridae, Subfamily Cricetinae. A generic account and key to the species of *Sigmodon* was presented in Baker and Shump (1978). The following 25 subspecies of *S. hispidus* were recognized by Hall and Kelson (1959; other subspecies then recognized have been removed to separate species *Sigmodon arizonae* and *S. mascotensis*):

- S. h. alfredi* Goldman and Gardner, 1947:57. Type locality I. N. Pruitt Farm, near William's Corner, 11 mi. N. Springfield, Baca Co., Colorado.  
*S. h. baileyi* Allen, 1903:601, see above.  
*S. h. berlandieri* Baird, 1855:333, see above (*pallidus* Mearns a synonym).  
*S. h. borucae* Allen, 1897:40, see above (*austerulus* Bangs a synonym).  
*S. h. chiriquensis* Allen, 1904:68. Type locality Boqueron, Chiriqui, Panama.  
*S. h. confinis* Goldman, 1918:21. Type locality Stafford, Graham Co., Arizona.  
*S. h. eremicus* Mearns, 1897:504. Type locality Cienega Well, 30 mi. S Monument No. 204, Mexican boundary line, on east bank Colorado River, Sonora.  
*S. h. exspatus* Allen, 1920:236. Type locality Big Pine Key, one of the southern Florida Keys, Monroe Co., Florida.  
*S. h. floridanus* Howell, 1943:73. Type locality Canal Point, Palm Beach Co., Florida.  
*S. h. furvus* Bangs, 1903:39. Type locality La Cieba, Atlantida, Honduras.  
*S. h. griseus* Allen, 1908:657. Type locality lowlands east of Lake Nicaragua, Chontales, Nicaragua.  
*S. h. hispidus* Say and Ord, 1825:354, see above.  
*S. h. inexoratus* Elliot, 1903:144. Type locality Octlan, Jalisco.  
*S. h. insulicola* Howell, 1943:74. Type locality Captiva Island, Lee Co., Florida.  
*S. h. komareki* Gardner, 1948a:97. Type locality Woodville, 616 ft., Jackson Co., Alabama.  
*S. h. littoralis* Chapman, 1889:118. Type locality East Peninsula, opposite Micco, Brevard Co., Florida.  
*S. h. microdon* Bailey, 1902:111. Type locality Puerto Morelox, Quintana Roo.  
*S. h. obvelatus* Russell, 1952:81. Type locality 5 mi. S Alpuyecá, 3,700 ft., Morelos.  
*S. h. saturatus* Bailey, 1902:111. Type locality Teapa, Tabasco.  
*S. h. solus* Hall, 1951:42. Type locality island 88 mi. S, 10 mi. W Matamoros, Tamaulipas.  
*S. h. spadicipygus* Bangs, 1898:192. Type locality Cape Sable, Monroe Co., Florida.  
*S. h. texianus* (Audubon and Bachman, 1853:229), see above.  
*S. h. toltecus* (Saussure, 1860:98), see above.

- S. h. tonalensis* Bailey, 1902:109. Type locality Tonalá, Chiapas.  
*S. h. virginianus* Gardner, 1946:137. Type locality Triplet, 160 ft., Brunswick Co., Virginia.  
*S. h. zanjonensis* Goodwin, 1932:1, see above.

**DIAGNOSIS.** *Sigmodon hispidus* differs from the *S. fulviventris* group in possessing large tail scales (0.75 mm wide rather than 0.5 mm wide) and a tail sparsely haired instead of heavily haired. The skull is generally long and narrow, basioccipital long and broad, palatal pits shallow, as opposed to a short and broad skull, long and narrow or short and broad basioccipital, and deeply marked palatal pits in *S. fulviventris* group (Baker, 1969).

*S. hispidus* differs from other members of the *S. hispidus* group by having a generally shorter hind foot (less than 34 mm, averaging 32 mm), shorter distance between temporal and occipital crests (less than 3.6 mm, averaging 3.2 mm) and the diameter of the foramen ovale less than three-fourths the diameter of M3. *S. hispidus* has a well-developed crest on the posterior of the palate (Zimmerman, 1970).

Cranial characters allow separation of *S. hispidus* from *S. arizonae*. The flattened ventral surface of the presphenoid is wider in *arizonae* than *hispidus* with lateral sides of the presphenoid visible only in *hispidus* (Severinghaus and Hoffmeister, 1978). The anterior spine on the infraorbital plate is more elongated and pointed in *arizonae*. The occipital shield of *arizonae* has a rounded dorsal ridge whereas it is angular in *hispidus*.

**GENERAL CHARACTERS.** Fig. 1 shows the external appearance of the hispid cotton rat. Typical adult sizes (in mm) are: total length 224 to 365, length of tail 81 to 166, length of hindfoot 28 to 41, length of ear 16 to 24 (Chipman, 1965; Hall and Kelson, 1959; Jimenez, 1971). Adult body weights range from 110 to 225 g for males and 100 to 200 g for females (Chipman, 1965). Sexual dimorphism has been reported for length of body (Chipman, 1965; Jimenez, 1971; McIntire et al., 1944), length of hindfoot (Jimenez, 1971), and body weight (Chipman, 1965). McClenaghan (1977) reported that northern populations (Kansas) exhibit greater morphological variation than southern (Mexico) populations.

The skull is illustrated in Fig. 2. Cranial measurements (in mm) for adults are (n = 27): condylobasal length, 40.9 (39.1 to 42.5); zygomatic breadth, 23.7 (22.1 to 25.4); height of braincase, 15.8 (14.8 to 17.3); length of nasal, 16.5 (15.3 to 18.0); alveolar length of maxillary toothrow, 7.6 (7.1 to 8.2); greatest length of



FIGURE 1. The hispid cotton rat (*Sigmodon hispidus texianus*). Photographed at the University of Houston Coastal Center by S. R. Spencer.

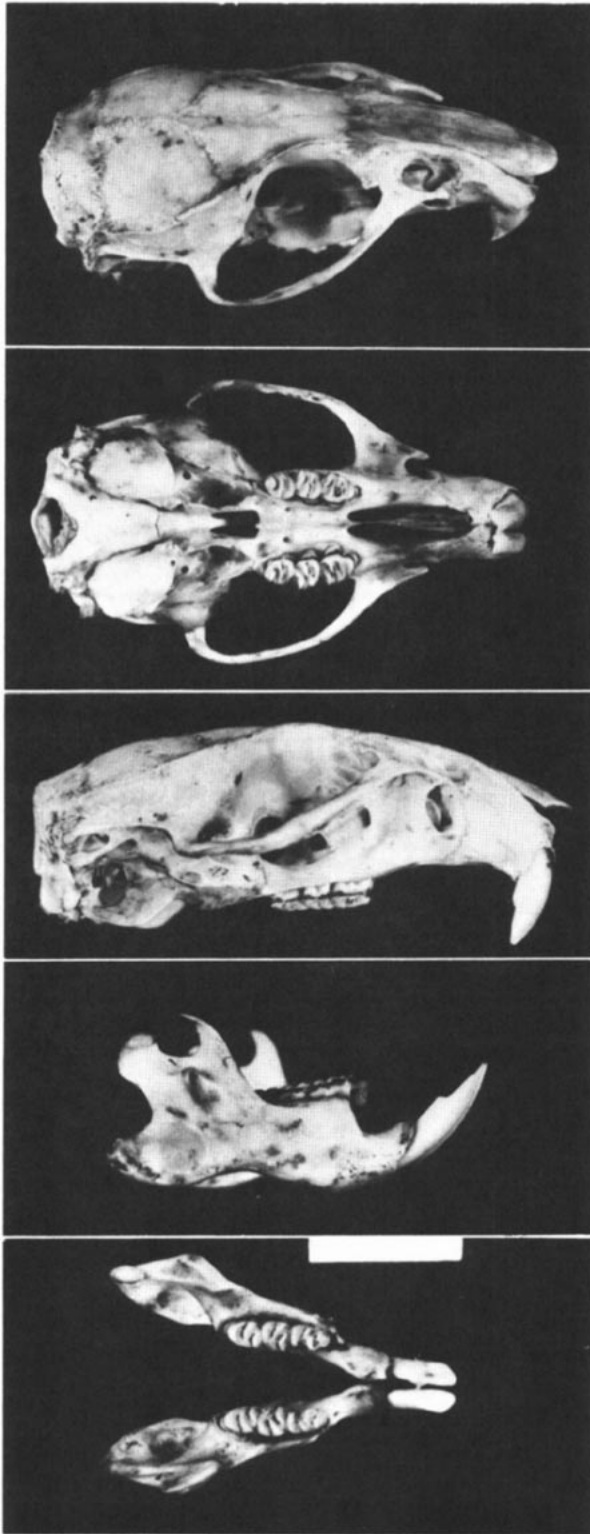


FIGURE 2. Dorsal, ventral, and lateral views of cranium and lateral and occlusal views of mandible of *Sigmodon hispidus texianus* (female from 27 km N Austin, Travis Co., Texas). Scale represents 10 mm.

skull, 42.2 (40.5 to 44.6); palatal length, 23.5 (21.7 to 24.9); length of rostrum, 16.6 (15.6 to 17.8); width of rostrum, 8.9 (8.0 to 9.9); least interorbital breadth, 5.6 (5.2 to 6.2); interparietal breadth, 12.2 (11.2 to 13.3); breadth of braincase, 16.4 (15.5 to 17.6); length of diastema, 12.3 (11.1–13.1); length of incisive foramen, 9.9 (9.5–10.5) (Jimenez, 1971).

