

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY  
THE AMERICAN MUSEUM  
OF NATURAL HISTORY

CENTRAL PARK WEST AT 79TH STREET  
NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2544

SEPTEMBER 3, 1974

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Emphasis on the Cotton Rat (*Sigmodon hispidus*)





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AMERICAN MUSEUM NOVITATES

NUMBER 2544, pp. 1-48, figs. 1-13, tables 1-8

Issued September 3, 1974

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ISSN 0003-0082

Price. \$2.87





## ABSTRACT

The small mammals of a pine flatwoods habitat in north-central Florida were studied during 1960 to 1972. *Didelphis virginiana*, *Cryptotis parva*, *Oryzomys palustris*, *Reithrodontomys humulis*, *Peromyscus gossypinus*, and *Rattus rattus* were live-trapped on the study plot. *Lasiurus seminolus*, *Scalopus aquaticus*, *Sylvilagus floridanus*, *Procyon lotor*, and *Geomys pinetis* were also recorded. Of the trappable species, *Cryptotis*, *Reithrodontomys*, *Peromyscus*, and *Sigmodon* were considered regular residents of the study plot, and data are given on their trappability, populations, body weight, sex ratio, reproduction, longevity, and movements. A portion of the study plot was burned in 1960, and the responses of the small mammal populations are documented. Information on mammals in various types of Florida flatwoods habitats is summarized. Data on *Sigmodon hispidus* from the present study and the literature are reviewed in an attempt to assess the relative influence of major climatic factors and local environmental conditions on selected ecological and life history parameters of this species. The relative importance of natality and mortality in population fluctuations of *Sigmodon* is also discussed.

## INTRODUCTION

Flatwoods, characterized by a tree layer comprised largely or entirely of pines, level topography, and imperfectly drained soils, constitute one of the major natural vegetation types of Florida. Like other pine-dominated associations in southeastern United States, flatwoods are maintained by periodic burning. In the absence of fire, succession proceeds toward a deciduous forest stand (Laessle, 1942). Although flatwoods originally covered extensive areas of the state (Davis, 1967), relatively undisturbed stands of this association are rapidly dwindling as the result of real estate development, conversion to improved pasture or other agricultural uses, management for wood production, and protection from fire.

Despite the fact that flatwoods constitute one of the principal terrestrial habitats of Florida, little is known about the animal communities of this association. The present paper gives the re-

sults of a study of the small mammals of a typical flatwoods stand in north-central Florida, approximately 4 miles northwest of Gainesville, Alachua County. As the cotton rat (*Sigmodon hispidus*) was the predominant species in the study area and appears to be a characteristic species of the flatwoods habitat in general, particular attention was given to its population ecology.

The area was studied intensively from June, 1960, through July, 1961. In December, 1960, part of the study plot was burned, providing an unexpected opportunity to observe the effects of fire on the vegetation and small mammal populations. Following the 14 months of continuous study, the area was livetrapped twice in 1962 and once in 1963. General observations on the vegetation were continued through 1972. In 1972, a major portion of the original study plot was re-trapped to assess possible long-term trends in the small mammal population and to determine whether or not differences in species composition and abundance, or both, could still be detected between the areas burned and not burned in 1960.

## DESCRIPTION OF THE STUDY AREA

**Vegetation.** The study area was a mature, relatively open, mixed stand of slash pine (*Pinus elliotii*) and longleaf pine (*P. palustris*). In 1960, the understory consisted of scattered saw palmetto (*Serenoa repens*), shrubs, and small deciduous trees. Principal species of the shrub layer included gallberry (*Ilex glabra*), fetterbush (*Lyonia lucida*), wax myrtle (*Myrica cerifera*), water oak (*Quercus nigra*), and sweet gum (*Liquidambar styraciflua*). Ground cover was well developed, with wire grass (*Aristida stricta*) the predominant component in the better drained sites and broomsedge (*Andropogon capillipes*) in moister areas. Various forbs were relatively frequent throughout the study plot, and extensive patches of bracken fern (*Pteridium aquilinum*) and runner oak (*Q. pumila*) occurred in some places. Sphagnum moss was often present in low spots.

The study plot was bordered on one side by a paved road and on another by a strip of low

swampy hardwoods. One of the remaining sides graded into relatively dry flatwoods with a well-developed understory of deciduous trees and shrubs and the other into lower, wetter flatwoods with areas of dense brush. Even before the fire, the vegetation of the study plot was not homogeneous. The portion toward the hardwood swamp had a greater number of small hardwood trees and shrubs, whereas the remainder was more open and had a denser ground cover of grasses and other herbs and fewer shrubs and small trees. This difference may have been a reflection of the previous fire history of the stand or, more likely, of variation in soils or other edaphic factors.

*Topography and soil.* The topography was generally level with scattered shallow depressions. Mean elevation was approximately 180 feet above sea level. The soil was fine sand underlain by an organic hardpan. As is typical of flatwoods, the study area became very dry during periods of low rainfall but quickly became wet in rainy periods because of the impeded soil drainage. Standing water was often present in the deeper depressions during the rainy season, and after exceptionally heavy rains much of the study area would be shallowly flooded for a day or two.

*Climate.* The nearest source of weather data applicable to the study area is the Department of Agronomy Weather Station at the University of Florida, approximately 5 miles away. The Gainesville region is characterized by high summer and low winter rainfall, with an annual average of 52.4 inches. Peak precipitation normally occurs in the June-September interval. Summer rainfall is mostly in the form of brief thunderstorms. Annual rainfall was considerably above normal in 1960 (62.9 inches) and slightly below in 1961 (47.8 inches) and 1962 (48.3 inches). Spring, summer, and fall of 1960 were wetter than usual; the rainfall in June (12.8 inches) was the highest on record for that month. November, 1960, was unusually dry, and rainfall in December and January was also slightly below normal. Spring, 1961, was drier than average, and there was also a shorter period of high summer rainfall that year, although August was unusually wet. Precipitation during fall and winter 1961-1962 was well below average, but in 1963 the cumula-

tive rainfall through March, the last month of trapping, was normal. Annual rainfall in 1971 was slightly below normal (50.3 inches), although the months of June and July were particularly dry. However, the winter of 1971-1972 (December-February) was considerably wetter than normal, with 10.8 inches of rainfall during the three-month period compared with a 60-year average of 8.4 inches.

Mean annual temperature in the Gainesville region is approximately 70° F., with mean maximum and minimum values of 81 and 59, respectively. June, July, and August are normally the warmest months of the year (mean daily temperature about 80° F.) and December, January, and February the coldest (mean daily temperature about 58° F.). Winter temperatures are generally above freezing, with occasional cold snaps of short duration. Nighttime temperatures often fall well below freezing during cold waves.

Temperatures in 1960-1961 for the most part did not depart from the normal pattern. However, December, 1960, and January, 1961, were unusually cold. Mean daily temperatures during these months were about 4 degrees below normal, and minimum temperatures dropped as low as 20° F. Mean daily temperatures in December, 1962, and January, 1963, were also approximately 3 degrees below normal.

Temperatures during 1971 did not depart markedly from normal, but the winter of 1971-1972, particularly December and January, was appreciably warmer than average. Mean daily temperatures in December and January were 66.4 and 63.9° F., respectively, compared with 60-year averages of 57.9 and 57.8° F. Mean daily temperature in February, 1972 (57.4° F.), was slightly cooler than normal (59.4° F.).

*Vertebrate Associates.* In addition to mammals, 76 other species of vertebrates were recorded on the study area. These included 11 amphibians, 12 reptiles, and 53 birds. The most common amphibians were the pine woods frog (*Hyla femoralis*), southern toad (*Bufo terrestris*), and oak toad (*Bufo quercicus*). The fence lizard (*Sceloporus undulatus*), southeastern five-lined skink (*Eumeces inexpectatus*), glass lizard (*Ophisaurus ventralis*), and black racer (*Coluber constrictor*) were the most conspicuous reptiles. Common birds occurring throughout the year in-



cluded the Rufous-sided Towhee (*Pipilo erythrophthalmus*), Red-bellied Woodpecker (*Centurus carolinus*), Carolina Wren (*Thryothorus ludovicianus*), Yellowthroat (*Geothlypis trichas*), Blue Jay (*Cyanocitta cristata*), Carolina Chickadee (*Parus carolinensis*), and Cardinal (*Richmondia cardinalis*). The Summer Tanager (*Piranga rubra*), Wood Pewee (*Contopus virens*), Pine Warbler (*Dendroica pinus*), Great Crested Flycatcher (*Myiarchus crinitus*), Bachman's Sparrow (*Aimophila aestivalis*), and Brownheaded Nuthatch (*Sitta pusilla*) were frequent in summer; and the House Wren (*Troglodytes aedon*), Eastern Phoebe (*Sayornis phoebe*), Robin (*Turdus migratorius*), Ruby-crowned Kinglet (*Regulus calendula*), Catbird (*Dumetella carolinensis*), and Myrtle Warbler (*Dendroica coronata*) were regularly present in winter.

*Effects of Fire.* Although the fire history of the stand prior to the beginning of the study was unknown, the condition of the vegetation and statements by local residents indicated that the area had not been burned for at least 10 years. On December 28, 1960, a large part of the original study area was burned by a fire of unknown origin. The fire was mostly confined to the more open section of the plot. The burned area was surveyed the following day. Except for an occasional basal rosette of a forb and sphagnum in damper depressions, the ground cover was almost completely destroyed (fig. 1). Shrubs appeared relatively undamaged above a foot or so from the ground, but within a few days most of the smaller shrubs lost their leaves. About half of the palmetto clumps were burned. The lower trunks of the taller (60-70 feet) pines were charred, some of the pine saplings were completely burned, and others appeared untouched. An exhaustive search of the burned area produced no evidence of mortality of small mammals or other vertebrates as the result of the fire. A small corn snake (*Elaphe guttata*) was found unharmed about a foot above ground on a still-warm charred trunk of a pine in the interior of the burned area. As the weather was cool at the time, it is possible that the snake had been attracted by the warmth of the burned tree.

Green shoots up to an inch in height appeared within 10 days after the fire. By this time the needles of some of the taller pines had turned

completely brown, whereas other trees of similar size still retained clusters of green needles in the upper crown. The needles of all smaller pines had become brown. Many cones had opened and fallen from the trees, and seeds were scattered abundantly over the ground of the burned area. Many birds, particularly Robins, Mockingbirds, and Yellow-shafted Flickers, were observed foraging on the burned area during this period. Mean soil temperatures (°F.) at 10 randomly selected locations in the unburned and burned areas during the day on January 30 were as follows (values for the burned area in parentheses): surface, 55.0(61.7); 1-inch depth, 53.1(58.8); 2-inch depth, 52.3(56.8); 4-inch depth, 51.8(54.7). Air temperature at the time was 59.0° F.

By mid-March, considerable regrowth of ground cover had occurred, and the general aspect of the burned area was bright green in contrast to the typical brown and dry winter condition of the unburned area. The general height of the ground cover in the burned area ranged from 6 to 12 inches, but the vegetation was still sparse and did not effectively screen the ground surface as in the unburned part of the study plot. Many forbs were coming in and much new growth of bracken fern and runner oak was evident. Forbs were much scarcer in the unburned area. Most of the palmettos in the burned area now had fully grown new leaves, and some had flowering stalks. In contrast, none of the palmettos in the unburned area had new leaf growth or flowering stalks at this season. The smaller shrubs in the burned area showed no signs of recovery.

The general height of ground vegetation in the burned area had reached 12 to 14 inches by late April, and from a distance the ground cover appeared dense. However, from above, the ground surface was still relatively well exposed in most places. Regrowth of wire grass was particularly evident, although the clumps were fairly sparse because of the absence of dead material. Sprouts had appeared at the base of many of the burned wax myrtles, and new needles were developing on pines that had not been killed.

It was now evident that none of the mature pines had been killed by the fire. Some of the longleaf pines between 1 and 6 feet tall had failed to recover but most young trees of this

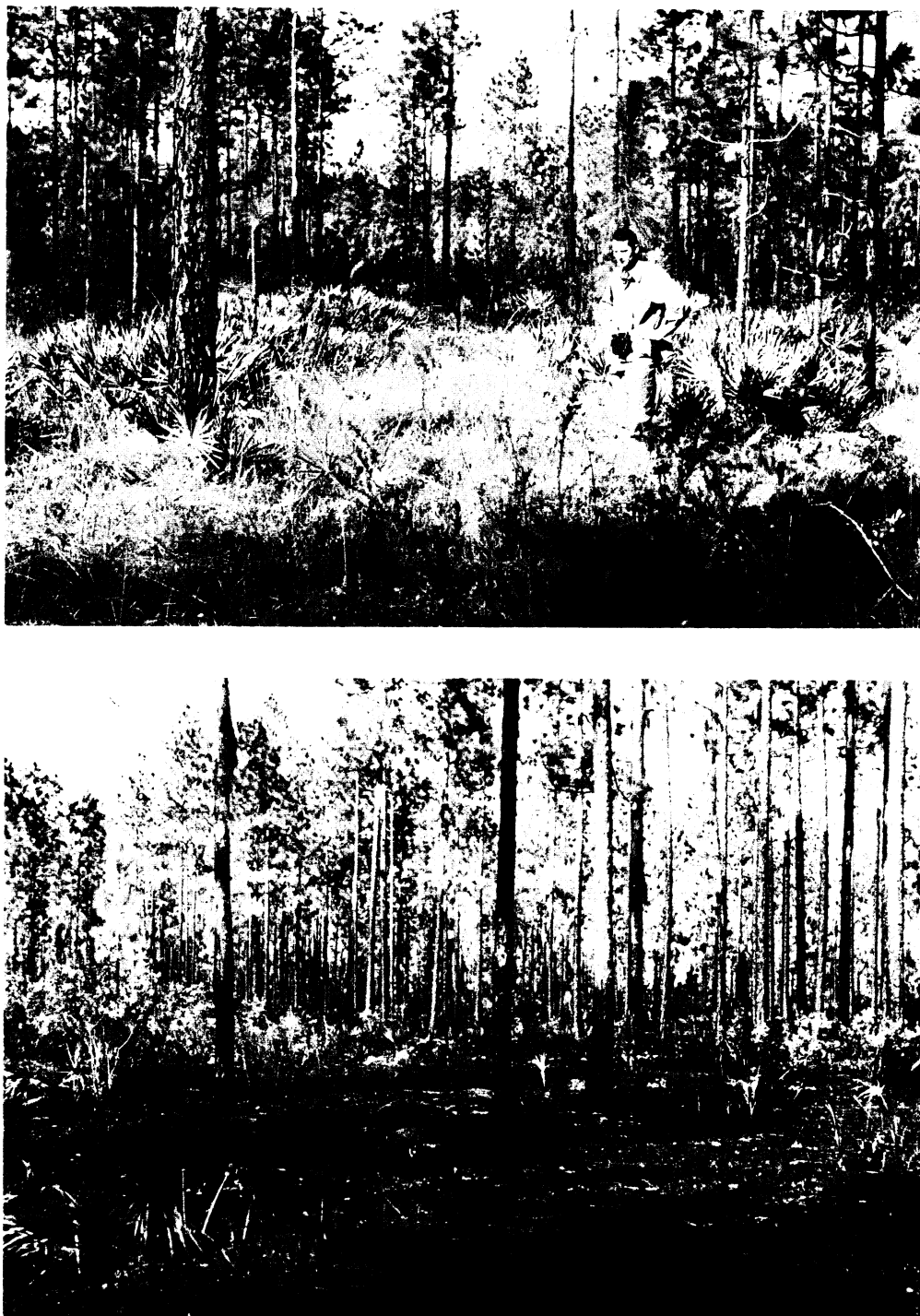


FIG. 1. Unburned (upper) and burned (lower) areas of the study plot in January, 1961.



species over 3 feet high survived. Forbs still appeared to be less frequent in the unburned areas and flowering seemed to be less advanced than in the burned area.

Mean soil temperatures ( $^{\circ}$  F.) at six random locations in the unburned and burned areas during the day on April 21 were as follows (values for burned area in parentheses): surface, 76.1 (83.5); 1-inch depth, 68.0 (79.5); 2-inch depth, 66.0 (77.0); 4-inch depth, 62.4 (73.8). Air temperature at the time was 80.1.

By October, the recovery of the ground vegetation was far advanced. Forbs were still more conspicuous on the burned area, and the grass cover was somewhat sparser, although now dense enough to generally obscure the ground surface from above. Many sprouts were growing from the bases of wax myrtle, fetterbush, water oak, and other shrubs and small trees whose above-ground parts had been killed by the fire. The bark of the mature pines was still conspicuously blackened. In general aspect, the burned area was still less shrubby and more open than the unburned part of the plot.