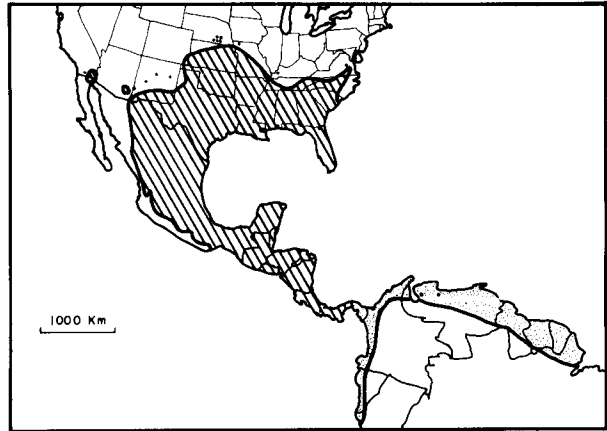


FIGURE 3. Map of southern North America and northern South America showing the distribution of *S. hispidus*. Cross-hatched area after Hall and Kelson (1959); stippled area after Hershkovitz (1955). Closed circles indicate range extensions described in text.

**DISTRIBUTION.** The geographic range of the hispid cotton rat extends northward from northern South America (Kiblisly, 1969) through most of Central America and Mexico and into the southeastern and southcentral United States (Fig. 3). *S. hispidus* extends from Florida north to Virginia, west to Kansas and Nebraska, southwest to southern New Mexico and southeastern Arizona. An isolated population near Yuma, Arizona, extends into western Mexico, southern Arizona, and southeastern California along the Colorado River and in the Imperial Valley.

Recent reports have documented extensions in the species range, primarily northward into central Virginia (Pagels and Adleman, 1971), Kentucky (Robinson and Quick, 1965), northern Missouri (Easterla, 1968), southern Nebraska (Farney, 1975; Genoways and Schlitter, 1967; Jones, 1960), and northern New Mexico (Mohlhenrich, 1961). Carey (1978) reported a western movement in Colorado and Dixon (1922) reported a spread westward from the Colorado River drainage into the Imperial Valley of California (see also Clark, 1972).

**FOSSIL RECORD.** The fossil record of *Sigmodon* was reviewed by Martin (1979). *Sigmodon* is believed to have evolved from a grass-eating cricetine ancestor which developed as a progressive offshoot from the main line of phyllotine rodent origin (Hershkovitz, 1962). The genus is presumed to be tropical American in origin, evolving either in South or Middle American grasslands in the late Pliocene (Baker, 1969; Hershkovitz, 1966; Hooper, 1949), although Martin (1979) suggested a North American origin. Martin (1979) speculated that *S. hispidus* dispersed into South America over the Panamanian land bridge during the early Blancan and radiated into its present habitat types during the Rancholabrean.

*Sigmodon hispidus* is known from the Rancholabrean in Florida, the Sangamon (third interglacial) in the Moore Pit Pleistocene fauna of northern Texas, and may have been present in this region throughout the Wisconsin glaciation (Slaughter, 1966, 1967). Cushing (1945) and Gilmore (1947) reported *Sigmodon* from the Mexican Quaternary and Recent deposits, respectively. *S. hispidus* reached Kansas during the late Pliocene and Early Pleistocene (Hibbard, 1960). This species was displaced southward into refugia in Florida and the American southwest during the Wisconsin glaciation (Blair, 1958) and again moved northward with the retreat of the glaciers. Serological evidence indicated that Florida and southwestern populations of *S. hispidus* did not rejoin, but that cotton rats from the Mexican plateau repopulated the area by moving northward (Dalby and Lillevik, 1969).

Speciation of *S. hispidus*, *S. arizonae*, and *S. mascotensis* probably occurred during the mid-Pleistocene (Zimmerman, 1970). Zimmerman (1970) surmised a pre-Wisconsin habitat separation of *hispidus* and *arizonae* in southern Arizona and the region west of the Sierra Madre Occidental in Mexico. When the climate of southern Arizona became warmer and drier with the retreat of the glaciers, *S. arizonae* may have been more adapted to invade this area quickly; this northward movement of *arizonae* may have isolated the population *hispidus* at Yuma (Zimmerman, 1970; see Fig. 3).

**FORM.** The pelage of *S. hispidus* is grizzled with blackish or dark brownish hairs, interspersed with buffy or grayish hairs. The sides are only slightly paler while the underparts are usually pale to dark grayish, sometimes faintly washed with buff. The tail is dark, coarsely annulated but only sparsely haired, the hairs not obscuring the annulations. Chipman (1965) described the pelage as remarkably uniform throughout the animal's life but with several molts occurring. Juvenile pelage becomes complete within a week after birth and is characterized by short hairs somewhat darker than those of the adult. A rapid molt to subadult pelage begins ventrally and ends dorsally and is completed within 5 to 6 weeks. Immediately after or slightly before the subadult molt is completed, the molt to adult pelage begins, following the same basic pattern but taking 2.5 to 3 months to complete. Usually another molt occurs at about 6 months of age but is irregular and has been termed a patch molt. Gardner (1948b) and Sherman (1951) described albino color phases of the cotton rat while Danforth and Schwenker (1949) described a coat color mutation they called "snowball" because of the white coloration. This mutation occurred twice in two related substrains both derived from stock originally collected in Alabama. Sherman (1951) noted that two individuals taken in Florida were browner and blacker than normal, respectively. Gennaro (1968) found that coat color varied in New Mexico and related the variation to soil color differences and past dispersal events.

Female cotton rats possess 10 mammae including three pectoral and two inguinal pairs (Hall and Kelson, 1959) or one inguinal, two abdominal and two pectoral pairs (Meyer and Meyer, 1944a). Meyer and Meyer (1944a) also encountered two animals which had an extra pair of abdominal mammae (making a total of 12), and one animal which lacked the anterior pectoral pair (making a total of 8). According to Chipman (1965) one-month old females showed no teat pigmentation while at 2 months all females showed some pigmentation and at 3 months all females showed dark brown pigmentation. A week or 10 days prior to the birth of a litter, the teats became enlarged and developed a black coloration. The dark brown coloration returned after weaning if there was not a new pregnancy.

Dental formula for *S. hispidus* is  $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$ , total 16. Dental characters were described by Hershkovitz (1955): incisors opisthodont, grooved or ungrooved; molar crowns high, plane, principle cusps lozenge-shaped; vestige of mesoloph absent; apices of major and first primary folds opposed and touching M1 and M2, confluent in M3 (M3 absent until 1 to 2 months of age (Chipman, 1965)); second secondary folds (posterior cingula) absent in upper molars; first secondary folds absent in lower second and third molars; anterior internal folds absent in first molars; second primary fold of M2 short, less than one-half of length of first primary. *S. hispidus* has the most hypsodont molars of any species of *Sigmodon* (Martin, 1979). Hypsodonty in cotton rats has been accompanied by the addition of accessory roots; *S. hispidus* has four well-developed roots on M1. Martin (1979) further suggested that the processes of lamination and involution are continuing in this species and the masticatory platform provided by the roots is becoming sturdier. In addition, root capture (the formation of a bridge of dentin between roots) is evident as a recent evolutionary adaptation to grazing in this species.

Sprague (1941) described the hyoid apparatus of *Sigmodon* and suggested that *Sigmodon* should not be placed with the Cricetinae. Hamilton (1946) noted that the baculum of *S. hispidus* was distinctively different than in other genera of Cricetinae, except for its great similarity to *Oryzomys palustris palustris*. Hooper (1962) described and illustrated the glans penis of *S. hispidus* in detail and compared it with those of other supposed sigmodont rodents. Rinker (1954) compared the myology of *Sigmodon*, *Oryzomys*, *Neotoma*, and *Peromyscus* and discussed their intergeneric relationships. Blank (1950) described the histology of the alimentary canal of the cotton rat and Goertz (1965a) related adrenal gland and spleen weights to age, sex, and season.

**FUNCTION.** McIntire et al. (1944) and Schweigert (1948a, 1948b) reviewed studies that determined the susceptibility of cotton rats to poliomyelitis and diphtheria infection. This led to increasing use of the cotton rat as an experimental laboratory animal and to studies of its nutritional requirements. Underhill (1973) reported *S. hispidus* was more efficient in utilizing a wide range of protein concentrates than *S. fulviventris* and suggested this may be related to the ubiquity of feeding habits of *S. hispidus*. Clark and Jungeblut (1940) determined that vitamin C was not required by cotton rats although McIntire et al. (1944) determined that cotton rats require thiamine, riboflavin, pantothenic acid, pyridoxine, and choline in approximately the same quan-

ties as the white rat. Increases in growth rates of 3% were noted when 2% liver extract was added to the diet. If sufficient tryptophan is included in the diet, tryptophan can be converted to niacin. Inositol also increased growth rates.

Oxygen consumption of resting cotton rats was measured by Baker and Dunaway (1969). Oxygen consumption ( $\text{cc g}^{-1} \text{h}^{-1}$ ) ranged from 2.8 to 4.0 at 5°C, from 1.9 to 2.7 at 15°C, and from 1.2 to 1.9 at 25°C; Baker (1974) and Wagner (1970) also found that oxygen consumption was temperature dependent. In animals exposed to 9°C for one month prior to testing (also at 9°C),  $\text{CO}_2$  production ( $\text{cc g}^{-1} \text{h}^{-1}$ ) was measured as  $2.62 \pm 0.11$  whereas animals exposed to ambient temperature for one month were measured as  $1.78 \pm 0.07$ . Bowers (1971) measured resting metabolic rate in several subspecies ( $\text{O}_2$  consumption in  $\text{cc g}^{-1} \text{h}^{-1}$ ) with the following results: *S. h. texianus*, 1.31 (0.96 to 1.56), Arkansas; *S. h. berlandieri*, 1.33 (1.02 to 1.75), Lubbock, Texas; *S. h. toltecus*, 2.42 (2.11 to 2.89), Veracruz and Isla del Toro, Mexico. McClure and Randolph (1980) reported allocation of energy to growth and thermoregulation in *S. hispidus*; Sealander and Guess (1970) investigated thermoregulatory responses to stress.

The increase in metabolic rate with decreasing temperature must be compensated for to increase survival. Fleharty et al. (1973) suggested that cotton rats expend considerable energy for thermoregulation during winter in the northern part of their range and that fat deposition during the growing season could provide this energy. This was confirmed by Cameron et al. (1979a) who found that cotton rats from Kansas store significantly more fat than rats from Texas in summer, autumn, and winter, but not in spring. Depletion of body fat in the Texas population corresponded with low abundance of preferred foods, seasonal cessation of reproduction, and seasonal hot weather during summer, whereas Kansas rats exhibited their lowest fat content in the spring following cold winter temperature.

Energy content of cotton rats ranged from 5.30 to 5.39 kcal/g dry weight or 1.74 kcal/g live weight (Fleharty et al., 1973; Golley, 1969). Caloric value was not influenced by sex or reproductive stage, but seasonal influences were manifest as changes in fat composition. Golley attributed the spring depression in fat (and hence energy) content of cotton rats to nutritional variation in food items. Cameron et al. (1979a) reported a similar phenomenon (see above). Energy value of two litters was given by Fleharty et al. (1973) as 5.65 kcal/g ash free weight (85.5% water, 12.3% ash) or 0.79 kcal/g live weight. Kaufman et al. (1976) estimated digestibility as 78% for field and 82% for laboratory conditions. Randolph et al. (1977) and Petrides and Stewart (1969) reported similar digestibility figures; Fleharty and Choate (1973) reported 69%.

Kirksey et al. (1975) found that the tail of the cotton rat is important in temperature regulation. The metabolic rate of normal rats was significantly higher than that of rats without tails between ambient temperatures of 4°C and 20°C. Internal temperatures also differed significantly within the same temperature range. Mean lower critical temperature for rats with tails was 30.8°C while for rats without tails it was 30.0°C, indicating significant heat loss from the tail in this species. Higher rates of water loss (6.8% greater) in rats without tails at high temperatures suggested difficulty in thermoregulating without a tail.

**ONTOGENY AND REPRODUCTION.** Information on fertilization and implantation came from the study of post-partum mating by Meyer and Meyer (1944a). Copulation generally occurred between 3 and 6 h and ovulation between 6.5 and 12 h after parturition. Eggs lost their cumulus cells 21 to 22 h after parturition and post-partum eggs in the two-cell stage were found in uterine flushes after 30 to 32 h. Eggs reached the eight-cell stage by 56 h post-partum and blastocysts still possessing zona pellucida were encountered by 74 to 76 h. Eggs were not encountered in uterine flushes at 94 to 97 h indicating the probable occurrence of implantation by this time. Meyer and Meyer (1944a) included photographs of *Sigmodon* sperm and eggs at various stages of development.

Gestation in cotton rats lasts approximately 27 days (Meyer and Meyer, 1944a; Randolph et al., 1977). Both studies found a bloody discharge on about day 10 of pregnancy; the latter study described the vulva as becoming dry and contracted, appearing closed, after day 10.

Litter size in *S. hispidus* ranged from 1 to 15 (Goertz, 1965b; Haines, 1961; Kilgore, 1970; Svihla, 1929). Animals from northern areas of the range had significantly larger litters. Kilgore (1970) found a mean litter size of 3.4 (range, 2 to 5;  $n = 5$ ) in Lubbock Co., Texas (33°35'N) and 7.3 (range, 4 to 15;  $n = 23$ ) in Douglas

Co., Kansas (38°57'N). Seasonal variation in litter size occurred in the northern population with April litters significantly smaller than those of July, September, and October. Bancroft (1969) reported reproduction in Douglas Co., Kansas, from early spring to late fall with a peak in August and a mean litter size of 7.6 (range, 6 to 9;  $n = 9$ ); Fleharty and Choate (1973) reported a mean litter size of 6.8 from Kansas. McClenaghan and Gaines (1978) reported an average litter size of  $9.0 \pm 0.3$  ( $n = 70$ ) with breeding restricted to frost-free seasons in this same area. Prenatal mortality averaged 1.2% from ova loss and 4.0% from resorption of embryos with no pattern attributable to season or population density. Larger litter size was explained as a response to a shortened breeding season and lack of winter reproduction.

Reproductive patterns in the southern part of the species range differed from those in the northern portions. Cameron (1977) reported reproductive peaks in fall and spring and a mean litter size of 4.8 (range, 2 to 7;  $n = 18$ ) for cotton rats in Texas. O'Farrell et al. (1977) reported a bimodal reproductive pattern in South Carolina with a mean litter size of 4.5 (range, 2 to 8;  $n = 139$ ); they found no seasonal difference in litter size. Cameron (1977) and Hall and Dalquest (1963) found cotton rats breed throughout the year in Texas and Veracruz, Mexico, respectively. Bowdre (1971) found no significant relationship between litter size and latitude in the southern portions of the range (from 8°41'N to 29°36'N); litter size ranged from a mean of 2.5 (21°35'N;  $n = 2$ ) to a mean of 6.3 (29°36'N;  $n = 6$ ). Smaller litters were found in moister habitats and larger litters in drier habitats; areas with marked seasonality in temperature or rainfall yielded females with larger litters.

The neonates of *S. hispidus* are well developed at birth. Svihla (1929) measured an average birth weight of 7.23 g (range, 6.5 to 8.0;  $n = 19$ ) and mentioned that they "are able to run about very well, though their eyes are still unopened." Meyer and Meyer (1944a) gave an average birth weight of 6.8 g (range, 3.5 to 8.0;  $n = 184$ ) and noted the average weight of young appeared to vary with the size of the mother and the number in the litter. The majority of the young opened their eyes between 18 and 36 h after birth with two of 197 opening their eyes within 2 h of birth. Three young did not open their eyes until 60 to 65 h after birth. Young are covered by a fine coat of light-colored hair at birth, thickest around the head, with a reddish-brown tint; the skin of the dorsal surfaces of the head, back, and tail is slate grey and the undersurfaces are pink. Young are easily sexed at birth due to the presence of a dark pigmented area in the scrotal region (Meyer and Meyer, 1944a).

Young cotton rats grow rapidly, gaining about 1 or 2 g per day (Fleharty and Choate, 1973; Meyer and Meyer, 1944a; Svihla, 1929). They can be weaned at 10 to 15 days of age with the earlier weaning resulting in retarded growth rates (Keys, 1958; Meyer and Meyer, 1944a; Svihla, 1929).

Jimenez (1971, 1972) found that body growth can be divided into three periods: from 1 to 40 days, length of all body dimensions increases rapidly; from 41 to 100 days, the increase is moderate; and from 101 days onward, there is practically no growth. In contrast, skull growth is divided into two phases: birth to 100 days and 100 days to maximum adult size. Most skull dimensions reach minimum adult size during the first 100-day period. Chipman (1965) followed developmental trends in 316 known-age cotton rats and judged that a combination of body length, molting stage, epiphyseal fusion, skull measurements, and dry-lens weight accurately aged cotton rats up to 6 months. Green and Jameson (1975) found a significant relationship between age and width of the zygomatic arch (a measurement that does not require sacrificing the animal) and classified animals with a width  $\leq 18.5$  mm as juveniles and those  $> 18.5$  mm as adults. Birney et al. (1975) found that body weight as a reliable criterion for age determination only through the first 70 days. Eye lens weight and insoluble lens protein were roughly equal in age predictability up to 130 days when insoluble protein became the best criterion.

Sexual maturation in males can be determined by the presence of sperm in the epididymis. Chipman (1965) found that testes descended and remained in the scrotal sac between 2 weeks and 1 month of age; sperm were found in the epididymis of two out of five 2-month old males and all 3-month old males observed. Meyer and Meyer (1944a) also observed this pattern with some variation. Seasonal variation in both sexes is very important (Ewing et al., 1965; Goertz, 1965b; Haines, 1961). Open vaginas are usually encountered between 30 and 40 days of age (Meyer and Meyer, 1944a) with earliest occurrence at 10 days and others not open by 50 days of age. Chipman (1965) observed a pregnancy with conception occurring at the age of 38 days, impregnation

was by a littermate. Meyer and Meyer (1944a) observed a conception at 40 days of age, also by a littermate. They also observed animals showing signs of estrus at the age of 10 days.