Subsequent changes in the vegetation of the burned area were more gradual, chiefly involving an increase in density of ground cover and further growth of shrubs. In April, 1963, 27 months after the fire, differences in the vegetation of the burned and unburned areas were still fairly obvious. In the years between 1963 and 1972, there was a steady increase in the number and size of hardwood trees, shrubs, and palmettos. The most pronounced changes occurred on the unburned part of the grid, particularly in the areas nearest the hardwood swamp. By 1972, this part of the grid was heavily invaded by water oaks and wax myrtle up to 20 feet in height. Extensive thickets of gallberry up to 6 feet in height and large patches of tall saw palmetto had also grown. Grass and other herbaceous ground cover was scarce in areas where the shrub layer was well developed and a heavy layer of pine straw covered the ground in many places. The changes in this portion of the plot were the result of the expansion of the swamp edge in the absence of burning. Although palmetto and hardwood growth became more prevalent in the burned area of the plot between 1963 and 1972, the changes in this area were less pronounced than in

the unburned portion. The general appearance of the burned area in 1972 was not markedly different from the preburn period in 1960. The stand remained relatively open, with a dense ground cover of grasses and other herbaceous plants.

## METHODS

Small mammals were livetrapped on a permanent study plot. The plot was initially 8.3 acres and contained a 13 by 13 grid of trap stations at 50-foot intervals. Approximately 80 percent (6.8 acres) of the original study area was burned. After the burn four more rows of 13 stations each were added at one end to include an additional 2.8 acres of unburned habitat, giving an unburned area of 4.2 acres and a total plot size of 11 acres.

The plot was trapped twice a month for five to seven days in June, July, and August, 1960; once a month for four or five days from September to July, 1961; six days in May, 1962; four days in August, 1962; five days in March, 1963; and two days in February, 1972. Prior to the burn, traps were set at 50-foot intervals over the entire grid except for the two trapping periods in July and one in August when traps were set at 100-foot intervals. From January to July, 1961, traps were set at a 50-foot spacing on the unburned portion of the grid and at 100-foot intervals on the burned area. In 1962 and 1963, only a 5.7-acre part of the grid, including both unburned (3.7 acres) and previously burned (2.0 acres) areas, was trapped at 50-foot intervals. Total trapping effort from 1960 through 1963 amounted to 11,094 trap nights.

Approximately 8.6 acres of the grid, including areas both burned and not burned in December, 1960, were livetrapped in February, 1972 (total trap nights, 276). Traps were set at or near original station markers at 50-foot intervals.

One large (3 by 3 by 9-inch) Sherman trap baited with rolled oats or a mixture of peanut butter, raisins, and rolled oats was set at each trap station. Cotton was placed in traps for nesting material during cold weather. Traps were checked once a day in cooler weather, and during hot weather were either closed in the morning and reset in the late afternoon or checked twice daily. Animals trapped from 1960 through 1963

were marked by toe clipping. Body weight and data on pelage and molt, ectoparasites, and reproductive condition were recorded at each capture. Individuals that died accidentally in traps were necropsied for internal data, and in 1960-1961 a small series of specimens was trapped from similar nearby habitat for laboratory examination. All animals trapped in 1972 were sacrificed and necropsied.

Numerical estimates of small mammals present on the portion of the study area trapped in a given period were based on the number of individuals actually trapped during that period plus those taken both in earlier and subsequent trapping periods and assumed to have been present during the interval in question. Such estimates are most reliable when trapping periods are closely spaced, because individuals skipping capture during one or more intervals will have a better chance of appearing in a subsequent trapping period and being added to the count of the periods missed. The greater the tendency for a given species to avoid trapping or the shorter its lifespan on the study area, the greater the bias toward underestimation of numbers when trapping periods are infrequent. Thus population estimates for the period 1960-1961 when trapping was done each month are presumably more reliable than those based on the widely spaced trapping periods in 1962-1963.

Because of variation in the size of the area actually trapped at different times during the study, abundance is expressed in terms of number of individuals per acre for ease of comparison. It is understood that these values are probably higher than true population density, as the traps presumably sampled a larger area than that actually covered by the grid.

"Longevity" as used in this paper refers to the period of known or assumed residence on the study plot as reflected in appearance of animals in traps. Individuals who failed to be captured in some months were assumed to have been present on the study area during the entire interval between first and last capture. For purposes of calculation, the animal was arbitrarily considered to have lived on the plot the entire month of its first and last appearance in traps, regardless of the actual dates of capture.

The percentage of the total months of resi-

dence, including months skipped between captures, that individuals of a given species actually appeared in traps was used as an index of trappability. Only animals trapped three or more months could be used for this calculation.

Several methods of expressing spatial activity patterns were employed. These are:

1. Average distance between successive captures ( $AvD$ ). Hayne (1949), Davis (1953), and Brant (1962) have discussed this measure of movements. For purposes of this study, average distance between successive captures within trapping periods ( $AvD_W$ ) is considered to be the best estimate of the extent of spatial activity of an individual or population at a given point in time, whereas average distance between all captures ( $AvD_T$ ) provides an index of movement over the entire period an individual or population was trapped.

2. Average distance between the last capture of the month of original capture and the first recapture of each subsequent month ( $AvD_B$ ). This measure is employed as an index of the tendency to shift activity loci, the assumption being that the difference between  $AvD_W$  and  $AvD_B$  reflects the degree of shifting of home range. Plotting  $AvD_B$  for each month following the month of original capture also gives an indication of the actual rate of home range shifting with time.

3. Maximum range length (MRL). The distance between the two most widely separated captures of a given individual.

4. Minimum home range (MHR). The area of the polygon produced by connecting peripheral points of capture with straight lines. MHR was calculated only for individuals with four or more nonlinear captures.

## RESULTS

Three hundred seventy-nine individuals of seven species were livetrapped on the study plot and recaptured 1792 times from June, 1960, to April, 1963 (table 1). The cotton rat (*Sigmodon hispidus*) was the principal species appearing in traps, accounting for 77 percent of the original captures and 95 percent of recaptures. The single opossum (*Didelphis virginiana*) trapped was a small juvenile. Opossum tracks were frequently



TABLE 1  
Species Distribution of Captures and Recaptures of Small Mammals  
on Study Area from June, 1960 through April, 1963

Species	Original Captures		Recaptures	
	Number	Percent	Number	Percent
<i>Didelphis virginiana</i>	1	0.3	0	—
<i>Cryptotis parva</i>	44	11.6	27	1.5
<i>Oryzomys palustris</i>	1	0.3	0	—
<i>Reithrodontomys humulis</i>	7	1.8	14	0.8
<i>Peromyscus gossypinus</i>	30	7.9	44	2.4
<i>Sigmodon hispidus</i>	292	77.0	1707	95.2
<i>Rattus rattus</i>	4	1.0	0	—
Totals	379		1792	

observed on the study area. The remaining species, all of which may be assumed to be potentially trappable, made up only about 23 percent of the original captures and 5 percent of recaptures. Of this group, only the least shrew (*Cryptotis parva*), cotton mouse (*Peromyscus gossypinus*), and Eastern harvest mouse (*Reithrodontomys humulis*) were apparently resident on the plot. The individuals of rice rat (*Oryzomys palustris*) and roof rat (*Rattus rattus*) were captured during a single trapping period only and in all probability were transients. As in earlier years, *Sigmodon* predominated in the catch in 1972. Of 92 animals trapped, 67 were cotton rats and 25 cotton mice.

In addition to the species trapped, five additional mammals were recorded on the study plot. A young seminoe bat (*Lasiurus seminolus*) was found clinging to a shrub about 2 inches above the ground during the day in July, 1960. No attempt was made to observe or collect bats in the study area, but it is likely that this and possibly one or two other species foraged over the area. Runways of the Eastern mole (*Scalopus aquaticus*) were seen in relatively well-drained sites along an old roadway that ran through the study plot. Cottontail rabbit (*Sylvilagus floridanus*) droppings were fairly common in all parts of the study area, and raccoon (*Procyon lotor*) tracks were observed on occasion.

Pocket gopher (*Geomys pinetis*) mounds occurred along the slightly elevated shoulder of the paved road bordering the grid, but no evidence of this species was found in the more

poorly drained study area itself. Although not actually recorded, the gray fox (*Urocyon cinereoargenteus*) and bobcat (*Lynx rufus*) probably ranged through the study area, as both were common in the general region.

More detailed consideration of the population dynamics and other aspects of the biology of the four small mammal species livetrapped on the plot and considered to be regularly resident on the area is given below.

## SPECIES ACCOUNTS

### *Cryptotis parva*

**Trappability.** Eight least shrews with a combined total residence of 48 months, were actually trapped in only 24 months (50%).

**Populations.** Numbers ranged from a maximum of 1.2 per acre in October, 1960, to a low of 0.2 per acre in June, 1961 (fig. 2). No shrews were trapped in 1962 or 1963. The reliability of these estimates is questionable, as there is reason to believe that shrews were not consistently trapped in proportion to their true abundance. Trap success tended to be higher in periods of wet weather, which may have forced shrews to be more active in drier sites. Also, the frequent gaps of several months between captures of the same individual give further indication of variation in trappability. Monthly population estimates were higher (0.7-1.2) from June to December, 1960, than from January to July, 1961 (0.2-0.6). The difference in average population levels between the two periods largely reflects

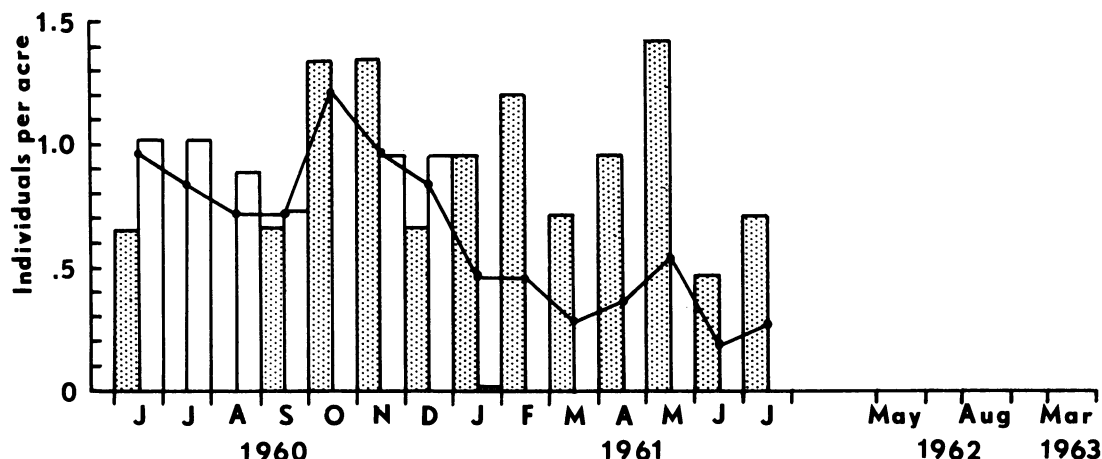


FIG. 2. Population levels of *Cryptotis parva*. Solid dots are estimates for the entire study plot. Stippled bars indicate numbers on the portion of the grid that was not burned in December, 1960, and open bars, numbers on the area burned.

the effect of the burn, as *Cryptotis* strongly avoided the burned area.

Figure 2 shows that in the seven-month period prior to the burn, shrews were generally distributed over the study area, but with a slight tendency to occur somewhat more frequently in the part of the plot subsequently burned. The average density on the "unburned" area during this period, based upon individuals taken only in that part of the grid, was 0.7 per acre compared with 1.0 per acre on the "burned" area. Comparable values for the seven-month period following the burn were 0.9 and 0.04 per acre, respectively. The only shrew recorded on the burned area was trapped in January, 420 feet from the edge of the unburned habitat.

**Weights.** Mean weight of 11 males and 15 females was 5.3 grams (3.4-6.7). The means and ranges for males and females separately were 5.0 (3.4-6.7) and 5.6 (3.6-6.7), respectively. The lightest shrews taken (3.4, 3.6, 3.8 grams) were obviously immature.

Several specimens handled over periods of several months exhibited significant weight changes. An adult male weighed 4.7 grams in September, 4.8 grams in March, 5.1 grams in May, and 6.5 grams in July. An adult female that was not obviously pregnant weighed 6.0 grams in October and 4.2 grams in December. Another was 4.8 grams in October and 4.4 grams in November. A third

female had the following weights (in grams) over a ninth-month interval: September 5.5; October, 5.2; April, 6.7; May, 6.4. These few data suggest that adults may tend to lose or exhibit a plateau in weight during the cold months and then gain weight rather rapidly the following spring and summer.

**Longevity.** The average period of residence on the study area of 15 males was 2.0 months. Ten of these were captured in only one month. Three individuals were known to be present for two months, one died in a trap three months after initial capture, and one was present for 11 months. Mean longevity of 16 females was 4.4 months. Of these, 10 were recorded in only one month and two for two months. One died in a trap after four months and another after nine months' residence on the area. Two others were recorded for six and seven months each.

**Movements.**  $AvD_W$  of two males and five females was 190 and 148 feet, respectively, and 164 feet for both sexes combined (table 2).  $AvD_B$  of five males and six females was 107 feet and 283 feet, respectively.

Average MHR of eight adults was 0.23 acres, with females being trapped over a considerably larger mean area than males (table 2). The lack of a prominent sex difference in  $AvD_W$  in contrast to the markedly greater values of  $AvD_B$ ,  $AvD_T$ , and MHR for females, suggests that females had a

TABLE 2  
Average Distance between Captures within Trapping Periods (AvDw) and between Trapping Periods (AvDb)  
and Minimum Home Range (MHR) of Adult *Cryptotis parva*, *Reithrodontomys humulis*, and *Peromyscus gossypinus*

Species	Sex	AvDw <sup>a</sup>			AvDb <sup>b</sup>			No. Ind.	Dist. (ft.)	No. Ind.	MHR <sup>b</sup>			Area (Acres)
		No. Ind.	No. Capt.	Dist. (ft.)	No. Ind.	No. Capt.	X No. Mos.				X No. Mos.	X No. Capt.	X Range	
<i>Cryptotis</i>	Male	2	3	190	5	10	3.8		107	3	2.7	3.7	0.19	0.03-0.36
	Female	5	5	148	6	11	3.7		283	5	2.7	3.4	0.25	0.07-0.80
	Combined	7	8	164	11	21	3.7		199	8	2.7	3.5	0.23	0.03-0.80
<i>Reithrodontomys</i>	Male	3	5	232	3	5	3.7		184	1	4	6	3.26	
	Female	2	3	267	1	1	2		150	2	1.5	3.0	0.27	0.18, 0.36
	Combined	5	8	245	4	6	3.2		178	3	2.3	4.0	1.27	0.18-3.26
<i>Peromyscus</i>	Male	12	18	63	7	7	1.0		74	2	2.0	3.5	0.20	0.15, 0.25
	Female	5	11	104	5	7	2.0		116	2	3.0	7.0	0.68	0.17, 1.20
	Combined	17	29	79	12	14	1.2		95	4	2.5	5.2	0.44	0.15-1.20

<sup>a</sup> 50-foot trap spacing.

<sup>b</sup> 50- and 100-foot trap spacing.

greater tendency than males to shift their home range with time but were not more mobile during any given period. In most cases, the shift in loci of captures was gradual. Only one of 13 shrews taken two or more times exhibited a shift in activity resulting in clearly discrete clusters of capture points. This was an adult female who between October and April moved from one side of the study plot to the other, the nearest capture points in the two areas being separated by about 500 feet. This individual was also the only one of six shrews assumed to be present in December on the portion of the grid subsequently burned that was later retrapped in the unburned area following the fire. Whether it moved as a result of the fire or sometime before is unknown.

*Sex Ratio.* Of a total of 30 shrews whose sex was determined, 14 (47%) were males and 16 (53%) females. The difference from equality is not significant (chi-square test,  $P > .05$ ).

*Reproduction.* Eight females with prominent teats suggesting current or recent lactation were captured in July (1), August (1), September (2), October (3), and June (1). Shrews believed to be pregnant on the basis of palpation were recorded in August (1) and April (1). The female examined in April had been lactating when handled the previous September. Among females that died in traps and were necropsied, pregnancies were recorded in June (1), August (1), and October (1). Numbers of embryos or fetuses were two, three, and three. Shrews weighing less than 4 grams were trapped in December, January, and February. Also possibly indicative of breeding activity was the capture in the same trap of an adult male and female in September. Taken together, the foregoing data indicate a relatively prolonged breeding season with a possible peak in late summer and fall. Some females may produce two litters in a season.

#### *Reithrodontomys humulis*

*Trappability.* Two harvest mice recorded three or more months on the study area were trapped in six (54%) of the total of 11 months of assumed residence.

*Populations.* This species was the least abundant of the four resident small mammals on the

plot. Numbers on the entire plot ranged from 0.4 per acre in July, 1960, to 0.1 in January, March, April, and May, 1961 (fig. 3). No harvest mice were taken on the study area after May, 1961. Except for the slight increases in July, 1960, and February, 1961, there were no obvious seasonal or yearly trends in abundance.

Prior to the fire, harvest mice were trapped either on the portion of the grid subsequently burned or in both parts of the study area. None was taken exclusively in the "unburned" part (fig. 3). Following the fire there was a decided shift of the species to the unburned area, mean abundance in the unburned and burned areas from January to May being 0.2 and 0.04 per acre, respectively. Harvest mice did not reappear on the burned area until March.

*Weight.* Mean weight of five adult males and two apparently nonpregnant adult females was 9.1 grams (6.8-10.7). Average weight of the males was 8.5 grams, and the two females weighed 10.4 and 10.7 grams.

*Sex and Age Ratios.* All (5 males, 2 females) harvest mice trapped were adult except one 5.0-gram juvenile male taken in February, 1961.

*Reproduction.* Males with enlarged testes and judged by external appearance to be fertile were recorded in February, May, June, July, August, and December. One individual handled in June, July, August, and December showed no evidence of change in reproductive status over this seven-month interval. One pregnant female was captured in February; and, on the basis of weight change and condition of the teats between captures, another female apparently gave birth to a litter in July.

*Longevity.* Two males and one female were recorded for only one month, one male and one female were present two months, while two males appeared on the plot for four and seven months. Mean longevity of all mice was thus 2.6 months (males 3.0, females 1.5).

*Movements.*  $AvD_W$  of five mice was 245 feet with little difference between sexes (table 2).  $AvD_B$  of four mice was 178 feet. The absence of an increase of  $AvD_B$  over  $AvD_W$  suggests that home ranges of these individuals were relatively stable.

Average MHR of one male and two female adults was 1.27 acres (table 2), with the male



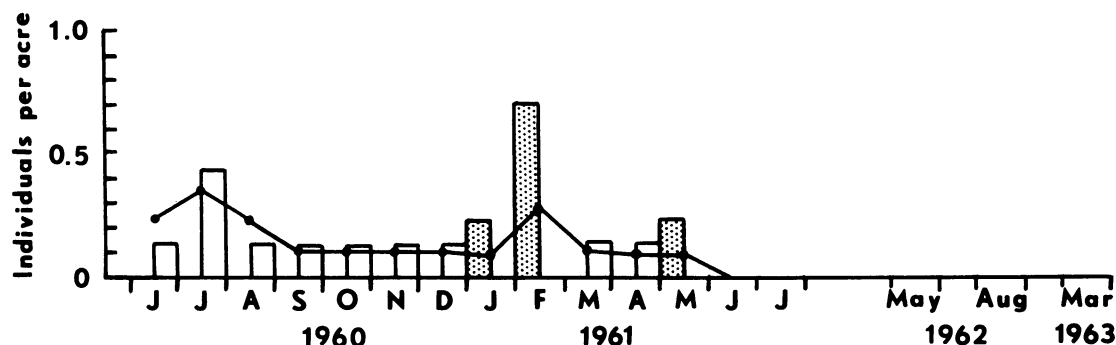


FIG. 3. Population levels of *Reithrodontomys humulis*. Solid dots are estimates for the entire plot. Stippled bars indicate numbers on the portion of the grid that was not burned in December, 1960, and open bars, numbers on the area burned.

having a much larger area than either of the females. Although the male had a longer residence time, his larger  $AvD_w$  suggests that his greater MHR was not simply due to a shifting of home range during his longer sojourn on the grid.

#### *Peromyscus gossypinus*

**Trappability.** Four cotton mice failed to be trapped in six of a total of 18 months' residence, giving an overall trappability of 67 percent.

**Populations.** Cotton mice occurred only sporadically and at low levels (approximately 0.1 per acre) in the seven months preceding the burn. They increased sharply in the interval following the fire, reaching maximum abundance (1.5 per acre) in April, 1961 (fig. 4). Estimated numbers of this species in May, 1962, and March, 1963, were lower than in the corresponding periods in 1961, whereas in February, 1972, the population was estimated at 2.9 per acre, exceeding all earlier values.

Before the fire, cotton mice were slightly more abundant (0.1 per acre) in the portion of the plot that was not subsequently burned than in the area burned (0.04 per acre). Cotton mice invaded the burned area immediately after the fire in January. In the seven-month period following the burn, the situation was reversed, with numbers in the burned area being higher (mean 0.5 per acre) than in the unburned area (mean 0.3 per acre). A single individual captured in May, 1962, was in the burned area, whereas one

cotton mouse trapped in March, 1963, was in the unburned portion.

In 1972, there was no significant difference in the distribution of this species on the formerly burned and unburned sections of the plot. Of the total of 15 individuals trapped on the first day in each part of the grid, seven (47%) were taken in the unburned and 8 (53%) in the burned area.

**Weights.** Mean weight of 16 adult males and 11 nonpregnant females was 22.6 grams. Means and ranges for each sex were: males 20.8 grams (17.5-28.1); females 24.1 grams (18.1-41.8).

**Sex and Age Ratios.** Of a total of 30 mice of known sex taken in the 1960-1963 period, 20 (67%) were males and 10 (33%), females. The difference from 50:50 approaches significance (chi square test,  $.10 > P > .05$ ). In contrast, the sex ratio of 19 adults trapped in 1972 was more nearly equal (53% males, 47% females).

Age classes were based on pelage characters. Individuals in juvenile pelage and showing no molt were classed as juveniles. Mice undergoing the postjuvenile molt were considered subadult, and individuals that had completed the postjuvenile molt were regarded as adults. Of the 30 mice handled between 1960 and 1963, 24 (80%) were adult, five (17%) subadult, and one (3%) juvenile. All subadults and the single juvenile were trapped between January and March. The age composition of the catch in 1972 consisted of 82 percent adults, 4 percent subadults, and 14 percent juveniles.

**Reproduction.** Only two pregnant females were recorded in the 1960-1963 period, one each

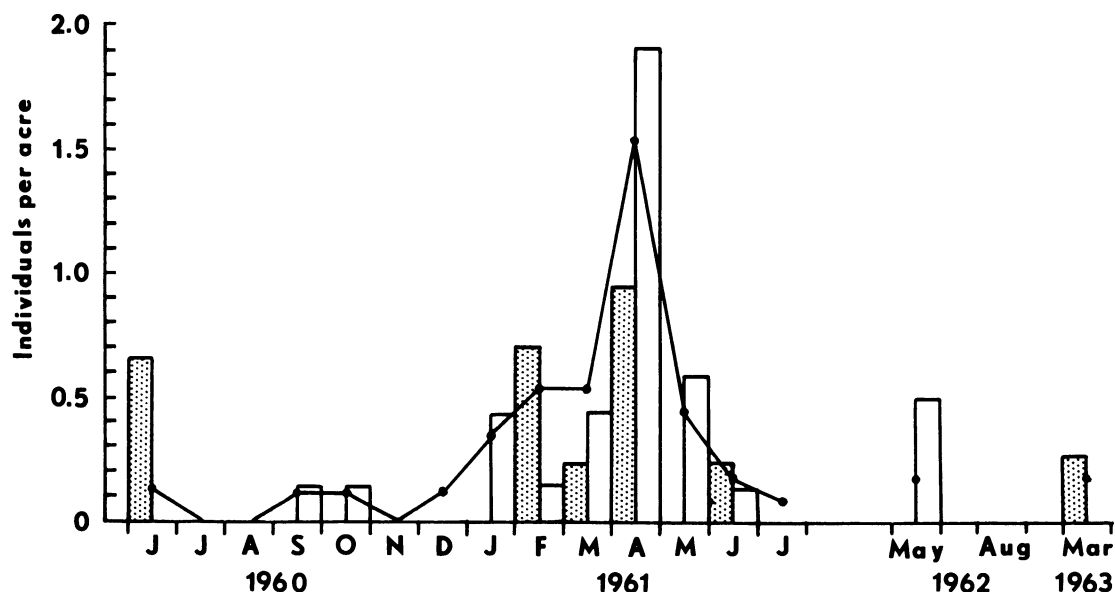


FIG. 4. Population levels of *Peromyscus gossypinus*. Solid dots are estimates for the entire plot. Stippled bars indicate numbers on the portion of the grid that was not burned in December, 1960, and open bars, numbers on the area burned.

in January and July. Of nine adult females captured in 1972, five (56%) were pregnant or lactating.

**Longevity.** Of the cotton mice trapped, 60 percent were recorded in only one month. Twenty males had an average longevity of 1.5 months. Average residence of 11 females was 2.0 months and for both sexes combined, 1.7 months. Five months (1 male, 1 female) was the longest period any individual was known to be present on the plot. Only one cotton mouse present on the grid before the burn, an adult male trapped on both the "unburned" and "burned" areas, was recorded on the study area following the burn. All other individuals of this species trapped on the area after the fire were new. There was no significant difference in the period of known residence of mice on the burned and unburned areas. The relatively short periods of residence, particularly of males, suggests that most of the cotton mice taken on the plot were transients.

**Movements.** Females showed a somewhat larger  $AvD_W$  and a slightly greater relative increase in  $AvD_B$ , indicating that they had less stable home ranges than males (table 2). Average

MHR of four adults was 0.44 acres (table 2). The smaller  $AvD_W$  but larger MHR of the two females compared with the males suggests that the larger average MHR of these females resulted from their longer residence on the study plot during which gradual shifts in movements had occurred.

#### *Sigmodon hispidus*

**Trappability.** Eighty-one cotton rats appearing three or more months on the study area were trapped in 359 (90.4%) of a combined total residence of 397 months. Fifty-six (69%) of these individuals had no gaps in their trapping records; 19 missed one month; two, two months; and six, three or more months. Although the differences were not marked, adult and subadult males exhibited a greater tendency to skip trapping periods than females in these age groups, whereas juvenile females missed more months than juvenile males.

The relationship between trappability and previous trap experience was also examined in this species. Table 3 gives the number and percentage of the total of new and previously trapped cotton rats taken each day of the first four days of the trapping period. Individuals with previous

TABLE 3  
Numbers and Percentages of Total Captures of New and Recaptured  
Cotton Rats on Days 1 through 4 of Trapping Periods from June, 1960 through April, 1963

Age	Day 1		Day 2		Day 3		Day 4	
	N	Percent	N	Percent	N	Percent	N	Percent
Adults								
New	15	9.8	51	33.3	40	26.1	47	30.7
Recaptured	192	52.3	103	28.1	49	13.3	23	6.3
Subadults								
New	5	10.6	12	25.5	18	38.3	12	25.5
Recaptured	48	52.7	21	23.1	16	17.6	6	6.6
Juveniles								
New	3	11.1	6	22.2	9	33.3	9	33.3
Recaptured	20	74.1	3	11.1	2	7.4	2	7.4
Total								
New	23	10.1	69	30.4	67	29.5	68	30.0
Recaptured	263	53.9	127	26.0	67	13.7	31	6.4

trap experience clearly had a higher probability of capture than naive animals, the population thus showing an alloresponsive (Type I) type of trap response as defined by Tanaka (1956, 1963). The difference in proportions of captures of new and previously trapped rats each day for the entire sample is highly significant (chi-square test,  $P < .001$ ). However, differences between age classes in trap response of new and previously trapped individuals are not significant ( $P > .05$ ), although "experienced" animals originally trapped as juveniles tend to have a higher probability of capture than those first trapped as subadults or adults.

The differential trap responses of new and previously trapped cotton rats introduces an obvious bias in any estimate of population size based upon numbers of individuals captured in a given interval or proportions of marked and unmarked individuals in samples. In the present study the effect of differential trap experience was assumed to be greatest at the beginning of trapping when the entire population was naive and to have diminished after the first month or two because trapping was intense enough to maintain a high proportion of "experienced" individuals in the population. The effect of experience with traps on numbers of individuals trapped was dramatically shown in the first

month of trapping, when the plot was trapped twice (June 17-21 and 24-30). The numbers of *Sigmodon* caught each day of the first trapping period were: 3, 18, 21, 19, 18 (total 79), whereas during the first five days of the second period the catch was: 16, 33, 40, 34, 30 (total 153). As weather conditions during each period were comparable, number of traps and methods were similar, and there was no evidence of an influx of new animals into the study area, the differences in numbers trapped during the two intervals appear to reflect an increasing familiarity with traps of an originally naive population. Green (1964) experienced a similar phenomenon in a study of *Sigmodon* in Oklahoma.

The lower trappability of naive animals in addition to the greater chance of failure to record animals that miss a trapping period when sampling periods are infrequent suggests that the density estimates for the isolated trapping periods in 1962, 1963, and 1972 are less reliable than those obtained during the 1960-1961 period of monthly trapping.

In addition to the difference in catchability of cotton rats attributable to experience with traps, individual differences in trappability may further complicate estimates of population size and other parameters based on trapping data (Wiegert and Mayenschein, 1966).

**Populations.** For the study plot as a whole, estimated numbers of cotton rats ranged from a high of 9.7 per acre in June, 1960, to a low of 1.8 in April, 1961 (fig. 5). The population declined in the late summer of 1960, reaching a low in September, and then increased to a second peak in December. This was followed by a steep drop in January following the fire, and a slower steady decline to the April, 1961, low. There was a gradual increase in population density from May to July, 1961.

Population trends on the unburned portion of the grid closely paralleled those of the entire plot except that the decline from December to January was less pronounced, and the population remained at about the same level from April through July, 1961.

Estimated population density for the entire grid in May, 1962, and March, 1963, was higher than in comparable periods in 1961. However, cotton rats were considerably less abundant on

the study area as a whole in August, 1962, than in August, 1960. In February, 1972, 67 individuals were trapped on approximately 8.6 acres of the original study area, giving an estimate of approximately 7.8 per acre. This value exceeds all other monthly estimates except June, 1960. Considering the brief and isolated trapping period in 1972 and that probably not all animals resident on the area trapped were caught, actual population density may have been higher than at any previous time.

Prior to the burn, cotton rats were relatively more abundant in the area of the grid that was not later burned. This appeared to reflect better developed ground cover in that part of the study area. In the seven-month period before the burn, the populations of the "burned" and "unburned" sections averaged 3.7 and 12.0 rats per acre, respectively. In the same time interval following the burn, mean population density of the unburned area was 5.4 rats per acre as com-

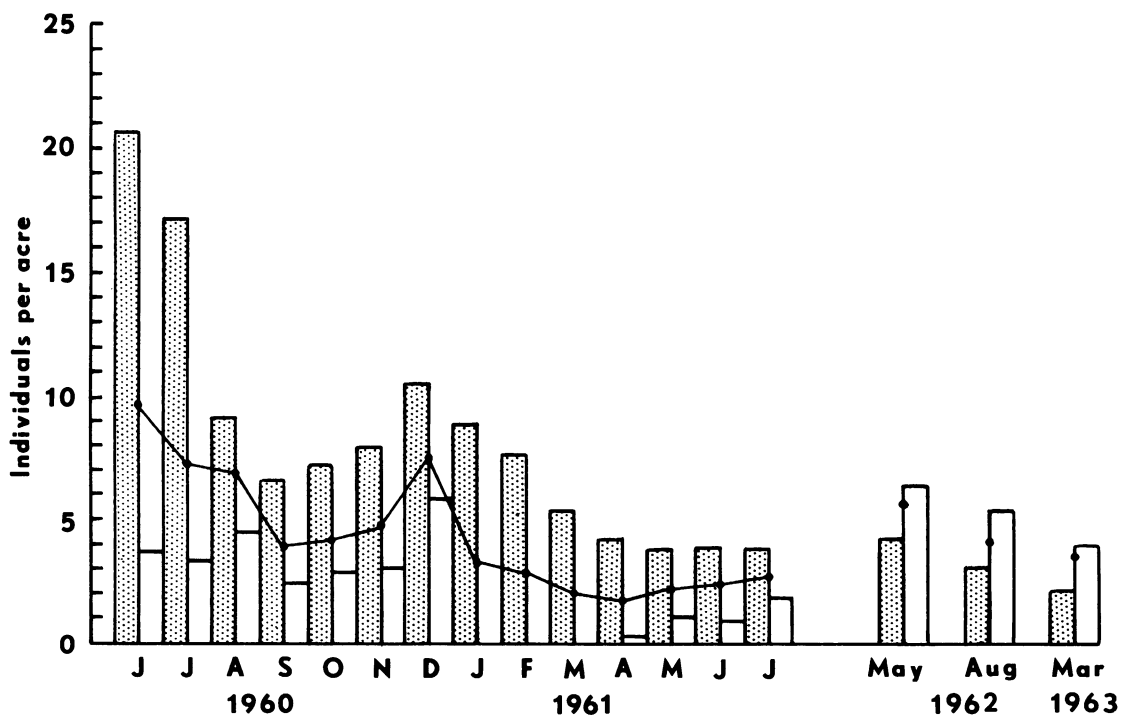


FIG. 5. Population levels of *Sigmodon hispidus*. Solid dots are estimates for the entire plot. Stippled bars indicate numbers on the portion of the grid that was not burned in December, 1960, and open bars, numbers on the area burned.



pared with 0.6 per acre in the burned section. No cotton rats reappeared on the burned area until April, 1963, by which time ground cover was fairly well re-established. The number of rats on the burned area increased gradually in the following months, whereas the number on the unburned area remained fairly constant.