Dunaway and Kaye (1964) reported average female body weights were heavier than those of males during breeding but not non-breeding seasons. Rate of weight gain was influenced by weather. The energy cost of reproduction was a function of litter size (Randolph et al., 1977); much of the energy accumulated during pregnancy was stored as fat and mobilized during lactation. Vaginal estrus was first described by Clark (1936) and then by Meyer and Meyer (1944a). Average cycle lengths were 8 to 9 days, with considerable variation. Proestrus was initiated by a period of marked leucocyte reduction and increased in nucleated epithelial cells which eventually composed the entire vaginal smear. Proestrus lasted from 12 to 21 h with a mean of 14 h. Estrus varied from 21 to 123 h, averaging 46 h, and consisted of great numbers of cornified cells. Metestrus lasted from 9 to 21 h, averaging 14 h, and first consisted of nucleated epithelial cells followed shortly by leucocytes. Diestrus varied from 42 to 156 h, averaging 116 h. In young females, a mass of white tissue protruded from the vagina which, when removed, formed an internal cast of the vagina. Chipman (1967) found that the cast consisted mainly of well-nucleated epithelial cells and suggested that all female cotton rats produce this cast upon reaching puberty. Meyer and Meyer (1944b) found that environmental disturbances (changes in light, noise) affected cycles of laboratory-confined cotton rats.

**ECOLOGY.** Trap biases which must be corrected to accurately describe parameters of *S. hispidus* populations have been reported. Wiegert and Mayenschein (1966) reported differential trappability affected density estimates. Social structure also influenced trapping success (Joule and Cameron, 1974; Summerlin and Wolfe, 1973); dominant animals were more prone to trapping than subordinates. This was caused by a neophobic response by subordinates, avoidance of traps with conspecific scent, or subordinate animals exhibiting less exploratory activity (Summerlin and Wolfe, 1971). Cameron (1977) employed temporary removal trapping to alleviate these biases; Hall (1974) suggested a correction factor based on age.

*Sigmodon hispidus* exhibited bimodal population fluctuations annually in the southern portion of its range (Texas: Cameron, 1977; Raun and Wilks, 1964; Georgia: Odum, 1955; Mexico: Petersen, 1973; and Florida: Layne, 1974). Maximum densities occurred during autumn and there were small spring peaks (Texas 14/ha, Georgia 69/ha, Mexico 51/ha, Florida 25/ha); minimum densities occurred during winter or summer (Texas 0.5/ha, Georgia 8/ha, Mexico 25/ha, Florida 10/ha). Density patterns were not bimodal in northern areas of the species range. Fleharty et al. (1972) reported an autumn peak (maximum density 20/ha) and a spring low (minimum density 0.02/ha) in Kansas. McClenaghan and Gaines (1978) reported similar phenology in eastern Kansas with a minor peak in early summer.

Cameron (1977) reported expectation of further life (average duration of residence for all individuals) for *S. hispidus* males as 1.96 months and females as 2.2 months. The longest period of residence for both sexes was 9 to 10 months. Petersen (1973) computed the mean expectation of further life for *S. hispidus* from Durango, Mexico, as 14.23 weeks.

*S. hispidus* is captured most frequently in grass-dominated habitats (Fleharty and Mares, 1973; Goertz, 1964; Kaufman and Fleharty, 1974; Odum, 1955). Goertz and Long (1973) reported *S. hispidus* in perennial grasses and forbs near edges of ponds. Grass height and density are important components of cotton rat habitat (Goertz, 1964; Kaufman and Fleharty, 1974). Cameron (1977) captured *S. hispidus* in areas of mixed grass and brush in coastal Texas. McClenaghan and Gaines (1978) trapped *S. hispidus* from old fields of cultivated brome in early stages of secondary succession.

Fleharty and Olson (1969) determined that the hispid cotton rat primarily ate grasses. They noted distinct dietary preferences and selection of food items from a wide environmental array. Kincaid (1975) and Gaertner (1968) showed seasonal utilization of insects by cotton rats.

Layne (1974) reported average home ranges for adults (0.35 ha), subadults (0.22 ha), and juveniles (0.35 ha). Fleharty and Mares (1973) computed a home range of 0.39 ha for males and 0.22 ha for females. Male *S. hispidus* have larger home ranges than females (Cameron et al., 1979c; Erickson, 1949; Fleharty and Mares, 1973; Goertz, 1964; Layne, 1974), but females have exclusive home ranges (Cameron et al., 1979c; Fleharty and Mares,

1973; Layne, 1974). Adults have larger home ranges than young adults (Cameron et al., 1979c; Layne, 1974).

Seasonal differences in movements appeared to be influenced by reproductive stage or availability of cover (Bigler and Jenkins, 1975; Briese and Smith, 1974; Fleharty and Mares, 1973; Layne, 1974; Smith and Vrieze, 1979). Cameron et al. (1979c) reported an average daily movement of about 13 m (combined sex and age); males averaged 17 m and females averaged 6.6 m. Bigler and Jenkins (1975) reported females moved slightly farther than males in Florida although they felt this may reflect grid size. Cameron et al. (1979c) determined that reproductive males moved farther than nonreproductive males; there was no such difference among females.

Dispersal of *S. hispidus* was positively correlated with density (Joule and Cameron, 1975); sex ratio and age structure of dispersers were similar to those of the source population. Lidicker (1975) characterized this pattern as pre-saturation dispersal.

Ramsey and Briese (1971) and Bigler et al. (1977) showed that intraspecific interactions affected density and movement patterns of *S. hispidus*. Aliens introduced into an experimental population were restricted to less preferred habitats, probably through behavioral interactions; this restriction decreased their survival (Bigler et al., 1977). Roads are effective barriers to *S. hispidus* movement (Joule and Cameron, 1974; Kozel and Fleharty, 1979).

Interspecific interactions have been reported between *S. hispidus* and several other rodent species. Raun and Wilks (1964) suggested competition with *Baiomys taylori* for favorable habitat in south Texas; cotton rats probably displaced pygmy mice into marginal areas through aggression. Petersen (1973) suggested competition between *S. hispidus* and *S. fulviventor* in Mexico because *fulviventor* was numerically and interactively dominant. Subsequent laboratory trials confirmed negative behavioral interactions (Petersen and Helland, 1978); *S. fulviventor* was more aggressive whereas *S. hispidus* avoided encounters. Over half of the encounters resulted in neutral or amicable behavior, suggesting that avoidance or peaceful coexistence were more important than aggression in the field. Baker (1971) suggested that *Sigmodon* may behaviorally exclude *Microtus*. Terman (1974) noted in the laboratory that *S. hispidus* excluded *Microtus ochrogaster* from confined areas except where cover was dense. Terman suggested that the frequency of contact was responsible for negative interactions. The concealing effect of thicker cover explained an increase in numbers of *M. ochrogaster* because of a decreasing number of interspecific contacts. Increases in density of *S. hispidus* caused decreases in density of *M. ochrogaster* because of increasing frequency of contact. Glass and Slade (1980) found *S. hispidus* negatively affected *M. ochrogaster* populations during the cotton rats' reproductive season. Cameron (1977) suggested behavioral (interference competition) interaction between *S. hispidus* and *Reithrodontomys fulvescens*.

Korschgen and Stuart (1972) documented a reliance by some avian predators on cotton rats in Missouri; deviations in the general prey usage pattern over a 20-year period were due to periodic concentrations on cotton rats (during years of high densities of cotton rats). Similarly, cotton rats were the primary food of barn owls in Texas (Raun, 1960). These authors suggested that utilization of cotton rats by avian predators resulted in decreased use of other prey. Schnell (1968) noted that avian predators were critically important in regulating densities of cotton rats in enclosures and that this was a density-dependent process. Avian predators reduced numbers of cotton rats to the carrying capacity whereas mammalian predators did not exert a density-dependent effect and were considered incidental (Weigert, 1972).

Roberts and Wolfe (1974) related social rank of cotton rats to their susceptibility to avian and mammalian predation. A mammalian predator (house cat) selected dominant animals more frequently whereas an avian predator (red-tailed hawk) selected subordinate animals. These differences were attributed to the predator's hunting strategy and the differential activity of dominants and subordinates.

Prairie cotton rats in western Kansas ingest less than 1% of the annual net primary production (Fleharty and Choate, 1973); 98% of this energy was utilized for maintenance costs. *S. hispidus* removed 0.4% of the annual primary production by clipping (Petryszyn and Fleharty, 1972). Seasonal variation in the energy budget reflected physiological adjustments to environmental variation (e.g., fat deposition, breeding).

Elemental composition varied significantly with age, sex and season in cotton rats (Gentry et al., 1975). Estimates of consumption, egestion, and assimilation of elements were used to

evaluate the influence of small mammals in nutrient flow in an ecosystem (Gentry et al., 1975; Kaufman et al., 1976). Two elements may be limiting to *S. hispidus*: Ca in the fall and P in the spring and fall.

*Sigmodon hispidus* exhibited a high resistance to radiation (Pelton and Provost, 1969). Survival of irradiated individuals was not different from that of controls in the laboratory or in a field enclosure. There was no change in radiosensitivity during the breeding season. Barrett (1969) and Pomeroy and Barrett (1975) determined that long-term effects of a pesticide (Sevin) inhibited breeding, with a concomitant decrease in population density. This latter effect resulted in an increase in population size of a competing species (*Mus musculus*).

*Sigmodon hispidus* supports a variety of internal and external parasites. Kinsella (1974), Mollhagan (1978), and Coggins (1972) listed helminth parasites (including trematode, cestode, and nematode species) from the digestive tract and pleural cavity. Host habitat and availability of intermediate hosts influenced the magnitude of the parasite load. Comparison between Texas and Florida suggested that aridity is partly responsible for the reduction of the helminth fauna in west Texas. Graves et al. (1974) noted that *S. hispidus* harbored the greatest number of flea species (15) in a study in southeastern New Mexico. The predominant flea (*Polygenis gwyni*) was prevalent during summer, whereas the next most abundant flea (*Eptedia wenwanni*, collected only from *S. hispidus*) was most abundant in fall and winter.

*Sigmodon hispidus* is a reservoir for a number of human diseases, including rabies, Chagas' disease, and Venezuelan equine encephalomyelitis (Bigler and Jenkins, 1975; World Health Organization, 1974).

**BEHAVIOR.** Cotton rats are active at all hours of the day and night, they exhibit a labile activity pattern influenced by biotic and/or abiotic factors (Calhoun, 1945). Cameron et al. (1979b) found activity peaks in southeast Texas field populations at 1900 and 0900 h with minimal activity from 2300 to 0500 h (a crepuscular pattern). Kilduff and Dube (1979) studied activity patterns in the laboratory. Activity began just after dark and declined until dawn under a 10L:14D photoperiod while there was a noticeable peak around dawn under 14L:10D. They concluded that *Sigmodon hispidus* is probably a nocturnal animal with a bimodal activity pattern and a labile pattern during dark hours. Stevenson et al. (1968) also found *Sigmodon* to be primarily nocturnal.

Esher et al. (1978) investigated the swimming behavior of hispid cotton rats. While swimming, cotton rats used mainly the hind feet for propulsion while holding the front feet near the body, never swimming under water. Fur of cotton rats was not as water repellent as that of the more aquatic rice rat (*Oryzomys palustris*), becoming wet almost immediately upon immersion and giving the animal a tendency to sink. Still, they concluded that narrow bodies of water do not form a significant barrier to cotton rats.

The building and utilization of nests by hispid cotton rats has been described (Baar et al., 1974; Dawson and Lang, 1973; Halloran, 1942; Hastings, 1957; Shump, 1978). Surface and burrow nests were made of woven grass and ranged from cup-shaped to hollow ball-shaped structures with a single entrance. Shump (1978) found that nests constructed by rats from Kansas were woven more tightly, significantly larger, and twice as insulative as Florida nests; he suggested that behavioral plasticity in nest-building was responsive to climatic conditions. Orientation of nest openings was most often toward the southeast to decrease cooling of the nest by cold northwest winds and allow penetration of sunlight on cold winter mornings (Shump, 1978). Shump and Christian (1978) analyzed the relation between soil type, burrowing activity, and nest type.

Harriman (1977) demonstrated that hispid cotton rats selected available food items and combined them into a nutritious diet. Cotton rats fed a diet consisting of types and amounts of foods selected by other cotton rats exhibited significantly greater weight gains than animals fed laboratory chow. In laboratory tests, Dewsbury (1970) and Lanier et al. (1974) found no evidence of food hoarding by cotton rats.

Copulation is characterized by the absence of a lock, a cessation of thrusting during intromission, multiple intromissions preceding ejaculation, and multiple ejaculations (Dewsbury, 1972, 1975). Post-ejaculatory copulation with no sperm transfer was observed.

Female cotton rats make exceptionally fine mothers (Meyer and Meyer, 1944a). During their study, no young were killed by their mothers even after both mothers and young were handled by the investigators. Females also made good foster mothers even

for young albino laboratory rats. Layne (1974) noticed that on four separate occasions, while juveniles or subadults were being handled in the field, an adult approached to within a few feet in response to squeaking by the young.

Wright and Pagels (1977) determined that hispid cotton rats climb in above-ground vegetation. In a trapping effort consisting of 279 trap-nights, five cotton rats were captured at a mean height of 202.2 mm (160.0–276.0) in vines of Japanese honeysuckle (*Lonicera japonica*).

Debusk and Kennerly (1975) found that homing in the cotton rat occurred from distances of 100 m to 1,500 m with success decreasing with distance. Of 266 rats displaced, 112 successfully returned to their home area with the highest proportion being those displaced up to 300 m. They concluded that cotton rats released up to 300 m away from their home areas probably were still on familiar ground but either navigation or random wandering could have been involved in instances of longer homing.

Liu (1971) described *S. hispidus* "as a solitary species, since its only prolonged social contact is between male and female, and even this contact depends upon the female's reproductive status." In the laboratory, male-female pair bonds are formed and are characterized by frequent physical contact (sleeping, huddling, and mutual grooming; huddling was also reported by Dunaway and Kaye, 1961). Males are dominant over females in these pairs.

Agonistic behavior is an important factor influencing social organization. Disorganized groups of *S. hispidus* exhibited significantly more agonistic encounters than organized groups and showed significant decreases in agonistic encounters after 24 h of interaction (Wolfe and Summerlin, 1968). They suggested that social behavior of hispid cotton rats in nature is characterized by a relative dominance system (Bronson, 1964). Summerlin (1968) described threat and appeasement postures for this species. Development of behavioral traits in young cotton rats is very rapid. Liu (1971) described the onset of adult characteristics and found that young could survive without maternal assistance at an age of five days.

**GENETICS.** The most widely distributed karyotype of *Sigmodon hispidus* consists of a 2n number of 52 and a FN of 52 and occurs from the eastern United States (Zimmerman, 1970) to Venezuela (Kiblicky, 1969). The karyotype consists of 48 acrocentric and two very small metacentric autosomes. Sex determination is of the XX/XY type; the X chromosome is usually large and subtelocentric and the Y chromosome varies from medium-small metacentric to submetacentric (Zimmerman, 1970). Zimmerman (1970) described chromosomal polymorphisms which included Robertsonian variation and pericentric inversions in autosomes and also polymorphism and geographic variation in the sex chromosomes. Chromosome numbers ranged from 2n = 51 (probably centric fusion) to 2n = 56 (addition of supernumerary chromosomes). Comparative male meiosis in seven species of cotton rats was described by Zimmerman (1974). Chromosomal and serological evidence suggested that a form similar to *S. hispidus* could have been the ancestor to all the species in the genus (Dalby and Lillevik, 1969; Zimmerman, 1970).

Johnson et al. (1972) investigated genetic variation among and within cotton rat populations by electrophoresis of 23 enzymatic and non-enzymatic proteins. Average heterozygosity was 2.14% (1.77 to 2.67%) with most of the heterozygosity contributed by two loci, PGM-3 and 6PGD. Average genetic similarity across populations,  $\bar{S} = 0.9834$  (0.976 to 0.998), indicated a high degree of geographic uniformity. However, Dalby and Lillevik (1969) assigned individuals to geographic regions based on five different transferrin patterns. McClenaghan (1980) and McClenaghan and Gaines (In press) reported higher mean levels of heterozygosity per individual (5.54%, Mexico and 4.04%, Kansas); marginal (Kansas) populations of *S. hispidus* exhibited higher levels of genetic variability than populations found centrally (Mexico) within the species distribution. McClenaghan (1980) found lower levels of heterozygosity (2.23 to 2.85%) at three localities within the isolated *S. hispidus* population in the Colorado River Valley of California and Arizona (see Fig. 3). Only two of 23 loci were polymorphic, the lower levels of variability presumably due to the founder effect. This isolated population is very similar genetically to cotton rats from the continuous range, possibly due to the adaptiveness of the "cotton rat ecomorph" (Zimmerman, 1970).

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#### LITERATURE CITED

- Allen, G. M. 1920. An insular race of cotton rat from the Florida Keys. *J. Mamm.*, 1:235–236.