The first cotton rats to appear on the burned area in April, 1961, were subadult males, and males predominated among the new animals captured on the burned area in May, June, and July. From April to July, 12 males and seven females were trapped on the burned area as compared with nine males and 10 females appearing for the first time in this interval on the unburned area. In both sexes, there was a higher proportion of young individuals among those rats trapped on the burned area. Seven (67%) of the males and six (85%) of the females taken on the burned area were juveniles or subadults as compared with four (44%) of the males and seven (70%) of the females captured on the unburned area. Although these data suggest that males and younger individuals had a greater tendency to invade the burned area than females and adults, the differences are not statistically significant (chi-square test,  $P > .05$ ).

In 1962 and 1963, the relative abundance of cotton rats in the burned and unburned sections was reversed from the 1960-1961 period (fig. 5). However, in 1972 the distribution of cotton rats in the two areas was similar to that in 1960-1961. Based on equal numbers of trap stations in the originally burned and unburned portions of plot, 39 percent of the animals were taken in the former and 61 percent in the latter on the first day of trapping in each.

*Age Composition.* Although not a highly reliable age criterion, particularly during winter (Chipman, 1965), body weight has been generally used as a basis for age categories in studies of cotton rats. Three age classes based on weight were recognized in this study: juvenile, less than 50 grams; subadult, 50-100 grams; and adult, over 100 grams. Although more or less arbitrary, these weight categories did tend to break down the population into fairly distinct classes of differing reproductive status (see Reproduction). The weight classes used here are the same as those employed by Dunaway and Kaye (1964)

and closely similar to Odum's (1955). Sealander and Walker (1955) and Goertz (1965b) recognized a greater number of age classes based on weight. However, considering the various factors besides chronological age that influence body weight, finer weight subdivisions probably do not add any greater precision to age estimates.

Based on the total number of cotton rats trapped on the study plot from 1960 through 1963, overall age composition of the population consisted of 42 percent adults, 33 percent subadults, and 25 percent juveniles. In comparison, the mean overall age ratio calculated from percentage age distributions at each trapping period was: adults, 52 percent; subadults, 35 percent; juveniles, 13 percent. Mean age composition based on age distributions at each sampling period is probably biologically more relevant than that calculated from total numbers of each age group captured during the entire study.

Seasonal variation in age composition was marked (fig. 6). Juveniles and subadults together ("young") comprised about 37 percent of the animals handled in June, 1961, and rose to about 50 percent in August. After a decline in September and October, young increased again to a peak of 88 percent in February, 1961. Young continued to predominate in the population during March and April then declined to about 27 percent in May. The proportion of juveniles and subadults increased again in June and July, reaching about the same levels as the previous year. A greater percentage of young was trapped in May, 1962, than in the same month in 1961, whereas in August, 1962, young made up only about 15 percent of the sample compared with 50 percent in 1960. The age composition of the March, 1963, sample agreed fairly well with that of March, 1961. The animals trapped in February, 1972, consisted of 34 percent adults, 41 percent subadults, and 25 percent juveniles.

Although there was a general correspondence between population size and percentage of young rats in the sample, the correlation was far from perfect. Both density and proportion of young were high in the period June to August, 1960, but density declined as the number of young increased. Similarly, while the increase in population from October to December was accompanied by an increase in young, the percentage of

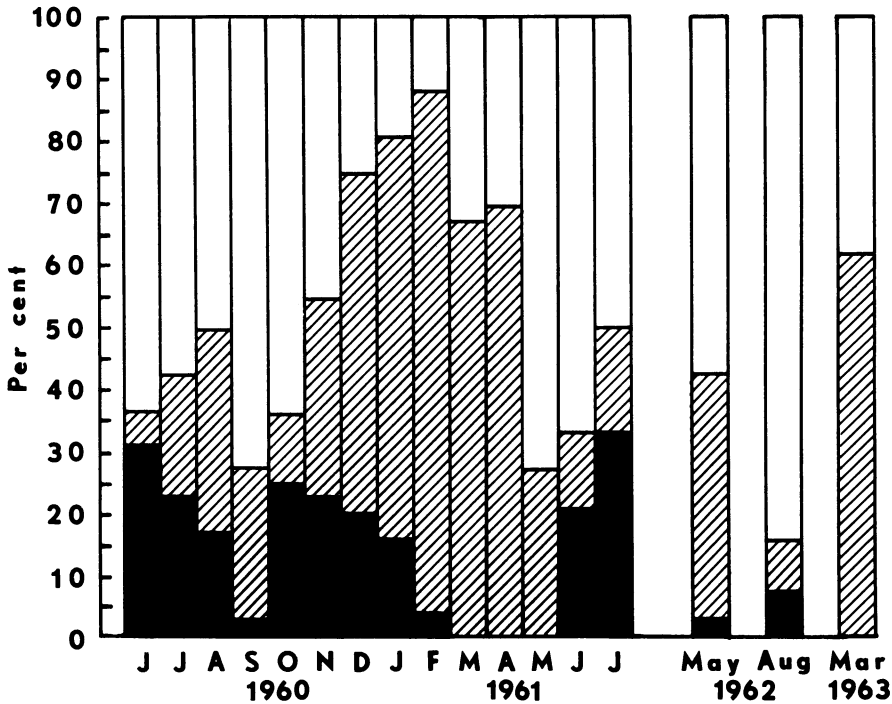


FIG. 6. Seasonal and yearly variation in age composition of cotton rats. Solid segments of bars represent juveniles; hatched segments, subadults; and open segments, adults.

young remained high for several months after, during which time the population was declining. As discussed more fully under Weight, the high proportion of young, particularly subadults, during the winter months is the result of slowing of growth or actual weight loss of individuals, so that during this season rats tended to remain in the juvenile or subadult categories for a longer period than during the warm months or even lost enough weight to drop back to a "younger" age class.

**Sex Ratios.** Of 271 animals handled from 1960 to 1963 whose sex was determined, 147 (54%) were males and 124 (46%), females. This ratio does not differ significantly from 50:50 (chi square test,  $P > .05$ ). Percentages of males in each age class were as follows (sample sizes in parentheses): juveniles (67), 43; subadults (90), 54; adults (114), 60. Neither the juvenile nor subadult sex ratios differ significantly from 50:50, whereas the difference in proportion of adult males and females is significant (chi-square

test,  $P < .05$ ). Although the sexes of juveniles and subadults do not differ significantly from equality, the data do hint at an increasing predominance of males in the catch in going from juvenile to adult age classes.

Figure 7 shows the proportions of juvenile, subadult, and adult males trapped each month of the study. There is a general tendency for the proportion of males to be lower in the fall and higher in winter and early spring. The juvenile and subadult sex ratios are rather erratic and do not show a clear-cut seasonal trend, in part probably because of the relatively small numbers of animals handled in some months. However, the trend is well marked in the adult age class.

The overall sex ratio of the sample collected in February, 1972, was 40 percent males and 60 percent females. Males constituted 44, 44, and 29 percent, respectively, of the adults, subadults, and juveniles, a reversal of the trend noted in 1960-1961 when males tended to exceed females during the winter months. However, unlike the

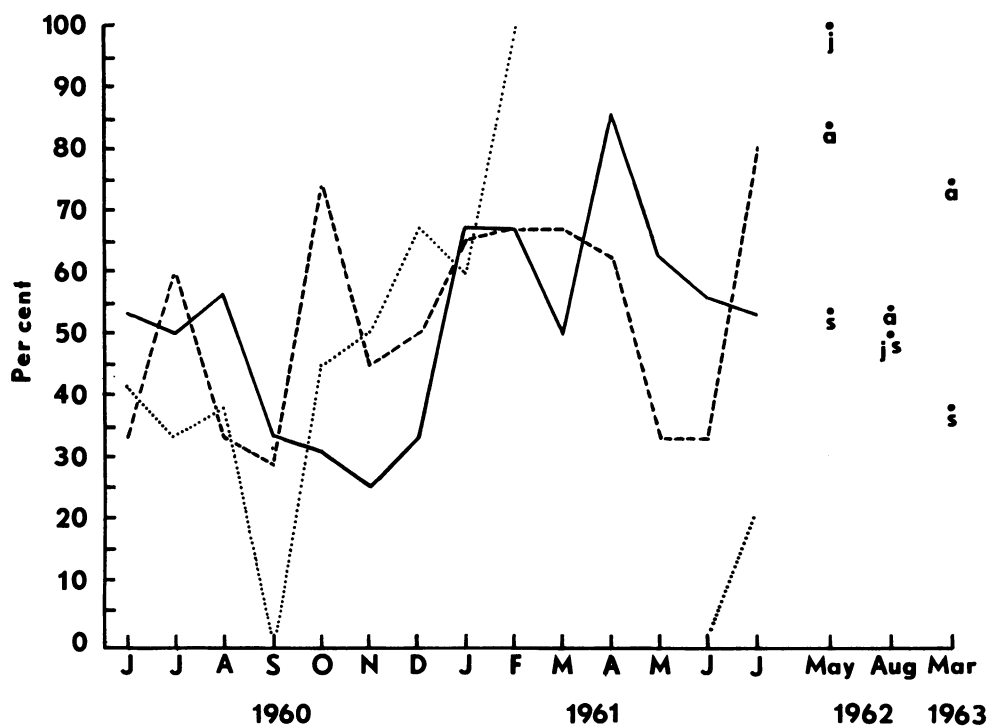


FIG. 7. Seasonal and yearly variation in percentage of male cotton rats. Solid line—adults, dashed line—subadults, dotted line—juveniles. Percentages of adults (a), subadults (s), and juveniles (j) in 1962 and 1963 indicated by solid dots.

winter of 1960-1961, there was intense breeding activity in February, 1972 (see below).

**Reproduction.** Male: Mean length and width of the testes of 13 adult males (mean body weight 127.5 grams) with abundant sperm in the cauda epididymis were 16.7 mm. (15.0-20.5) and 9.6 mm. (7.0-11.5), respectively. The average weight of paired testes of nine specimens in this series was 1.25 grams. The smallest fertile male necropsied weighed 56.2 grams and was trapped in July, 1960. The testes of this specimen were 11.0 by 7.0 mm.; sperm were not abundant in the epididymis. The three next smallest fertile males examined were taken in June, August, and December, 1960. Their body weights and testis measurements (in parentheses) were as follows: 99.6 grams (15.0 by 6.0 mm.), 82.5 grams (13.5 by 9.0 mm.), and 91.5 grams (19.0 by 11.0 mm.). All had abundant epididymal sperm. Other males within the same weight range (94.1-97.8

grams) examined in December had testes with average measurements of only 6.0 by 3.0 mm. and were not reproductively active. Males thus appeared to reach puberty at an earlier age in summer than in winter.

Condition of the cremaster (scrotal sac) was used as a general criterion of reproductive status of live-trapped cotton rats. The cremaster of individuals in full breeding condition was enlarged, sparsely haired, and often heavily pigmented. Except in January, March, and April, in which only 25.0, 66.7, and 75.0 percent, respectively, of the adult males showed some development of the cremaster, all males in the adult weight class had developed cremasters. The reduction in the proportion of sexually active adults in January, March, and April was at least partly due to the entrance of young nonbreeding animals into the adult weight class, although it is also possible that the reproductive tract of some mature adults

may actually have undergone regression during midwinter.

**Female:** The smallest female with a perforate vulva was trapped in August, 1960, and weighed 61.7 grams. The smallest unquestionably pregnant female, weighing approximately 90 grams, was recorded in October, 1960. An 83.5-gram individual examined in September, 1960, was believed to be pregnant on the basis of palpation.

Within the subadult weight class, 15.9 percent of the females had open vulvas, 1.1 percent were pregnant, and 1.1 percent were lactating. Subadults with perforate vulvas were noted in June (50%), July (50%), September (80%), December (13.3%), and May (1961, 75.0%; 1962, 16.7%). As in the case of males, these data suggest that females tended to reach sexual maturity at an earlier age during the warmer months of the year.

Among females in the adult weight class, 53.7 percent had perforate vulvas, 17.2 percent were pregnant, and 8.2 percent were lactating. The

percentages of reproductively active adult females during each month of the study are shown in figure 8. These data indicate a bimodal breeding season in 1960-1961, with peaks in spring and fall.

Two females each gave birth to three young while in traps. Additional data on litter size in this population in 1960-1961 was obtained from embryo and placental scar counts of animals dying in traps on the study area or collected for necropsy in similar habitat about a half mile from the study plot. The mean number of embryos or fetuses in six specimens was 4.0 (2-6). Placental scars in five specimens varied from three to seven (mean 4.6). The mean of combined embryo and placental scar counts was 4.3.

The majority of the adult females in the population apparently had at least two litters during the breeding season. Of eight females resident on the grid from June or July through October,

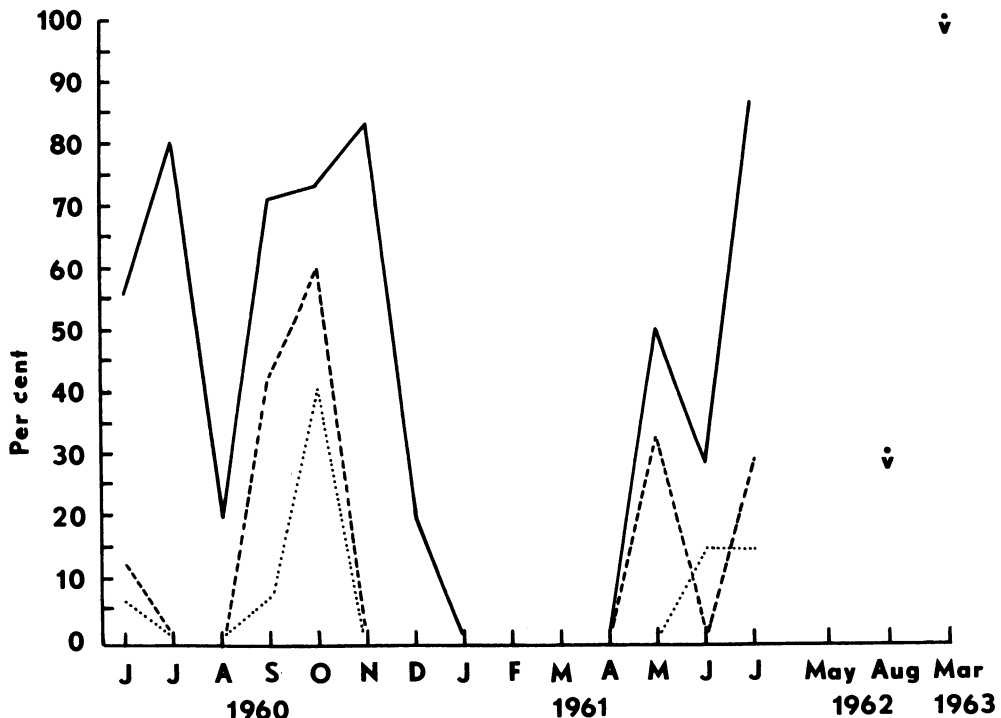


FIG. 8. Seasonal and yearly variation in frequency of perforate vulvas (solid line, "v"), pregnancy (dashed line), and lactation (dotted line) in adult female cotton rats.



1960, seven (87.5%) bore at least two litters in the interval. Two of these animals were lactating or pregnant in June and again in October, whereas the remainder apparently gave birth to two litters in the two-month period September-October. Of seven females followed from August through October, two had two litters each in September and October. One was pregnant both in September and October, 1960, and again in May and July, 1961.

All 13 adult females trapped in February, 1972, were either lactating (1), pregnant (8), or both pregnant and lactating (4). Of 15 subadults examined, 73 percent were either lactating (2) or pregnant (9). The smallest breeding subadult, a nulliparous individual in early pregnancy, weighed 54.7 grams. None of 12 juveniles was in breeding condition. In sharp contrast to 1960-1961, the data from February, 1972, indicate a high level of midwinter breeding. The number of embryos in 11 adults ranged from one to six, with a mean of 4.2, whereas the number of embryos in eight subadults varied from two to four, with a mean of 3.2.

*Body Weight.* Mean and maximum (in parentheses) weights of 65 adult males and 42 non-pregnant adult females were 140.1 (203.6) and 130.2 (178.2) grams, respectively. In 1960-1961 monthly mean weight of adults was highest (149.3 grams) in September and lowest in February (114.2 grams) and March (114.1 grams). Average monthly body weight ranged from 127.8 to 149.3 grams from June through November and from 114.1 to 123.0 grams from December through May. Mean weights in June and July were 133.4 and 142.7 grams, respectively. Average weights in May, 1962 (119.2 grams), August, 1962 (134.3 grams), March, 1963 (121.7 grams), and February, 1972 (122.1 grams) suggest seasonal trends similar to 1960-1961.