- Allen, J. A. 1897. Additional notes on Costa Rican mammals, with descriptions of new species. *Bull. Amer. Mus. Nat. Hist.*, 9:31–44.
- 1903. List of mammals collected by Mr. J. H. Batty in New Mexico and Durango, with descriptions of new species and subspecies. *Bull. Amer. Mus. Nat. Hist.*, 19:587–612.
- 1904. Mammals from southern Mexico and Central and South America. *Bull. Amer. Mus. Nat. Hist.*, 20:29–80.
- 1908. Mammals from Nicaragua. *Bull. Amer. Mus. Nat. Hist.*, 24:647–670.
- Audubon, J. J., and J. Bachman. 1853. The viviparous quadrupeds of North America. V. G. Audubon, New York, 3:1–257.
- Baar, S. L., E. D. Fleharty, and M. F. Artman. 1974. Utilization of deep burrows and nests by cotton rats in west-central Kansas. *Southwestern Nat.*, 19:440–444.
- Bailey, V. 1902. Synopsis of the North American species of *Sigmodon*. *Proc. Biol. Soc. Washington*, 15:101–116.
- Baird, S. F. 1855. Characteristics of some new species of North American mammalia collected chiefly in connection with the United States Surveys of a Railroad Route to the Pacific. *Proc. Acad. Nat. Sci., Philadelphia*, 7:333.
- Baker, C. E. 1974. Measurement of small mammal metabolism by infrared gas analysis. *J. Mamm.*, 55:664–670.
- Baker, C. E., and P. B. Dunaway. 1969. Retention of  $^{134}\text{Cs}$  as an index to metabolism in the cotton rat (*Sigmodon hispidus*). *Health Physics*, 16:227–230.
- Baker, R. H. 1969. Cotton rats of the *Sigmodon fulviventer* group. Pp. 177–232, *In Contributions in mammalogy* (J. K. Jones, Jr., ed.). *Misc. Publ. Mus. Nat. Hist., Univ. Kansas*, 51:1–428.
- 1971. Nutritional strategies of myomorph rodents in North American grasslands. *J. Mamm.*, 52:800–805.
- Baker, R. H., and K. A. Shump, Jr. 1978. *Sigmodon fulviventer*. *Mamm. Species*, 94:1–4.
- Bancroft, W. L. 1969. Notes on reproduction of three rodents of Douglas County, Kansas. *Trans. Kansas Acad. Sci.*, 72:67–69.
- Bangs, O. 1898. The land mammals of peninsular Florida and the coast region of Georgia. *Proc. Boston Soc. Nat. Hist.*, 28:192.
- 1903. Birds and mammals from Honduras. *Bull. Mus. Comp. Zool.*, 39:139–159.
- Barrett, C. W. 1969. The effects of an acute insecticide stress on a semi-enclosed grassland ecosystem. *Ecology*, 49:1019–1035.
- Bigler, W. J., and J. H. Jenkins. 1975. Population characteristics of *Peromyscus gossypinus* and *Sigmodon hispidus* in tropical hammocks of south Florida. *J. Mamm.*, 56:633–644.
- Bigler, W. J., et al. 1977. Response of a cotton rat population to increased density. *Amer. Midland Nat.*, 97:10–17.
- Birney, E. C., R. Jenness, and D. D. Baird. 1975. Eye lens proteins as criteria of age in cotton rats. *J. Wildl. Mgmt.*, 39:718–728.
- Blair, W. F. 1958. Distributional patterns of vertebrates in the southern United States in relation to past and present environments. Pp. 433–468, *In Zoogeography* (C. L. Hubbs, ed.), American Association for the Advancement of Science, 51:1–509.
- Blank, O. E. 1950. A histological study of the alimentary canal of the cotton rat, *Sigmodon hispidus*. *Anat. Rec.*, 108:421–439.
- Bowdre, L. P. 1971. Litter size in *Sigmodon hispidus*. *Southwestern Nat.*, 16:126–128.
- Bowers, J. R. 1971. Resting metabolic rate in the cotton rat *Sigmodon*. *Physiol. Zool.*, 44:137–148.
- Briese, L. A., and M. H. Smith. 1974. Seasonal abundance and movement of nine species of small mammals. *J. Mamm.*, 55:615–629.
- Bronson, F. H. 1964. Agonistic behavior in woodchucks. *Anim. Behav.*, 12:470–478.
- Calhoun, J. B. 1945. Diel activity rhythms of the rodents, *Microtus ochrogaster* and *Sigmodon hispidus hispidus*. *Ecology*, 26:251–273.
- Cameron, G. N. 1977. Experimental species removal: demographic responses by *Sigmodon hispidus* and *Reithrodontomys fulvescens*. *J. Mamm.*, 58:488–506.
- Cameron, G. N., E. D. Fleharty, and H. A. Watts. 1979a. Geographic variation in the energy content of cotton rats. *J. Mamm.*, 60:817–820.
- Cameron, G. N., W. B. Kincaid, and B. A. Carnes. 1979b. Experimental species removal: temporal activity



- patterns of *Sigmodon hispidus* and *Reithrodontomys fulvescens*. J. Mamm., 60:195-197.
- Cameron, G. N., et al. 1979c. Daily movement patterns of *Sigmodon hispidus*. Southwestern Nat., 24:63-70.
- Carey, A. B. 1978. Distributional records for the prairie vole and the hispid cotton rat in Colorado. J. Mamm., 59:624.
- Chapman, F. M. 1889. Description of a new subspecies of the genus *Sigmodon* from southern Florida. Bull. Amer. Mus. Nat. Hist., 2:118.
- Chipman, R. K. 1965. Age determination of the cotton rat (*Sigmodon hispidus*). Tulane Studies Zool., 12:19-38.
- 1967. Shedding of the vaginal epithelium of the cotton rat. J. Mamm., 48:308-310.
- Clark, A. R., and C. W. Jungeblut. 1940. Vitamin C metabolism in eastern cotton rats. J. Nutrition, 20:427-432.
- Clark, D. O. 1972. The extending of cotton rat range in California—their life history and control. Pp. 7-14, in Proceedings of the 5th Vertebrate Pest Conference (R. E. Marsh, ed.), California Vertebrate Pest Committee, Davis, 204 pp.
- Clark, F. H. 1936. The estrous cycle of the cotton rat, *Sigmodon hispidus*. Contrib. Lab. Vert. Gen., Univ. Michigan, 2:1-2.
- Coggins, J. R. 1972. Internal parasites of the cotton rat *Sigmodon hispidus* (Say). J. Elisha Mitchell Sci. Soc., 88:205-206.
- Cushing, J. E., Jr. 1945. Quaternary rodents and lagomorphs of San Josecito Cave, Nuevo Leon, Mexico. J. Mamm., 26:182-185.
- Dalby, P. L., and H. A. Lillevik. 1969. Taxonomic analysis of electrophoretic blood serum patterns in the cotton rat, *Sigmodon*. Publ. Mus. Michigan State Univ., Biol. Ser., 4:65-101.
- Dalquest, W. W. 1953. Mammals of the Mexican state of San Luis Potosí. Louisiana State Univ. Studies, Biol. Ser., 1:1-229.
- Danforth, C. H., and V. Schwentker. 1949. Snowball: a repeated mutation in the cotton rat. J. Heredity, Wash., 40:252-256.
- Dawson, G. A., and J. W. Lang. 1973. The functional significance of nest building by a neotropical rodent (*Sigmodon hispidus*). Amer. Midland Nat., 89:503-509.
- Debusk, J., and T. E. Kennerly, Jr. 1975. Homing in the cotton rat, *Sigmodon hispidus* Say and Ord. Amer. Midland Nat., 93:149-157.
- Dewsbury, D. A. 1970. Food hoarding in rice rats and cotton rats. Psychol. Rep., 26:174.
- 1972. Copulatory behavior of cotton rats (*Sigmodon hispidus*). Z. Tierpsychol., 30:477-487.
- 1975. Diversity and adaptation in rodent copulatory behavior. Science, 190:947-954.
- Dixon, J. 1922. Rodents and reclamation in the Imperial Valley. J. Mamm., 3:136-146.
- Dunaway, P. B., and S. V. Kaye. 1961. Cotton rat mortality during severe winter. J. Mamm., 42:265-268.
- 1964. Weights of cotton rats in relation to season, breeding, and environmental radioactive contamination. Amer. Midland Nat., 71:141-155.
- Easterla, D. A. 1968. Hispid cotton rat north of the Missouri River. Southwestern Nat., 13:364-365.
- Elliot, D. G. 1903. A list of mammals collected by Edmund Heller in the San Pedro Martin and Hanson Laguna mountains and the accompanying coast regions of Lower California with descriptions of apparently new species. Field Columbian Mus., Publ. 79, Zool. Ser., 3:199-232.
- Erickson, A. B. 1949. Summer populations and movements of the cotton rat and other rodents on the Savannah River refuge. J. Mamm., 30:133-140.
- Esher, R. J., J. L. Wolfe, and J. N. Layne. 1978. Swimming behavior of rice rats (*Oryzomys palustris*) and cotton rats (*Sigmodon hispidus*). J. Mamm., 59:551-558.
- Ewing, L. L., P. M. Green, and A. M. Stebler. 1965. Metabolic and biochemical changes in testis of cotton rat (*Sigmodon hispidus*) during breeding cycle. Proc. Soc. Exp. Biol. Med., 118:911-913.
- Farney, J. P. 1975. Natural history and northward dispersal of the hispid cotton rat in Nebraska. Platte Valley Review, 3:11-16.
- Fleharty, E. D., and J. R. Choate. 1973. Bioenergetic strategies of the cotton rat, *Sigmodon hispidus*. J. Mamm., 54:680-692.
- Fleharty, E. D., J. R. Choate, and M. A. Mares. 1972. Fluctuations in population density of the hispid cotton rat: factors influencing a "crash." Bull. Southern California Acad. Sci., 71:132-138.
- Fleharty, E. D., M. E. Krause, and D. P. Stinnett. 1973. Body composition, energy content and lipid cycles of four species of rodents. J. Mamm., 54:426-438.
- Fleharty, E. D., and M. A. Mares. 1973. Habitat preference and spatial relations of *Sigmodon hispidus* on a remnant prairie in west-central Kansas. Southwestern Nat., 18:21-29.
- Fleharty, E. D., and L. E. Olson. 1969. Summer food habits of *Microtus ochrogaster* and *Sigmodon hispidus*. J. Mamm., 50:475-486.
- Gaertner, R. A. 1968. Seasonal variations in the energy budgets of the harvest mouse, *Reithrodontomys fulvescens*, and the cotton rat, *Sigmodon hispidus*. Unpubl. Ph.D. dissert., Univ. Arkansas, Fayetteville, 149 pp.
- Gardner, M. C. 1946. A new cotton rat from Virginia. Proc. Biol. Soc. Washington, 59:137.
- 1948a. An undescribed eastern cotton rat. Proc. Biol. Soc. Washington, 61:97-98.
- 1948b. Albino cotton rats. J. Mamm., 29:185.
- Gennaro, A. L. 1968. Color variation of the hispid cotton rat in New Mexico. J. Mamm., 49:317-318.
- Genoways, H. H., and D. A. Schlitter. 1967. Northward dispersal of the hispid cotton rat in Nebraska and Missouri. Trans. Kansas Acad. Sci., 69:356-357.
- Gentry, J. B., et al. 1975. Elemental flow and standing crops for small mammal populations. Pp. 205-222, in Small mammals: their productivity and population dynamics (F. B. Golley, K. Petrusewicz, and L. Ryszkowski, eds.). Cambridge Univ. Press, Cambridge, 451 pp.
- Gilmore, R. M. 1947. Report on a collection of mammal bones from archeologic cave-sites in Coahuila, Mexico. J. Mamm., 28:147-165.
- Glass, G. E., and N. A. Slade. 1980. The effect of *Sigmodon hispidus* on spatial and temporal activity of *Microtus ochrogaster*: evidence for competition. Ecology, 61:358-370.
- Goertz, J. W. 1964. The influence of habitat quality upon density of cotton rat populations. Ecol. Monogr., 34:359-381.
- 1965a. Adrenal and spleen weights in cotton rats in relation to age, sex and season. J. Mamm., 46:699-700.
- 1965b. Reproductive variation in cotton rats. Amer. Midland Nat., 74:329-340.
- Goertz, J. W., and R. C. Long. 1973. Habitats of five species of rat in Louisiana. Amer. Midland Nat., 90:460-465.
- Goldman, E. A. 1918. Five new mammals from Arizona and Colorado. Proc. Biol. Soc. Washington, 31:21-25.
- Goldman, E. A., and M. C. Gardner. 1947. Two new cotton rats. J. Mamm., 28:57-59.
- Golley, F. B. 1969. Caloric value of cotton rats (*Sigmodon hispidus* Say and Ord). Pp. 143-147, in Energy flow through small mammal populations (K. Petrusewicz and L. Ryszkowski, eds.). Polish Scientific Publ., Warsaw, 298 pp.
- Goodwin, G. G. 1932. Two new mammals from Guatemala. Amer. Mus. Novitates, 528:1-2.
- Graves, G. N., et al. 1974. Sylvatic plague studies in southeast New Mexico. I. Flea-host relationships from six years' study. J. Med. Entomol., 11:488-498.
- Green, A., and D. L. Jameson. 1975. An evaluation of the zygomatic arch for separating juvenile from adult cotton rats (*Sigmodon hispidus*). J. Mamm., 56:534-535.
- Haines, H. 1961. Seasonal changes in the reproductive organs of the cotton rat. Texas J. Sci., 13:219-230.
- Hall, D. O. 1974. Reducing a maturity bias in estimating populations: an example with cotton rats (*Sigmodon hispidus*). J. Mamm., 55:477-480.
- Hall, E. R. 1951. Mammals obtained by Dr. Curt von Wedel from the Barrier Beach of Tamaulipas, Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 5:33-47.
- Hall, E. R., and W. W. Dalquest. 1963. The mammals of Veracruz. Univ. Kansas Publ., Mus. Nat. Hist., 14:165-362.
- Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. The Ronald Press Co., New York, 2:547-1084 + 79.
- Halloran, A. F. 1942. A surface nest and the young of *Sigmodon* in Texas. J. Mamm., 23:91.
- Hamilton, W. J., Jr. 1946. A study of the baculum in some North American Microtinae. J. Mamm., 27:378-387.
- Harriman, A. E. 1977. Self-selection of diet by hispid cotton rats (*Sigmodon hispidus*). Psychol. Rep., 41:343-346.
- Hastings, C. E. 1957. Nest of the cotton rat. J. Mamm., 38:416.
- Hershkovitz, P. 1955. South American marsh rats, genus *Hol-*

- ochilus* with a summary of sigmodont rodents. Fieldiana-Zool., Chicago Mus. Nat. Hist., 37:639-673.
- 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana-Zool., Chicago Mus. Nat. Hist., 46:1-524.
- 1966. Mice, land bridges and Latin American faunal interchange. Pp. 725-751, in *Ectoparasites of Panama* (R. L. Wenzel and V. J. Tipton, eds.). Field Mus. Nat. Hist., Chicago, 861 pp.
- Hibbard, C. W. 1960. An interpretation of Pliocene and Pleistocene climates in North America. 62nd Ann. Rep., Michigan Acad. Sci., Arts, Letters, 1959-60, pp. 5-30.
- Hooper, E. T. 1949. Faunal relationships of recent North American rodents. Misc. Publ. Mus. Zool., Univ. Michigan, 72:1-28.
- 1962. The glans penis in *Sigmodon*, *Sigmomys*, and *Reithrodontomys* (Rodentia, Cricetinae). Occas. Papers Mus. Zool., Univ. Michigan, 625:1-11.
- Howell, A. H. 1943. Two new cotton rats from Florida. Proc. Biol. Soc. Washington, 56:73-76.
- Jimenez, J. J. 1971. Comparative post-natal growth in five species of the genus *Sigmodon*. I. External morphological character relationships. Rev. Biol. Trop., 19:133-148.
- 1972. Comparative post-natal growth in five species of the genus *Sigmodon*. II. Cranial character relationships. Rev. Biol. Trop., 20:5-27.
- Johnson, W. E., et al. 1972. XIV. Biochemical genetics of sibling species of the cotton rat (*Sigmodon*). Studies in Genetics VII. Univ. Texas Publ., 7213:297-305.
- Jones, J. K., Jr. 1960. The hispid cotton rat in Nebraska. J. Mamm., 41:132.
- Joule, J., and G. N. Cameron. 1974. Field estimation of demographic parameters: influence of *Sigmodon hispidus* population structure. J. Mamm., 55:309-318.
- 1975. Species removal studies. I. Dispersal strategies of sympatric *Sigmodon hispidus* and *Reithrodontomys fulvescens* populations. J. Mamm., 56:378-396.
- Kaufman, D. W., and E. D. Fleharty. 1974. Habitat selection by nine species of rodents in north-central Kansas. Southwestern Nat., 18:443-452.
- Kaufman, D. W., et al. 1976. Digestibility and elemental assimilation in cotton rats. Acta Theriol., 21:147-156.
- Keys, C. E. 1958. The rate of development of *Sigmodon hispidus* as compared with some other rodents. Trans. Kentucky Acad. Sci., 19:25-27.
- Kiblicky, P. 1969. The chromosomes of the hispid cotton rat, *Sigmodon hispidus*, from two localities in Venezuela. J. Mamm., 50:810-811.
- Kilduff, T. S., and M. G. Dube. 1979. The effects of seasonal photoperiods on activity of cotton rats and rice rats. J. Mamm., 60:169-176.
- Kilgore, D. L., Jr. 1970. The effect of northward dispersal on growth rate of young, size of young at birth, and litter size in *Sigmodon hispidus*. Amer. Midland Nat., 84:510-520.
- Kincaid, W. B. 1975. Species removal studies: III. Niche dynamics and competition in *Sigmodon hispidus* and *Reithrodontomys fulvescens*. Unpubl. M.S. thesis, Univ. Houston, Houston, Texas, 53 pp.
- Kinsella, J. M. 1974. Comparison of helminth parasites of the cotton rat, *Sigmodon hispidus*, from several habitats in Florida. Amer. Mus. Novitates, 2540:1-12.
- Kirksey, E. R., J. F. Pagels, and C. R. Blem. 1975. The role of the tail in temperature regulation of the cotton rat, *Sigmodon hispidus*. Comp. Biochem. Physiol., 52A:707-711.
- Korschgen, L. J., and H. B. Stuart. 1972. Twenty years of avian predator-small mammal relationships in Missouri. J. Wildl. Mgmt., 36:269-282.
- Kozel, R. M., and E. D. Fleharty. 1979. Movements of rodents across roads. Southwestern Nat., 24:239-248.
- Lanier, D. L., D. Q. Estep, and D. A. Dewsbury. 1974. Food hoarding in murid rodents. Behav. Biol., 11:177-187.
- Layne, J. N. 1974. Ecology of small mammals in flatwoods habitat in north-central Florida, with emphasis on the cotton rat (*Sigmodon hispidus*). Amer. Mus. Novitates, 2544:1-48.
- Lidicker, W. Z., Jr. 1975. The role of dispersal in the demography of small mammals. Pp. 103-128, in *Small mammals: their productivity and population dynamics* (F. B. Golley, K. Petruszewicz, and L. Ryszkowski, eds.). Cambridge Univ. Press, Cambridge, 451 pp.
- Liu, E. S. 1971. The ethology of the cotton rat, *Sigmodon hispidus*. Unpubl. M.S. thesis, Univ. Florida, Gainesville, 85 pp.
- Martin, R. A. 1979. Fossil history of the rodent genus *Sigmodon*. Evol. Monogr., 2:1-36.
- McClenaghan, L. R., Jr. 1977. Genic variability, morphological variation and reproduction in central and marginal populations of *Sigmodon hispidus*. Unpubl. Ph.D. dissert., Univ. Kansas, Lawrence, 136 pp.
- 1980. The genetic structure of an isolated population of *Sigmodon hispidus* from the lower Colorado River Valley. J. Mamm., 61:304-307.
- McClenaghan, L. R., Jr., and M. S. Gaines. 1978. Reproduction in marginal populations of the hispid cotton rat (*Sigmodon hispidus*) in northeastern Kansas. Occas. Papers Mus. Nat. Hist., Univ. Kansas, 74:1-16.
- 1981. Genic and morphological variation in central and marginal populations of *Sigmodon hispidus*. Pp. 202-213, in *Mammalian population genetics* (M. H. Smith and J. Joule, eds.), Univ. Georgia Press, Athens, 380 pp.
- McClure, P. A., and J. C. Randolph. 1980. Relative allocation of energy to growth and development of homeothermy in the eastern wood rat (*Neotoma floridana*) and hispid cotton rat (*Sigmodon hispidus*). Ecol. Monogr., 50:199-219.
- McIntire, J. M., B. S. Schweigert, and C. A. Elvehjem. 1944. The nutrition of the cotton rat (*Sigmodon hispidus hispidus*). J. Nutrition, 27:1-9.
- Mearns, E. A. 1897. Preliminary diagnoses of new mammals of the genera *Sciurus*, *Castor*, *Neotoma* and *Sigmodon*, from the Mexican border of the United States (preprint of Proc. U.S. Natl. Mus., 20:504, 1898).
- Meyer, B. J., and R. K. Meyer. 1944a. Growth and reproduction of the cotton rat, *Sigmodon hispidus hispidus*, under laboratory conditions. J. Mamm., 25:107-129.
- 1944b. The effect of light on maturation and the estrous cycle of the cotton rat, *Sigmodon hispidus hispidus*. Endocrinology, 34:276-281.
- Mohlhenrich, J. S. 1961. Distribution and ecology of the hispid and least cotton rats in New Mexico. J. Mamm., 42:13-24.
- Mollhagan, T. 1978. Habitat influence on helminth parasitism of the cotton rat in western Texas, with remarks on some of the parasites. Southwestern Nat., 23:401-408.
- Odum, E. P. 1955. An eleven year history of a *Sigmodon* population. J. Mamm., 36:368-378.
- O'Farrell, M. J., et al. 1977. Reproductive patterns of some small mammals in South Carolina. Florida Scientist, 40:76-84.
- Pagels, J. F., and R. G. Adleman. 1971. A note on the cotton rat in central Virginia. Virginia J. Sci., 22:195.
- Pelton, M. R., and E. E. Provost. 1969. Effects of radiation on survival of wild cotton rats (*Sigmodon hispidus*) in enclosed areas of natural habitat. Pp. 39-45, in Proc. Second Nat. Symp. on Radioecology (D. J. Nelson and F. C. Evans, eds.). CONF-670503. U.S. Dept. Commerce, Springfield, Va., 774 pp.
- Petersen, M. K. 1973. Interactions between the cotton rats, *Sigmodon fulviventer* and *S. hispidus*. Amer. Midland Nat., 90:319-333.
- Petersen, M. K., and M. J. Helland. 1978. Behavioral interactions in *Sigmodon fulviventer* and *S. hispidus*. J. Mamm., 59:118-124.
- Petrides, G. A., and P. G. Stewart. 1969. Determination of energy flow in small mammals using <sup>51</sup>chromium. Pp. 131-142, in *Energy flow through small mammal populations* (K. Petruszewicz and L. Ryszkowski, eds.). Polish Scientific Publ., Warsaw, 298 pp.
- Petryszyn, Y., and E. D. Fleharty. 1972. Mass and energy of detritus clipped from grassland vegetation by the cotton rat (*Sigmodon hispidus*). J. Mamm., 53:168-175.
- Pomeroy, S. E., and G. W. Barrett. 1975. Dynamics of enclosed small mammal populations in relation to an experimental pesticide application. Amer. Midland Nat., 93:91-106.
- Ramsey, P. R., and L. A. Briese. 1971. Effects of immigrants on the spatial structure of a small mammal community. Acta Theriol., 16:191-202.
- Randolph, P. A., et al. 1977. Energy costs of reproduction in the cotton rat, *Sigmodon hispidus*. Ecology, 58:31-45.
- Raun, G. G. 1960. Barn owl pellets and small mammal populations near Mathis, Texas, in 1956 and 1959. Southwestern Nat., 5:194-200.
- Raun, G. G., and B. J. Wilks. 1964. Natural history of *Baiomys taylori* in southern Texas and competition with *Sigmodon hispidus* in a mixed population. Texas J. Sci., 16:28-49.
- Rinker, G. C. 1954. The comparative myology of the mam-