Individuals within each age class exhibited seasonal trends in body weight. Figure 9 illustrates changes in body weight of juveniles trapped at fairly regular intervals, usually monthly, for periods of two or more months. Young in the 18- to 40-gram range at initial capture usually gained weight rapidly for the first month or so. However, some juveniles had distinctly slower growth rates. The summer cohort (juveniles first trapped in June, July, or August) had a somewhat higher

average early growth rate with fewer distinctly slower growing individuals than the fall cohort (juveniles first captured in traps from October to December). Growth of young born later in the season also tended to level off at a lower weight. One juvenile male repeatedly trapped between October and April and another handled frequently from November to July exhibited a marked reduction in growth or actual loss of weight during the winter months followed by resumption of rapid growth in spring and summer. This was probably the typical pattern of young surviving over winter. Considering all (20) juveniles handled for two or more months in the November-April period, four showed actual weight losses from one month to the next ranging from 0.13 to 0.82 percent (mean 0.43) of the previous month's weight per day.

As expected, subadults grew slower than juveniles (fig. 10). Most individuals in this age class experienced an obvious plateau in growth from about November to March followed by greatly accelerated growth the following spring. Fifteen of 23 subadults handled sufficiently often during the November-April period to allow me to detect weight trends actually lost from 0.01 to 1.14 percent (mean 0.32) of the previous month's weight per day. In contrast, no individual first captured as a subadult outside of the winter period lost weight.

As reflected in monthly mean weights of the adult cohort, most individual adults (fig. 11) tended to gain weight from June to about September and then level off or actually lose weight from October on. Although none of the larger (120-150 grams) animals of either sex survived on the grid until the following spring, the data suggest that large adults surviving winter would probably show significant increases in weight the following spring. Most of the curves of adult males first appearing in October or later probably represent young animals that have just entered the adult weight class. If so, the decline in average adult weight in winter reflects both actual weight loss of older animals as well as a shift in age composition to younger and slower growing animals during this season. All 11 adults handled often enough between October and April to reveal individual weight trends lost weight during this period, the losses varying from 0.01 to 0.87

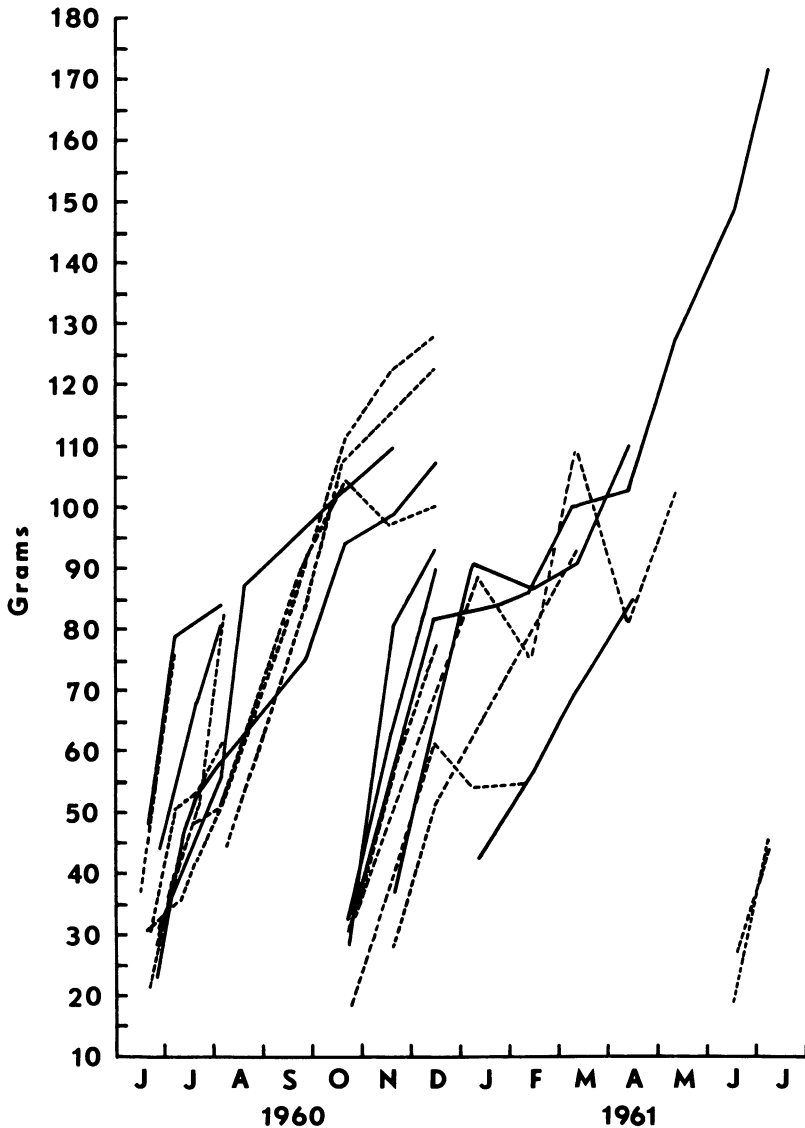


FIG. 9. Trends in body weight of individual cotton rats first trapped as juveniles. Males are represented by solid lines, females by dashed lines.

percent (mean 0.39) of the previous body weight per day, excluding any gains and losses attributable to pregnancy and birth.

*Longevity.* Based on data for the 14 months of continuous study (June, 1960-July, 1961), the average period of residence on the study plot for both sexes and all age groups combined was 2.9 months. This calculation excludes individuals

that died in traps and animals trapped for the first time in July, 1961. Two females originally trapped as subadults were recorded on the study area during the entire 14-month period. An adult and juvenile male and a juvenile female trapped in October, 1960, were still present in July, 1961, 10 months later. The average longevity on the study plot of each age class was as follows:

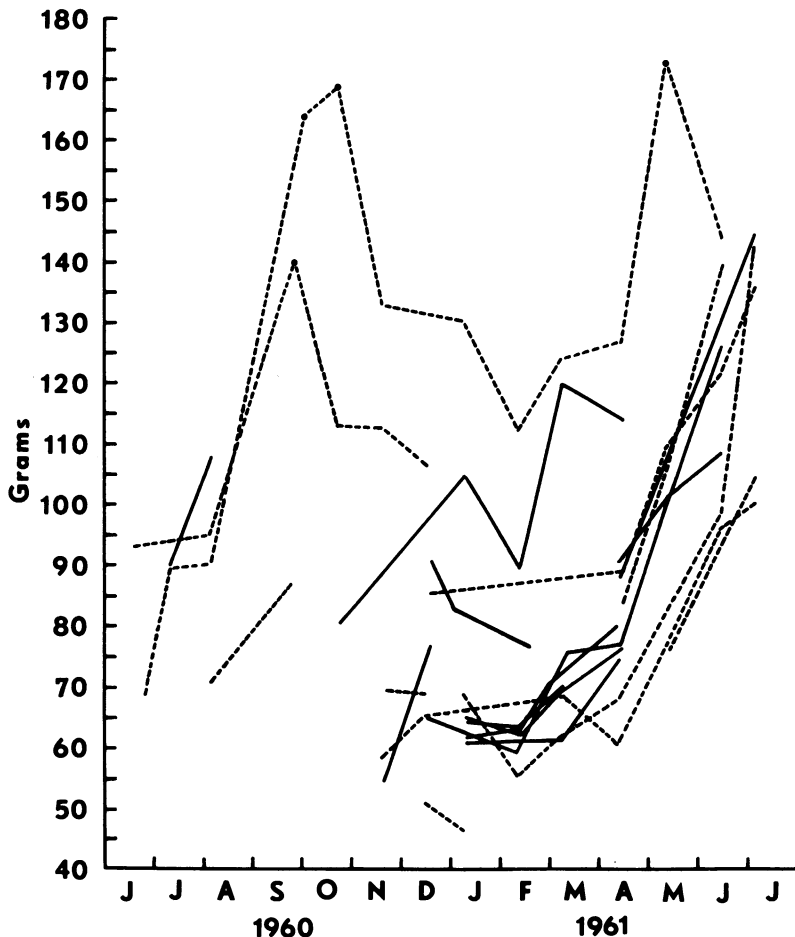


FIG. 10. Trends in body weight of individual cotton rats first trapped as subadults. Males are represented by solid lines, females by dashed lines.

adults, 3.1 months (males 3.1; females 3.2); subadults, 3.1 months (males 2.2; females 3.8); juveniles, 2.9 months (males 2.8; females 3.0). These figures suggest little difference in longevity of cotton rats differing in age at initial appearance on the study plot. In each age group males had lower average survival than females, but only in the case of subadults does the difference approach statistical significance (chi-square test,  $.10 > P > .05$ ).

Age-specific survival over monthly intervals between June, 1960, and July, 1961, is shown in figure 12. Average percentages of each age class survival from month to month during this inter-

val were: adults 70; subadults 72; juveniles 64. Males and females in the adult and juvenile classes did not differ appreciably in average monthly survival, but sex differences among subadults were more marked (males 61%, females 77%).

Cotton rats in each age group exhibited seasonal variation in monthly survival. The percentage of adults carrying over from one month to the next declined moderately in the August-September period and more sharply between December and January. Highest survival of adults was between November and December and January and April. Survival trends of subadults gener-

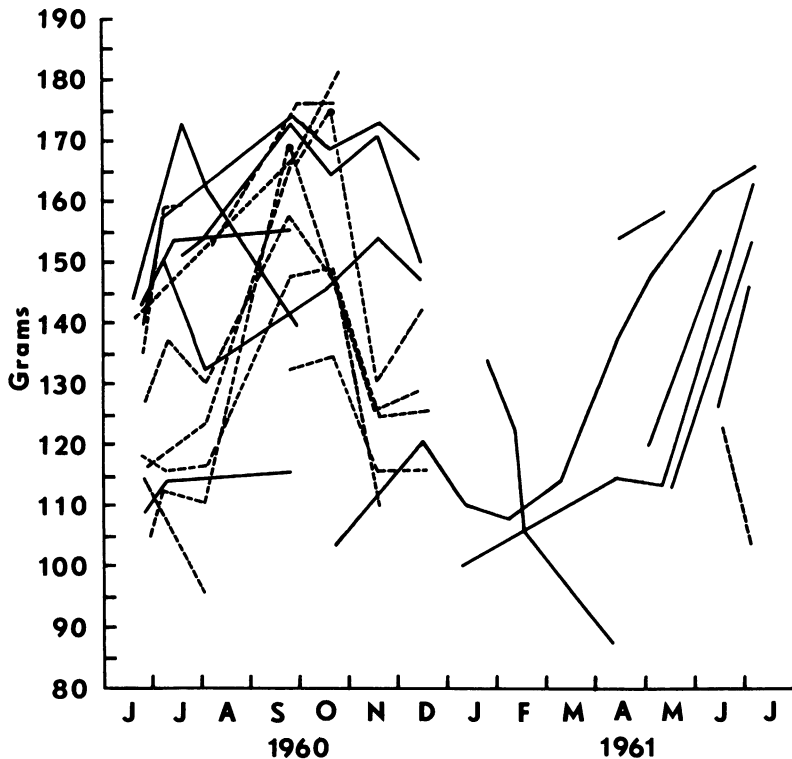


FIG. 11. Trends in body weight of individual cotton rats first trapped as adults. Males are represented by solid lines, females by dashed lines.

ally paralleled those of adults, although the decline between December and January was less marked, the percentages of survival between January and April were lower, and the decline in survival between April and May was more pronounced. The juvenile curve is more erratic, in part probably because of small sample size in some months. The data suggest, however, that juveniles had lower survival during late summer and early fall, with an increase between November and December. Although juveniles showed a decline in survival over the December-January period, the decrease was less pronounced than in August-September unlike the case of adults and subadults. Juveniles first appearing in January had a relatively high survival rate. Although in all age classes survival rates of males and females were not always in close agreement in a given month, there seemed to be no consistent pattern of sex differences.

The marked reduction in survival in all age

classes from December to January is at least partly attributable to the fire. Whether turnover normally increases in this period is open to question, but in view of the immediately preceding and succeeding high survival rates this is probably not the case. The records of rats present in December before the fire but not recorded in January after the fire show that individuals living on both the unburned and burned sections were involved. However, although the difference is not statistically significant (chi-square test,  $P > .05$ ), there was a tendency for a greater loss of animals from the burned sector. Of 24 rats trapped entirely or partially on the unburned part of the grid in December, 11 (45%) were trapped in the unburned area in January. Thirteen (30%) of the 42 rats trapped in December on the part of the grid that later was burned appeared in the traps on the unburned area in January.

Subadults showed highest survival between December and January of any age class on both



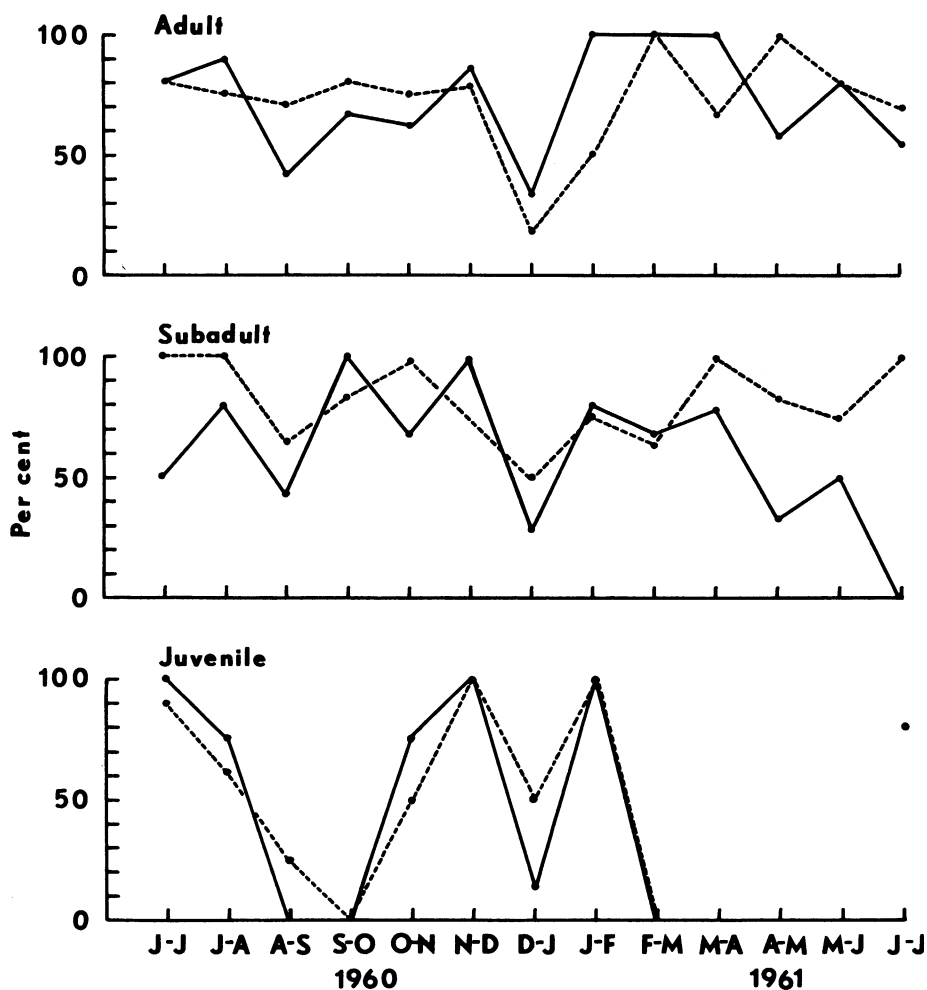


FIG. 12. Survival of juvenile, subadult, and adult cotton rats over monthly intervals. Solid line indicates males, dashed line, females.

unburned (71%) and burned (37%) parts of the grid. Among adults, 33 percent of the animals survived on the unburned part and 12 percent from the burned portion. Comparable values for juveniles were 37 and 20 percent, respectively.

Most of the snakes, raptors, and mammalian carnivores observed on the study area are potential predators on *Sigmodon*, but only two actual records of predation were obtained. Cotton rat remains were found in Barred Owl pellets collected on the study area in June, 1960, and in July, 1960, a *Sigmodon* released from a trap was captured by a corn snake (*Elaphe guttata*) that

appeared to have been lying in wait on the runway upon which the trap was set.

**Movements.** Although only data from the 50-foot trap spacing were used for calculations of  $AvD_w$ , the effect of grid size on apparent movement was examined.  $AvD_w$  of 18 adults (7 males, 11 females) based on captures of the same individuals at 50-foot spacing in June and 100-foot spacing in July, 1960, and 50- and 100-foot spacing in August, 1960, were compared. In the June-July period,  $AvD_w$  was 76 feet at the 50-foot spacing and 97 feet at the 100-foot interval. Comparable values in August were 87 and 97 feet

at the 50- and 100-foot intervals, respectively. Of the 30 pairs of values at the two grid sizes available for the 18 animals,  $AvD_W$  was higher at the 100-foot than at the 50-foot interval in 17 cases, less in 11 cases, and the same in two instances. Despite the differences in the mean distances for the two grid sizes, there was no significant ( $P < .37$ , one-tailed) tendency for  $AvD_W$  to increase at the 100-foot spacing on the basis of a sign test (Siegel, 1956).

$AvD_W$  ranged from 95 feet for subadults to 114 feet for adults (table 4). Although  $AvD_W$  of subadult and juvenile males was slightly higher than that of females in the same age class, the differences were not significant (Mann-Whitney U test,  $P > .05$ ). However, adult males had significantly larger home ranges than females (Mann-Whitney U test,  $P < .003$ ).  $AvD_B$  indicates that both juveniles and subadults tended to have less stable home ranges than adults (table 4). Males and females in all age groups were closely similar in the relative extent of shifting of loci of activity between trapping periods.

Although small sample sizes in some months complicate seasonal comparisons of movement patterns, the data suggest seasonal variation in

$AvD_W$  in all age groups, with possible sex differences, at least in the case of adults, in the magnitude of such trends (fig. 13). The curve of monthly  $AvD_W$  of adult males is roughly bimodal; the distance generally increased from June through November, 1960, then declined sharply in December to the lowest point in the study. From January to May the distance increased steadily, declining again in June and July, 1961. The average distance between captures of 16 adults between September and November was significantly greater than that of eight adults from December through February (Mann-Whitney U test,  $P < .001$ ). Adult females showed less indication of seasonal variation in movements, although the data for this sex suggest a slight increase in mobility in September compared with the June-August level followed by a steady decline until December. The erratic fluctuations beyond this point probably chiefly reflect the small number of individuals for which data are available. Unlike males, the difference in  $AvD_W$  of females between September and November ( $N = 35$ ) and December and February ( $N = 10$ ) was not significant (Mann-Whitney U test,  $P > .05$ ).

TABLE 4  
Movement Patterns of Age and Sex Groups of Cotton Rats as Indicated by Average Distance  
between Recaptures within Months ( $AvD_W$ ) and between Months ( $AvD_B$ )

Age and Sex Group	No. Ind.	$AvD_W^a$		Dist. (ft.)	No. Ind.	$AvD_B^b$	
		$\bar{X}$ No. Meas.	$\bar{X}$ No. Mos.			$\bar{X}$ No. Intervals	Dist. (ft.)
Adult							
Male	31	6.2	2.7	139	34	4.2	163
Female	33	8.0	2.7	92	29	3.7	145
Combined	64	7.1	2.7	114	63	3.9	154
Subadult							
Male	29	3.3	2.2	101	22	2.5	219
Female	28	5.2	2.2	91	15	4.3	202
Combined	57	4.2	2.2	95	37	3.3	209
Juvenile							
Male	20	4.0	1.4	119	18	3.2	224
Female	22	3.5	1.3	108	22	3.7	222
Combined	42	3.8	1.3	113	40	3.5	222

<sup>a</sup>50-foot trap spacing.

<sup>b</sup>50- and 100-foot trap spacing; based on two trapping periods each in July and August, 1960, and monthly intervals thereafter.

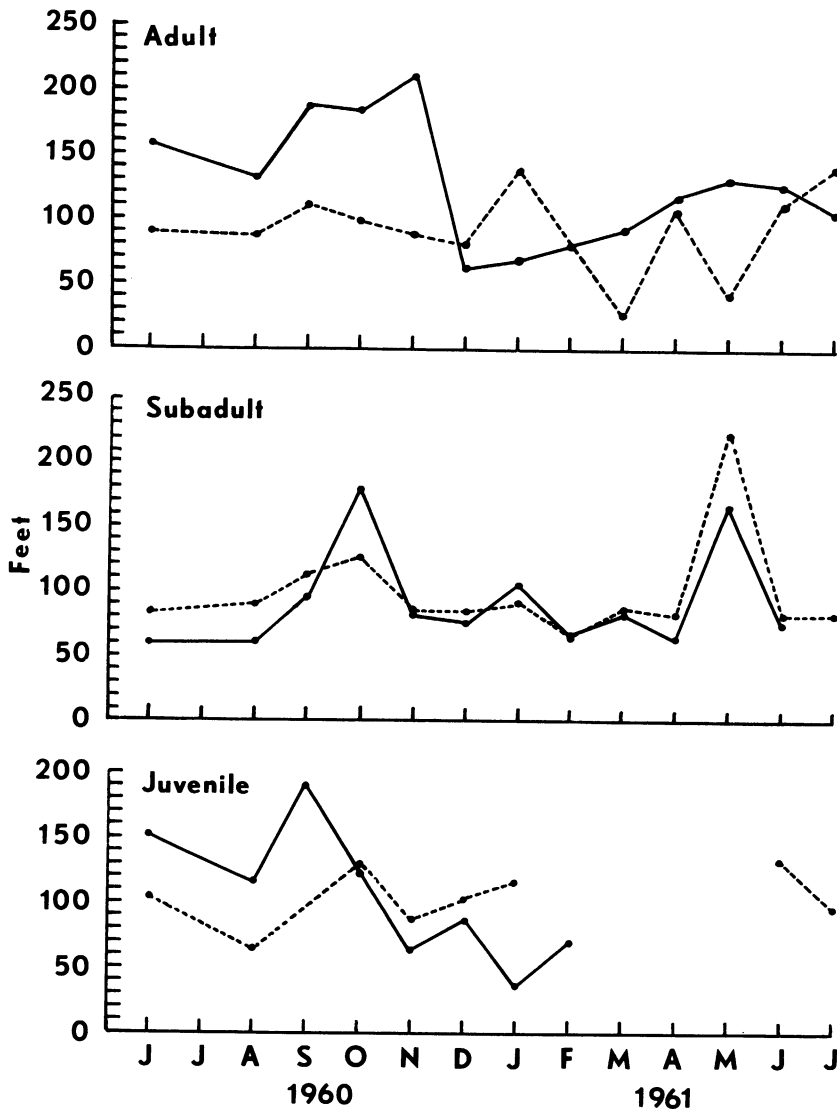


FIG. 13. Seasonal variation in movements of juvenile, subadult, and adult cotton rats as reflected in average distance between captures within trapping periods ( $AvD_w$ ). Males and females are indicated by solid and dashed lines, respectively.

Seasonal patterns of  $AvD_w$  of adult males and females appear to be more or less inversely related. The annual peaks of mobility in males occur at times of decreasing or low mobility of females, whereas maximum monthly  $AvD_w$  of females (January) corresponds to the period (December-January) of least movement in males. The peaks of male mobility and reduction of

female movements also roughly coincide with maximum incidence of pregnancy.

Subadult males and females show increased mobility in fall and spring, but the number of individuals involved is small (fig. 13). However,  $AvD_w$  of six individuals in October and May was significantly greater than that of 74 cotton rats in the interval from November through April

(Mann-Whitney U test,  $P < .05$ ). Males moved less than females in June and August, but during most of the remaining period of the study the curves of the two sexes are similar.

As juveniles were not present in all months of the study, seasonal trends in movements of this age group cannot be compared on the basis of a full annual cycle (fig. 13). In the period from June, 1960, to January, 1961, juvenile males exhibited greater variation in average distance between successive captures than females. Males were more mobile than females from June through October but  $AvD_w$  of males declined markedly thereafter, whereas that of females tended to fluctuate around the same level. The  $AvD_w$  of seven juvenile males in the three-month period August-October, 1960, was significantly higher than that of 13 animals between November and January (Mann-Whitney U test,  $P < .025$ ). However, mean distances of six females in each period did not differ significantly ( $P > .05$ ).

In general, all age groups tended to be more mobile during warmer months when food was presumably more abundant than during winter when food was presumably scarcer. Thus level of spatial activity may reflect factors other than food scarcity or low temperatures per se. Reduced movement in winter may have been due to social inhibition in the form of increased aggressiveness or territoriality as a result of environmental stress. The sharp reduction in adult male movements in December and January likewise may result from increased aggressiveness of adult females with recently weaned young, as this period correlates with maximum abundance of juveniles in the population. The increase in  $AvD_w$  of subadults in fall and spring may be indicative of increased dispersal, with perhaps a "tighter" social structure during winter resulting in more stable and restricted movement patterns in this season.

Capture records of adults were examined for possible sex and seasonal differences in degree of overlap of movements as reflected in the frequency with which different individuals were recorded at the same trap station. In June, July, and August, 26 adult males were captured at 91 different trap stations. Two or more different males were recorded at the same station in 37 (41%) of the cases, whereas in the remainder

(59%) only one male was trapped at the site. In comparison, of 96 captures of 25 females, only 31 percent involved two or more females at the same station. Of 34 captures of eight males in September, October, and November, 21 percent involved overlap at the same station. In the case of females ( $N = 14$ ), 16 percent of 71 captures were superimposed. Although these data suggest that during both seasons females showed less tendency to occur at the same sites than males, the differences are not significant in either period (chi-square test,  $P > .05$ ). However, the reduced overlap at trap stations of both males and females in the September-November compared with the June-August interval is significant (chi-square test,  $P < .05$  for males and  $< .001$  for females).

In the June to August period, both adult males and females were recorded at 64 (48%) of a total of 132 active trap stations, whereas from September through November both sexes were recorded at only 19 (21%) of 87 active stations. The difference in proportions is significant (chi-square test,  $P < .001$ ). These data thus suggest that home ranges of adult males and females tend to be more exclusive in the fall than during the summer months.

The more extensive recapture data available for *Sigmodon* than for other small mammals on the study plot provide a basis for examining the relationships between several linear indices of movement patterns and a commonly used areal estimate, minimum home range. Table 5 gives values of MHR,  $AvD_w$ ,  $AvD_T$ , and MRL for the same individuals. Age group designations refer to the age at original capture. Thus, a percentage of the individuals included under juveniles or subadults were actually in the adult class during part of their sojourn on the study plot. In none of the age groups was MHR size strongly correlated with either period of residence or number of captures. Correlation coefficients between MHR and months of residence and MHR and number of captures were as follows: months: juveniles, 0.256; subadults, 0.550; adults, 0.165; number of captures: juveniles, 0.491; subadults, 0.415; adults, 0.511.

Minimum home range size ranged from 0.03 to 3.66 acres. Individuals first caught as adults or juveniles had closely similar mean MHR size,

TABLE 5  
Comparison of Several Indices of Home Range Size for the Same Individual Cotton Rats

Age and Sex Group	No. Ind.	$\bar{X}$ No. Mos.	$\bar{X}$ No. Capt.	AvD <sub>W</sub> (feet)	AvD <sub>T</sub> (feet)	$\bar{X}$ MRL (feet)	$\bar{X}$	MHR (acres) SE	Range
<b>Adult</b>									
Male	25	3.9	13.0	158	163	390	1.07	0.16	0.17-3.06
Female	18	4.6	18.6	108	108	314	0.59	0.16	0.11-2.54
Combined	43	4.2	15.3	137	140	358	0.87	0.12	0.11-3.06
<b>Subadult</b>									
Male	14	3.5	9.0	125	143	319	0.58	0.12	0.06-1.50
Female	10	4.9	17.0	95	106	269	0.50	0.12	0.11-1.08
Combined	24	4.1	12.3	113	128	298	0.55	0.08	0.06-1.50
<b>Juvenile</b>									
Male	11	4.4	16.0	119	114	314	0.78	0.26	0.03-2.63
Female	18	3.8	18.3	113	124	367	0.90	0.20	0.11-3.66
Combined	29	4.0	17.4	115	120	347	0.86	0.16	0.03-3.66

0.87 and 0.86 acres, respectively, whereas subadults had a smaller mean MHR size (0.55 acres). Adult males had markedly larger MHR than females. There was no well-marked sex difference in MHR in the subadult or juvenile groups, although subadult males had a slightly larger MHR than females and the reverse was true among juveniles.

Mean values of MHR, AvD<sub>W</sub>, AvD<sub>T</sub>, and MRL show general agreement in trends and relative magnitude of differences. Among age groups, all measures except AvD<sub>T</sub> give the same ranking with regard to relative extent of movements (adults > juvenile > subadult) and even the mean values of AvD<sub>T</sub> are closely similar. Likewise, all measures indicate greater movement of males than females in the adult and subadult classes, and, with the exception of AvD<sub>W</sub>, the reverse among juveniles. Thus, mean values of the several measures compared here all lead to generally similar conclusions about the movement patterns of the groups in question. However, correlation between minimum home range size and the various linear indices of home range at the individual level varies greatly, ranging from 0.018 to 0.877 (table 6). In general, the strongest correlation between the several measures is that between MHR and MRL. This does not, however, necessarily mean that either or both of these measures is the most biologically significant expression of the movement patterns of an individual or popula-

tion. Wolfe (1968) demonstrated a closer correlation between minimum home range and successive distances between captures in *Peromyscus leucopus* than found in the present study for the cotton rat.

## DISCUSSION

### Species Composition and Relative Abundance of Flatwoods Mammals

Previous studies, mainly in northern peninsular Florida, providing information on mammals in various flatwoods habitats include those of Barrington, 1949 (longleaf pine-palmetto flatwoods); Ivey, 1947 (loblolly pine-slash pine flatwoods); Layne, 1968 (longleaf pine, slash pine, and mixed longleaf-slash pine flatwoods); Pearson, 1954 (longleaf pine, slash pine, and scrubby flatwoods); Pournelle, 1950 (longleaf-slash-pond pine flatwoods); Moore, 1946 (longleaf pine, slash pine, and scrubby flatwoods); Rand and Host, 1942 (south Florida slash pine flatwoods); and Starner, 1956 (longleaf pine-wire grass flatwoods). On the basis of these and the present study, 25 species of small mammals have been recorded from flatwoods habitats in Florida (table 7). In addition, flatwoods are utilized by the three large mammals native to the state—white-tailed deer, *Odocoileus virginianus* (Newman and Griffin, 1950; Dickson, 1955); black

TABLE 6  
Correlation Coefficients (r) between Minimum  
Home Range Size of *Sigmodon* and Three  
Indices of Mobility Based on Recapture Distances

Age	Sex	AvD <sub>W</sub>	AvD <sub>T</sub>	MRL
Adult	Male	0.345	0.394	0.877
	Female	0.018	0.251	0.045
Subadult	Male	0.414	0.245	0.238
	Female	0.441	0.258	0.816
Juvenile	Male	0.213	0.328	0.799
	Female	0.772	0.637	0.734

bear, *Ursus americanus* (Pearson, 1954; Harlow, 1962); and panther, *Felis concolor* (Tinsley, 1970). Small mammals most frequently reported from flatwoods associations include *Didelphis virginiana*, *Scalopus aquaticus*, *Lasiurus seminolus*, *Sylvilagus floridanus*, *Sciurus niger*, *Geomys pinetis*, *Peromyscus gossypinus*, *Sigmodon hispidus*, *Urocyon cinereoargenteus*, and *Procyon lotor*. Of these, the cotton rat is the only species that has been recorded in this habitat in every study. No Florida mammal is exclusive to flatwoods, although the fox squirrel is highly characteristic of types with an open understory. When we consider only the small mammals susceptible to capture in standard live or snap traps, *Sigmodon*, *Peromyscus gossypinus*, and *Cryptotis parva* constitute the most typical flatwoods species. Based on those studies in which some quantitative indication of relative abundance is given, *Sigmodon* ranks as the most common flatwoods mammal followed by *P. gossypinus* and *Cryptotis* in that order.

Major environmental variables influencing small mammal composition and abundance in flatwoods sites are probably soil moisture and the nature of the understory, the latter in part being determined by the frequency of fire. The size of the flatwoods area and adjacent habitat types are also important factors. Of the various types of flatwoods listed in table 7, scrubby flatwoods and longleaf pine flatwoods have comparatively dry, well-drained soils, whereas slash pine and pond pine flatwoods have more poorly drained soils. With regard to understory conditions, flatwoods may range from a grass and forb ground cover with few shrubs to a dense under-

story of palmettos and/or deciduous shrubs or small trees.

*Peromyscus floridanus* and *P. polionotus* are not generally characteristic of flatwoods and occur only in the driest types. *Geomys* is also restricted to better drained flatwoods sites. The presence and relative abundance of *P. gossypinus* is correlated with the development of deciduous growth. It appears to be more prevalent in flatwoods that are burned infrequently, although, as the present study shows, it may temporarily invade burned sites to exploit a new food supply if suitable habitats are present nearby. The present study also illustrates the response of the cotton mouse to an increase of deciduous cover in flatwoods, assuming that the data for 1960-1963 and 1972 indicate general population trends of this species and not merely low or high points in year to year variation. In the 1960-1963 period, *P. gossypinus* comprised only about 8 percent of the mammals trapped on the study plot, whereas about 10 years later, during which hardwood growth had increased in much of the study area, cotton mice accounted for approximately 27 percent of the total catch. The occurrence of the golden mouse, *Ochrotomys nuttalli*, in flatwoods is apparently also related to the development of hardwood growth.

Some indication of species diversity and relative abundance of small mammals in flatwoods compared with other terrestrial habitats in Florida is given by catch per unit of trapping effort data for 19 habitat types provided by Rand and Host, 1942; Moore, 1946; Barrington, 1949; Pearson, 1954; and Starner, 1956 (table 8). As the types of traps, methods of trapping, season of study, and other factors varied among these studies, the data are at most only broadly comparable. Among the habitats listed in table 8, flatwoods rank seventh in average number of species and thirteenth in relative abundance of small mammals, thus appearing to be generally intermediate in species diversity and abundance of small mammals.