- malian genera, *Sigmodon*, *Oryzomys*, *Neotoma*, and *Peromyscus* (Cricetinae) with remarks on their intergeneric relationships. Misc. Publ. Mus. Zool., Univ. Michigan, 83:1-124.
- Roberts, M. W., and J. L. Wolfe. 1974. Social influences on susceptibility to predation in cotton rats. J. Mamm., 55:869-872.
- Robinson, T. S., and F. W. Quick. 1965. The cotton rat in Kentucky. J. Mamm., 46:100.
- Russell, R. J. 1952. A new cotton rat (genus *Sigmodon*) from Morelos, Mexico. Proc. Biol. Soc. Washington, 65:81-82.
- Saussure, H. 1860. Note sur quelques mammiferes du Mexique. Rev. Mag. Zool., Ser. 2, 12:3-11.
- Say, T., and G. Ord. 1825. Description of a new species of Mammalia, whereon a genus is proposed to be founded. J. Acad. Nat. Sci. Philadelphia, 4:352-356.
- Schnell, J. H. 1968. The limiting effects of natural predation on experimental cotton rat populations. J. Wildl. Mgmt., 32:698-711.
- Schweigert, B. S. 1948a. Further studies on nutritional requirements of the cotton rat (*Sigmodon hispidus hispidus*). Proc. Soc. Exp. Biol. Med., 68:522-525.
- 1948b. Nutritional requirements of the cotton rat and hamster. Vitamins Hormones, 6:55-67.
- Sealander, J. A., and C. E. Guss. 1970. Effect of forced swimming on body temperatures and eosinophil levels in cotton rats (*Sigmodon hispidus*). J. Mamm., 51:348-357.
- Severinghaus, W. D., and D. F. Hoffmeister. 1978. Qualitative cranial characters distinguishing *Sigmodon hispidus* and *Sigmodon arizonae* and the distribution of these two species in northern Mexico. J. Mamm., 59:868-870.
- Sherman, H. B. 1951. Aberrant color phases of the cotton rat, *Sigmodon*. J. Mamm., 32:217.
- Shump, K. A., Jr. 1978. Ecological importance of nest construction in the hispid cotton rat (*Sigmodon hispidus*). Amer. Midland Nat., 100:103-115.
- Shump, K. A., Jr., and D. P. Christian. 1978. Differential burrowing by hispid cotton rats (*Sigmodon hispidus*: Rodentia). Southwestern Nat., 23:681-709.
- Slaughter, B. H. 1966. The Moore Pit local fauna; Pleistocene of Texas. J. Paleol., 40:78-91.
- 1967. Animal ranges as a clue to late-Pleistocene extinction. Pp. 155-167, in Pleistocene extinctions; the search for a cause (P. S. Martin and H. E. Wright, Jr., eds.). Yale Univ. Press, New Haven, 453 pp.
- Sprague, J. M. 1941. A study of the hyoid apparatus of the Cricetinae. J. Mamm., 22:296-310.
- Smith, A. T., and J. M. Vrieze. 1979. Population structure of Everglades rodents: responses to a patchy environment. J. Mamm., 60:778-794.
- Stevenson, M., G. Deatherage, and T. J. LaVaquer. 1968. Effects of light-dark reversal in the activity cycle of *Sigmodon hispidus*. Ecology, 49:1162-1163.
- Summerlin, C. T. 1968. A study of the social behavior of the cotton rat, *Sigmodon hispidus*. Unpubl. M.S. thesis, Univ. Alabama, University, 31 pp.
- Summerlin, C. T., and J. L. Wolfe. 1971. Social influences on exploratory behavior in the cotton rat, *Sigmodon hispidus*. Comm. Behav. Biol., 6:105-109.
- 1973. Social influences on trap response of the cotton rat, *Sigmodon hispidus*. Ecology, 54:1156-1159.
- Svihla, A. 1929. Life history notes on *Sigmodon hispidus hispidus*. J. Mamm., 10:352-353.
- Terman, M. R. 1974. Behavioral interactions between *Microtus* and *Sigmodon*: a model for competitive exclusion. J. Mamm., 55:705-719.
- Underhill, A. 1973. Use of Neotropical rodents in protein efficiency studies. Lab. Anim. Sci., 23:499-503.
- Wagner, C. K. 1970. Oxygen consumption, ambient temperature and excretion of phosphorus-32 in cotton rats. Ecology, 51:311-317.
- Wiegert, R. G. 1972. Avian versus mammalian predation on a population of cotton rats. J. Wildl. Mgmt., 36:1322-1327.
- Wiegert, R. G., and J. C. Mayenschein. 1966. Distribution and trap response of a small wild population of cotton rats (*Sigmodon h. hispidus*). J. Mamm., 47:118-120.
- Wolfe, J. L., and C. T. Summerlin. 1968. Agonistic behavior in organized and disorganized cotton rat populations. Science, 160:98-99.
- World Health Organization. 1974. Ecology and control of rodents of public health importance. Report of a WHO Scientific Group. Tech. Rep. Series, 533:1-42.
- Wright, D. E., and J. F. Pagels. 1977. Climbing activity in the hispid cotton rat, *Sigmodon hispidus*, and the eastern meadow vole, *Microtus pennsylvanicus*. Chesapeake Sci., 18:87-89.
- Zimmerman, E. G. 1970. Karyology, systematics and chromosomal evolution in the rodent genus, *Sigmodon*. Publ. Mus. Michigan State Univ., Biol. Ser., 4:385-454.
- 1974. Comparative male meiosis in seven species of cotton rats, genus *Sigmodon*. Cytologia, 39:113-120.

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