#### Effects of Fire on Small Mammal Populations

All small mammal species were apparently affected by the fire in late December, 1960. Except for a single shrew trapped in the burned area

TABLE 7  
Mammals Reported by Various Authors from Flatwoods Habitats in Florida

(Numbers in parentheses indicate relative abundance based on trapping effort. Type of association given in text.)

Species	Barrington, 1949	Ivey, 1947	Layne, 1968	Pearson, 1954	Pournelle, 1950	Moore, 1946	Rand and Host, 1942	Starnes, 1956	Present Study
<i>Didelphis virginiana</i>	X	X	-	X	X	X	-	-	X
<i>Cryptotis parva</i>	-	-	X	-	X(2)	X(3)	-	X(2)	X(2)
<i>Blarina brevicauda</i>	-	-	-	-	-	X(4)	-	-	-
<i>Scalopus aquaticus</i>	X	X	-	X	-	X	-	X	X
<i>Pipistrellus subflavus</i>	-	-	-	-	X	-	-	-	-
<i>Nycticeius humeralis</i>	X	-	-	-	-	-	-	-	-
<i>Lasiurus seminolus</i>	X	-	-	X	X	-	-	-	X
<i>Sylvilagus floridanus</i>	X	X	X	X	-	X	X	X	X
<i>Sciurus niger</i>	X	-	X	X	X	X	-	-	-
<i>Glaucomys volans</i>	X(4)	-	-	-	-	X	-	-	-
<i>Geomys pinetis</i>	-	-	-	-	X	X	X <sup>a</sup>	X	X
<i>Reithrodontomys humulis</i>	X(3)	-	-	-	-	-	-	-	X(4)
<i>Peromyscus gossypinus</i>	X(2)	-	X	-	X(1)	X(1)	X(2)	-	X(3)
<i>Peromyscus floridanus</i>	-	-	X	-	-	X(4)	-	-	-
<i>Peromyscus polionotus</i>	-	-	X	-	-	-	-	-	-
<i>Ochrotomys nuttalli</i>	-	X	-	-	X(3)	-	-	-	-
<i>Sigmodon hispidus</i>	X(1)	X	X	X	X(2)	X(2)	X(1)	X(1)	X(1)
<i>Oryzomys palustris</i>	-	-	X	-	-	-	X(3)	-	X(6)
<i>Rattus rattus</i>	-	-	-	-	-	-	-	-	X(5)
<i>Urocyon cinereoargenteus</i>	X	-	-	X	-	X	X	-	-
<i>Procyon lotor</i>	X	X	-	X	-	X	-	-	X
<i>Ursus americanus</i>	-	-	-	X	-	-	-	-	-
<i>Spilogale putorius</i>	-	-	-	-	-	-	X	-	-
<i>Mephitis mephitis</i>	-	-	-	X	-	-	X	-	-
<i>Lynx rufus</i>	-	X	-	X	-	X	-	-	-

<sup>a</sup>Does not occur in area of study.



TABLE 8  
Number and Relative Abundance of Trappable Small Mammal Species in Florida Habitats  
(See text for sources of data.)

Habitat	No. of Examples Studied	No. of Species (mean and range)	Trapnights per Individual (mean and range)
Mesic hammock	3	2.7(2-3)	21(14-27)
Coastal hammock	1	1	15
Live oak hammock	1	1	86
Hydric hammock	2	2.0(1-3)	12(12-13)
Bayhead	1	6	35
Hardwood river swamp	3	1.5(1-2)	14(10-21)
Cypress pond/swamp	2	2.0(1-3)	68(33-104)
Flatwoods	7	2.3(1-5)	43(15-98)
Sand pine scrub	2	2.5(1-4)	37(36-38)
Palmetto-oak scrub	1	2	13
Longleaf pine-turkey oak	1	1	83
Longleaf pine-bluejack oak	1	1	60
Coastal savannah	1	1	80
Salt marsh	1	3	9
Oldfield	1	3	40
Ruderal	1	1	98
Marginal thicket	2	5(3-7)	18(7-30)
Pond border	1	5	26
Grass field-swamp edge	1	4	56
Ecotone between mesic hammock and longleaf pine flatwoods	1	1	17

in January, *Cryptotis*, *Reithrodontomys*, and *Sigmodon* disappeared from the burned area for the first two months after the fire. *Cryptotis* was not recorded in the burned area for the remainder of the study. Harvest mice did not reappear until March. Cotton rats were not trapped on the burned area until April, and their relative abundance in this portion of the grid still had not approached that in the unburned portion by July, when regular trapping was discontinued.

The reappearance of harvest mice and cotton rats on the burned area appeared to be primarily correlated with redevelopment of ground cover. Baker (1940), Stickel and Stickel (1949), Goertz (1964), and others have emphasized the importance of well-developed ground cover to *Sigmodon*. However, population pressure, mobility, and other behavioral and ecological characteristics of the population in the unburned areas may also have influenced the timing and rate of reinvasion of the burned area. For example, Arata (1959) believed that the failure of cotton

rats to reappear in a burned over longleaf pine-turkey oak site after ground cover conditions were seemingly suitable was due to low populations in adjacent unburned areas.

As there was no evidence of any mortality from the fire itself, the disappearance of animals from the burned area was apparently due to emigration and failure to settle in the unburned area. Had *Sigmodon* been actively breeding during the winter of 1960-1961 as in 1971-1972, there might have been significant mortality of young in the nest. In the absence of direct mortality from the fire, the greater disappearance of cotton rats from the burned compared with the unburned area suggests that animals dispersing from the fire were prevented from settling in the unburned part of the grid by social pressure from residents and were thus forced to move on or were subjected to higher mortality from predators. Schnell (1964) found that aliens suffered higher mortality than residents in experimental populations. The fact that there was a slight, although

not statistically significant, tendency for better survival of juveniles and subadults than adults from the burned area, suggests that young moving from the burned to unburned area were more readily tolerated by residents. In this connection, Inglis (1955) reported that in captive populations adults were more likely to ignore young than other adults, with whom they frequently fought.

The low survival of rats on the unburned area, if not a seasonal phenomenon, which seems unlikely, might have been due to a general disruption of the social system of the resident population as a result of the influx of many new individuals. In this connection, Wolfe and Summerlin (1968) provided experimental evidence that local populations of *Sigmodon* are socially structured. In a study of the effects of fire on a snowshoe hare population, Keith and Surrendi (1971) also concluded that intensified social interaction caused by animals moving from a burned to unburned habitat was principally responsible for dispersal of young hares from the unburned area.

Over the period 1960-1972 there were shifts in relative abundance of cotton rats between the burned and unburned parts of the study area that may reflect responses to changes in the nutritional quality or other characteristics of the vegetation as a result of burning. Before the fire, cotton rats were relatively more abundant on the part of the grid that was not later burned. However, in 1962-1963 they were proportionally more abundant in the burned area. In 1972, cotton rats were again relatively commoner on the originally unburned area. These trends suggest that the "unburned" part of the study are provided "intrinsically" better cotton rat habitat but that for a few years following the fire the burned area offered superior conditions in the form of better food resources, vegetative cover, or other factors.

The response of cotton mice to the fire was markedly different from the other resident small mammals. This species was relatively scarce prior to the burn but appeared in numbers on the burned area a short time following the fire. The short residence times and generally small size of the majority of cotton mice trapped on the plot suggest that most were transients and that the rapid invasion of the burned area by this opportunistic species was in response to increased food availability in the form of pine and perhaps other

kinds of seeds and insects. Tevis (1956) also noted a rapid invasion by *Peromyscus* of burned areas of slash in western United States. However, Arata (1959) found no change in numbers of *Peromyscus floridanus* and *Peromyscus polionotus* on a recently burned-over longleaf pine-turkey oak plot in northern Florida.

As the numbers of cotton mice built up on both the unburned and burned areas after January, their invasion of the study plot might have been due to population pressure in nearby more typical habitats as well as a direct response to food abundance resulting from the fire. Cotton mice in the area typically breed in fall and early winter and thus high populations and possible food shortage in adjacent habitats might have caused individuals to move onto the grid even if there had been no fire.

#### COMPARATIVE POPULATION ECOLOGY OF *SIGMODON HISPIDUS*

Although incomplete in a number of respects and not always in a form suitable for detailed comparison, data presently available from this and previous studies of the cotton rat provide a basis for a comparison of selected life history and ecological characteristics of populations of this species in a wide variety of habitats and over a broad geographic area extending from about latitude 28° to 39°N and longitude 33° to 102°W. Of particular interest in such comparisons is the degree to which the life history parameters of this species of Neotropical origin may be adjusted to major climatic regimes and local environmental conditions in North America.

##### Population Levels and Fluctuations

Maximum densities of the cotton rat reported by various authors for grassland or other open grass-forb habitat types in Georgia, Kansas, Louisiana, Oklahoma, South Carolina, Tennessee, and Texas range from about two to 19 per acre, with a rough average of about eight to nine per acre (Stickel and Stickel, 1949; Howell, 1954; Negus, Gould, and Chipman, 1961; Provo, 1962; Goertz, 1964; Raun and Wilks, 1964; Schnell, 1968; Petryszyn and Fleharty, 1972). The highest population level encountered in the flatwoods habitat, approximately nine or 10 per acre, is thus

well within the range of estimates for other habitats in different geographic areas. On the basis of present data, there seems to be no obvious relationship between maximum density and habitat type or geographic locality. However, such exceptionally high numbers (subjectively estimated as several hundred rats per acre) reported during cotton rat irruptions in the west (Davis, 1958) have not been encountered in southeastern United States.

Both an annual cycle of abundance and pronounced longer term population fluctuations have been recorded in different habitats and geographic regions. A seasonal cycle with high summer or fall densities and low numbers from winter to spring was described by Komarek (1937), Odum (1955), Sealander and Walker (1955), Dunaway and Kaye (1961a), Provo (1962), Goertz (1964), Green (1964), and Petryszyn and Fleharty (1972). However, Dunaway and Kaye as well as Goertz found that seasonal variation in abundance was less pronounced in some habitats than others, and there was no distinct annual cycle in the Texas population studied by Raun and Wilks (1964). Odum (1955) referred to the seasonal cycle of the cotton rat as a "northern" type, as opposed to the "reversed" cycle with peak abundance in late winter or spring characterizing some species of *Peromyscus* in the south (Pournelle, 1952; McCarley, 1954).

Although somewhat obscured by a superimposed general population decline during the 14 months of continuous study, a seasonal pattern of abundance was also discernible in the flatwoods population of this study. As longer term trends in population may partially mask or distort normal seasonal patterns and most investigations of *Sigmodon* population biology have been of relatively short duration, it is difficult to compare results of different studies to determine possible relationships between habitat or geographic factors and the magnitude and timing of the seasonal cycle. However, the data of this study indicate that in at least some habitats and years there is as well-marked an annual cycle in southern populations of the species as in those near the northern limits of the range. This does not, of course, imply that the causative factors are necessarily the same.

Annual peak population in a drained lake bed

in Tennessee studied by Dunaway and Kaye (1961a) increased from 9.8 to 43.1 per 100 trapnights in three successive years then went to extinction in spring of the fourth year. Cotton rats in an old field habitat studied by the same authors went from a maximum of 12.6 per 100 trapnights in the fall of one year to zero by the following spring. Maximum numbers on one grass-forb-tree study plot in Oklahoma went from a high of about 19 per acre (41.8 per 100 trapnights) in October, 1959, to zero in March, 1960, then increased to 6.9 per 100 trapnights by September, 1961. On another study plot in the same area, populations were more stable, with maximum numbers of 2.8 and 2.4 per 100 trapnights in 1960 and 1961 (Goertz, 1964). In a prickly pear-short grass prairie area in Texas studied from 1958 to 1963 (Raun and Wilks, 1964), cotton rats first appeared in April, 1959, and remained low until fall. The population increased to about 12 per acre in June, 1960, then began to decline. No cotton rats were trapped on the area after February, 1961. Stoddard (1931) noted yearly fluctuations in abundance of cotton rats in southeastern United States and suggested that these might be cyclic. Komarek (1937) also reported pronounced year to year changes in abundance in Tennessee and Georgia and stated the possibility of a four- or five-year cycle in these regions. In an 11-year period, Odum (1955) observed three well-marked autumn peaks and additional evidence of two- and four-year intervals of increased abundance in an old field habitat in Georgia. As noted above, population irruptions of plague proportions have been reported in western United States. Such an outbreak in Texas and adjacent states was documented by Haines (1963).

The limited long-term data available for the Florida population indicate about a three-fold variation in yearly peak levels of abundance. This is a considerably smaller range of variation than occurred in populations studied by Odum (1955), Dunaway and Kaye (1961a), Goertz (1964), and Raun and Wilks (1964), some of which actually went to extinction. Although these previous studies were done in widely separated geographic areas (Tennessee, Georgia, Oklahoma, Texas) the habitats were all open, predominantly grass-forb types. It is possible, there-

fore, that the less pronounced population fluctuations in flatwoods indicate that this habitat provides a more stable environment for *Sigmodon* than grass-forb habitats.

Goertz (1964) suggested that cotton rat populations may be more variable at the northern periphery of the range because of less favorable climatic conditions. On this basis, the apparently greater stability of the flatwoods population might reflect a milder and less variable climatic regime rather than properties of the vegetation *per se*. However, available data do not seem to offer conclusive support for Goertz's hypothesis. Goertz and Dunaway and Kaye (1961a) in their studies near the northern limit of the range found that populations in the same area but in habitats of differing quality showed marked differences in maximum abundance and magnitude of annual fluctuations during the same period of time. The variability in annual population size in old fields and other open habitat types in southern parts of the range is also as pronounced as in more northern areas (Odum, 1955; Raun and Wilks, 1964). Furthermore, the most dramatic population irruptions of cotton rats also appear to occur in more southerly parts of the range. Present evidence seems to indicate, therefore, that habitat type has a strong modulating influence on major climatic factors so that populations in some habitats in the interior of the range may be as unstable as those in better quality habitats near the northern range limits.

An additional factor that may tend to dampen climatic effects on northern peripheral populations may be selection in those populations for relatively less sensitivity to extreme weather conditions, as has been suggested in the case of some insects (Watt, 1968).

Although present data do demonstrate that cotton rat populations may vary considerably from year to year and that populations over a broad geographic area may be synchronized, the fluctuations do not appear to be regularly cyclic.

#### Reproduction

*Sex Ratios.* Although the overall sex ratio in this study did not depart significantly from 50:50, there was a slight preponderance of males. Males did comprise a significantly higher percentage of the adult age class. Other studies have

shown a similar tendency toward more males in the total sample handled (Komarek, 1937; Meyer and Meyer, 1944; Erickson, 1949; Stickel and Stickel, 1949; Sealander and Walker, 1955; Dunaway and Kaye, 1961a; Goertz, 1965b). Insofar as direct comparison of data from different studies is possible, there seems to be no definite relationship between overall sex ratio and habitat or geographic factors.

Seasonal variation in sex ratio has been widely reported in cotton rat populations. Dunaway and Kaye (1961a) found a higher proportion of males in late winter than in early spring and increased prevalence of females during the breeding season. In the period May to September, Erickson (1949) recorded an increase in the proportion of females in June and July when high numbers of immatures appeared in samples. Goertz (1965b) observed a slight but not statistically significant preponderance of females over males when density was high and a significantly higher proportion of males to females when density was low. Komarek's (1937) data indicate an approximately balanced sex ratio from June through September with males predominating at other seasons. Sealander and Walker (1955) trapped a higher percentage of males from February to April, with females increasing in May and June. Seasonal changes in sex ratios, particularly in the adult age class, also occurred in the present study. Males declined in fall and increased in winter and early spring. There seems to be no distinct difference in the magnitude of the seasonal changes in sex ratios in different habitats or geographic areas, although the timing may vary somewhat.

Causes of seasonal variation in sex ratios have been suggested by various authors. Dunaway and Kaye (1961a) concluded that the proportion of males declined during the breeding season because of higher predation, and Goertz (1965b) implied that density may be involved, with a more balanced ratio occurring at higher densities. Sealander and Walker (1955) hypothesized that an increase in proportion of females might represent a compensatory mechanism operating at low density to restore reproductive potential. Neither Goertz's nor Sealander and Walker's explanations give any indication of how the change in relative numbers of males and females is achieved, al-

though a varying sex ratio at birth or differential mortality would presumably be involved.

My data suggest an alternative explanation of seasonal variation in cotton rat sex ratios, namely, that it is attributable to changes in behavioral interactions between males and females which in turn influence the relative trappability of the sexes. The increase in percentage of females in 1960-1961 was strongly correlated with breeding activity, particularly appearance of high numbers of juveniles on the study area. That this is not simply a case of two independent variables being correlated with a third (season per se) is shown by the data from February, 1972. In the late winter-early spring period of 1961 there was no breeding and males exceeded females, whereas there was intense breeding during the same period in 1972 and females were then more abundant than males. This suggests that during the breeding season mobility or other aspects of the behavior of males are affected by adult females in such a way that their trappability relative to females is reduced. Possibly females become more aggressive or territorial at this time and thus inhibit movements of males. Several lines of circumstantial evidence support this interpretation. One is that the seasonal variation in sex ratios is most pronounced in that age class, adult, which is reproductively most active and presumably most aggressive. In addition, adult males did show reduced movements and there was apparently less overlap of male and female home ranges during peak periods of juvenile abundance which might indicate increased territoriality of females.

Results of several laboratory studies lend further credence to this explanation of seasonal sex ratio variation. In a captive colony observed by Inglis (1955) old females dominated all other individuals and adult males were most frequently harassed. Summerlin (1968) found that in small experimental populations females in estrus were more aggressive than when not and initiated most of the agonistic encounters. Estrous females were never displaced by a male in aggressive encounters and sometimes became the dominant member of the population. James L. Wolfe (personal commun.) suspects that females in advanced pregnancy or nursing young also exhibit increased aggressiveness. Field observations in the

course of this study suggest that females may continue to be more aggressive even after the young have left the nest. The occurrence of double captures of adult females with juveniles or subadults and response of adults when young were being handled suggests that the mother-young group may remain together for some time after the young have been weaned. I recorded two double captures involving adult females with juveniles or subadult females in June, one of an adult female and juvenile in August, and another of an adult female and subadult in December. Dunaway and Kaye (1961a) found that young may remain within the mother's home range for up to 94 days. During the present study on four occasions between October and December, 1960, while an observer was handling juveniles or subadults removed from traps, an adult boldly approached to within a few feet in response to the squeaking of the young. This behavior might be interpreted as aggressive. Summerlin and Wolfe (1973) found that socially subordinate cotton rats exhibited less exploratory activity and a greater neophobic response than dominant individuals, which together lowered the probability of their entering traps. Thus, if increased aggressiveness of breeding females in field populations is associated with increased dominance status, this could result in greater trappability of adult females relative to males.

Finally, differential mortality seems to be ruled out as a cause of the seasonal difference in sex ratio in the present study. In addition to lack of any significant difference in overall longevity of adult males and females, there was little correlation between monthly survival rates of males and females and trends in the sex ratio.

The foregoing explanation also appears to account for the seasonal sex ratio changes reported by other authors. In each study where seasonal sex composition data are accompanied by reproductive information, relative increase in the proportion of females is correlated with breeding activity, particularly with appearance of young.

*Age at Puberty.* The earliest age at which laboratory-raised males become fertile is about 40 days at a body weight of approximately 60-70 grams (Meyer and Meyer, 1944; Chipman, 1965). In wild populations, Haines (1961) observed ear-

liest spermatogenic activity in an individual weighing 60 grams, and Odum (1955) believed that males began breeding at a weight of about 65-70 grams. These minimum body weights at puberty are comparable with that of the Florida population (56.2 grams). Meyer and Meyer (1944) reported a tendency in laboratory-raised males for earlier sexual development from March through June than in fall, and a similar trend in wild populations is suggested by my field data.

The earliest age of successful mating recorded by Meyer and Meyer (1944) in laboratory-raised females was about 40 days at an average body weight of about 70 grams. Chipman (1965) reported the youngest breeding age of captive females born in the spring as 38 days (body weight about 60 grams), as compared with 57 days (body weight about 100 grams) for individuals born in September and October. The smallest pregnant females observed by Goertz (1965a) in field populations were 51-53 grams in weight and may have conceived at 40-45 grams. Odum (1955) did not record pregnancies in females who weighed less than 60 grams. In this study, the smallest pregnant live-trapped females were in the 80-90 gram range, whereas the smallest pregnant female autopsied weighed 54.7 grams. As in the case of males, there appeared to be a tendency for females born in the warmer months to become reproductively active at an earlier age than those born later in the season. The unusually high percentage of pregnant or lactating subadults in the February, 1972, sample compared with the period 1960-1961 indicates yearly variation in age at puberty.

On the basis of the presently limited data on sexual development in wild cotton rat populations, especially taking into consideration variation attributable to the influence of various environmental factors on growth rate and sexual development in a given population, there is no evidence of any major geographic or habitat trend in age at puberty of either sex.

*Litter Size and Frequency.* Goertz (1965a) summarized variation in litter size of *Sigmodon hispidus* in different localities. Sealander and Walker (1955), Haines (1961), Kilgore (1970), and Bowdre (1971) provided additional data on litter size in populations in Arkansas, Kansas, Texas, and various Mexican and Central Ameri-

can localities. Mean litter sizes given in these papers vary from 2.0 to 12.0 with an overall average of 5.3 and range of one to 17. In comparison, the mean litter size of 4.3 (two to seven) recorded in the present study is somewhat low.

Based upon data from two localities, Lawrence, Kansas, and Lubbock, Texas, Kilgore (1970) concluded that there had been a significant increase in litter size of the northern population. Mean litter size in the Kansas population ranged from 5.2 to 8.6 in different months, although a single sample of five litters from Texas had a mean of 3.4. Although the difference between the two localities was statistically significant, it seems questionable whether the difference reflects climatic factors. Both Goertz (1965a) and Kilgore (1970) indicated that litters born in colder months are smaller than those produced in warmer months. Kilgore's Texas sample was taken in April, whereas the Kansas data include samples taken in April (mean 5.2), July (mean 7.8), September (mean 8.6), and October (mean 7.1). Thus the two samples are not comparable with respect to seasonal distribution. Furthermore, considerable differences in litter size have been reported for different populations in the same region or in the same population from one year to the next. For example, populations in nearby habitats studied by Dunaway and Kaye (1961a) had mean litter sizes of 5.4 and 7.7 during the same time period, and in an old field habitat in Georgia mean litter size was 5.7 in high density years and 4.1 in low density years (Odum, 1955). Variation in mean litter size may also result from differences in age composition of the samples. For example, in the present study, mean embryo counts in adult and subadult females in 1972 were 4.2 and 3.2, respectively. Finally, considerably larger average litter sizes have been reported by other authors from localities as far or farther south than Lubbock, Texas (e.g., Burt, 1933; Inglis, 1955; Haines, 1961).

Bowdre (1971) examined the question of latitudinal variation in litter size in the south temperate and tropical part of the range (latitude 29° 36' N-8° 41' N) at localities within 100 meters of sea level to avoid the complication of altitudinal effects. He found no significant latitudinal trend but did demonstrate a correlation between litter size and climatic regime, with

larger litter size being associated with areas of pronounced climatic seasonality and smaller litter size with areas of year-round stable temperatures and ample rainfall.

To further examine the possibility of a latitudinal trend in litter size of the cotton rat, I calculated the correlation coefficient between mean litter size and latitude for 11 localities extending from about latitude  $20^{\circ} 45'$  to  $38^{\circ} 57'$  N, using the data of Brimley, 1923; Svihla, 1929; Burt, 1933; Sealander and Walker, 1955; Odum, 1955; Dunaway and Kaye, 1961a; Goertz, 1965a; Kilgore, 1970; and the present study. In studies where two or more mean values were given for the same population at different times or different populations in the same region, I used the average of these values as representative of mean litter size for that locality. The calculation yielded a correlation coefficient of 0.175, which does not differ significantly from zero.

Published information on numbers of litters produced per year by female cotton rats is fragmentary. Meyer and Meyer (1944) stated that a number of females in a laboratory colony produced six or more litters in a 10-month period and one individual had nine litters in 10 months. Females in natural populations probably seldom if ever achieve this level of production. Goertz (1965a) indicated that some females produced three or four litters a year in the Oklahoma populations he studied, and in Arkansas, Sealander and Walker (1955), using the formula of Emlen and Davis (1948), estimated an average of six litters per year. Actual records of pregnancy in this study indicated that some females produced three litters in a 12-month period but evidence of two litters per year was more frequent. Based on Emlen and Davis's (1948) formula and 23 days as the period of detectable pregnancy following Sealander and Walker (1955), calculated average frequency of litters in adult females for the 12-month period June 1960-May, 1961, was 2.9, which agrees fairly well with actual observations. The much lower calculated frequency of pregnancy obtained in this study compared with that of Sealander and Walker (1955) may be at least partly because of the differences in the nature of the data rather than an actual population difference. Sealander and Walker de-

termined percentage of pregnancy from autopsy data and assumed 23 days as the period of visible pregnancy. However, it is unlikely that pregnancy can be detected as early by palpation of a live individual so that use of a 23-day period of detectable pregnancy is probably not justified with this method. For example, if frequency of litters is calculated using 14 rather than 23 days as the period during which pregnancy is detectable by palpation, an estimate of 4.7 litters per year is obtained. However, considering the short average longevity of cotton rats, it is doubtful if many individual females actually achieve this level of productivity.

In summary, available data give no indication of a latitudinal gradient in either litter size or frequency in the cotton rat. Rather, most variation in these parameters seems to reflect local environmental conditions.

*Breeding Season.* Breeding in a laboratory colony under fairly constant conditions occurred throughout the year with no tendency to decrease in winter (Meyer and Meyer, 1944). Although pregnancies in field populations in various parts of the range have been recorded in every month (Goertz, 1965a), all studies of wild populations involving periodic sampling have shown distinct seasonality in reproductive activity, with a general pattern of increased breeding in the spring to fall period and no or reduced reproduction in the winter months.

Reproduction in Tennessee populations studied by Dunaway and Kaye (1961a) occurred mainly between April and October, although sporadic breeding took place in winter. There was evidence of a bimodal pregnancy curve, with peaks in June or July and September or October. Sealander and Walker (1955) recorded breeding in Arkansas from April to December, with an indication of two periods of increased activity within this interval: a major period from February or March through July and a lesser period from late September or October through November. In Oklahoma, Goertz (1965a) recorded reproductive activity in every month except December and January, but there were distinct seasonal trends. Highest percentages of pregnancy in snap-trapped females occurred in May and September, with an indication of a midsummer lull in breeding activity. Under favorable



conditions some breeding took place in winter, but in cold winter years with high population density breeding ceased. Green (1964) found pregnant females in another Oklahoma population from May to October and believed that the length of the breeding season was related to population density. Haines (1961) recorded pregnancies in cotton rats in Texas from February to October, with the greatest number occurring from February to July.

Reproductive activity in the Florida population followed the same general pattern as observed elsewhere. In 1960-1961, pregnant or lactating females occurred from April through November and had a distinctly bimodal distribution, with a lesser spring-early summer peak and a greater late summer-fall peak. There was no evidence of winter breeding in 1960-1961, 1961-1962, or 1962-1963, but the sample in February, 1972, indicated a high level of breeding during the winter of 1971-1972.

From the above data it appears that seasonality of reproductive activity in *Sigmodon* populations is as well defined in the southern part of the range as near the northern limits. This leads to the question of what factors regulate reproduction in this species and whether the generally similar seasonal patterns in different parts of the range are produced by the same factor or combination of factors.

Odum (1955) emphasized that the typical breeding cycle of *Sigmodon* was similar to many northern rodents, in contrast to such southern species as *Peromyscus gossypinus* which breed mainly in fall and early winter. As cotton rats have shown no evidence of a distinct breeding cycle under uniform laboratory conditions (Meyer and Meyer, 1944), an endogenous cycle keyed to day length can probably be ruled out as a major cause of the seasonal cycle in wild populations. Temperature, either in summer or winter, has most often been suggested or implied to be the critical environmental factor influencing cotton rat reproduction. Odum (1955) suggested that, unlike other southern rodents that do not breed in summer, the cotton rat may suffer less from direct effects of high summer temperature on reproduction but is more sensitive to low winter temperatures. Haines (1961) agreed with this interpretation but cited a decline in testis and

vesicular gland size in August coincident with maximum daily temperature as possible evidence of an inhibiting effect of high temperature on reproduction in the species. Goertz (1965a) also suggested that the apparent midsummer decline in reproductive activity in Oklahoma was due to high temperature. Dunaway and Kaye (1961a) and Sealander and Walker (1955) whose data also show a midsummer depression in breeding do not comment on possible causes. Goertz (1965a) found that seasonal variation in size of sex organs was more pronounced in cold winters than in mild ones and that breeding occurred at a reduced level in warmer winters but ceased in cold winters when populations were also high. Dunaway and Kaye (1961a) recorded a pregnancy in February of one year after a period of warm weather. However, no winter pregnancies occurred the following winter which was warmer throughout.

The midsummer decline in reproductive activity in the flatwoods population coincided with the months of highest average daily temperatures and thus may have been due to an inhibiting effect of high temperature as suggested by other authors. However, a similar effect could have been produced by a synchronization of breeding activity in spring, with females entering a "rest" period in midsummer after production of several litters. The trend might also have reflected a shift in age composition, with older females responsible for the spring peak then dropping out of the population and younger, recently maturing females composing the bulk of the breeding population in late summer and fall.

The pattern of winter breeding and consequent density levels of this population also shows a relationship to temperature. The winters of 1960-1961, 1961-1962, and 1962-1963 were relatively cool. In contrast the winter of 1971-1972 was unusually warm. Mean daily temperatures in December and January, normally the coldest months of the year, were 66.4 and 63.9° F., respectively, compared with 60-year mean values of 58.0 and 57.8° F. Judging from the age composition and high incidence of pregnancy and lactation in the February, 1972, sample, a high level of reproductive activity had occurred during that winter. Unusual abundance of cotton rats was also observed in other habitats

in the Gainesville area (J. M. Kinsella, personal commun.) and elsewhere in Florida (L. M. Ehrhart, personal commun.; unpubl. data) during the winter of 1971-1972, suggesting increased winter breeding and perhaps better survival over a wide area of the state as a result of the unusually warm weather.

In addition to a possible direct effect of low temperature on reproductive physiology of cotton rats, the decline in reproduction in winter may also reflect a reduction in the quantity or quality, or both, of food, although increased energetic demands for heat production under low temperatures would also increase the relative stress of nutritional deprivation. Winter decline in nutritional resources may be relatively more important than low temperatures per se in the southern parts of the range. Circumstantial evidence for this is the fact that there is no obvious difference in the magnitude of the reproductive cycle of populations in southern and northern areas despite the milder winters in the south. In addition, deterioration of physical condition as reflected in individual weight loss appears to be as pronounced in southern as in northern populations.

Low rainfall contributing to drying of vegetation may also combine with low temperature to reduce food abundance or quality in cotton rat populations in southern United States. Thus, in years of warm winters with above normal rainfall there may be more green vegetation available resulting in enhanced reproduction. Data on the stimulating effects of green vegetation on reproduction in various rodents and lagomorphs has been summarized by Pinter and Negus (1965). This suggestion is supported by the data of the present study. The winter of 1971-1972 was not only much warmer than average but also wetter. December and January rainfall totaled 8.08 inches compared with 5.19, 2.54, and 3.90 for 1960-1961, 1961-1962, and 1962-1963, respectively, and a 60-year average of 5.12 inches. Negus, Gould, and Chipman (1961) also noted that a build-up of cotton rats to plague proportions in Texas was preceded by springs of high rainfall and luxuriant plant growth following a seven-year drought period.

The suggestion offered here that, at least in the more southerly parts of the range, climatic

factors acting on food supply rather than directly on reproductive physiology may be largely responsible for seasonal and multiannual variation in reproductive activity of *Sigmodon* agrees with the model of population regulation of *Oryzomys palustris* proposed by Negus, Gould, and Chipman (1961). This model may also apply to southern *Peromyscus* species such as *P. gossypinus* (Pournelle, 1952; Odum, 1955) and *P. floridanus* (unpubl. data) in which breeding activity tends to peak in fall and early winter and declines to lowest levels during the summer months. Although this "reversed" cycle has previously been attributed to a direct inhibitory effect of high summer temperatures on reproductive physiology, an alternative explanation is that the increased reproductive activity in fall is a response to a higher nutritional plane resulting primarily from acorn and other seed production at this season. Thus, it is possible that the phase differences in the reproductive cycles of the primarily granivorous *Peromyscus* and herbivorous *Sigmodon* in the same region reflect variation in the periods of abundance of their respective foods rather than direct temperature effects.

Behavioral and physiological considerations support this interpretation. By means of nocturnal or crepuscular activity and nest site selection the animals probably avoid high daytime temperatures in summer. For example, while average maximum daily temperatures in June, July, and August in the Gainesville region are about 90° F., mean minimum nighttime temperatures are only about 70° F. *Peromyscus*, being more strictly nocturnal and probably being able to utilize cooler refugia than cotton rats, are probably more successful in avoiding extreme summer temperatures. However, casual observations suggested that cotton rats on the study area tended to be less active during the middle of the day in summer than in winter. Metabolic studies also indicate that the cotton rat is more tolerant of high temperature than such species as *Peromyscus gossypinus*. For example, oxygen consumption at 40° C. measured with an open flow system and a Beckman F3 paramagnetic oxygen analyzer was 57 percent above the thermoneutral level in *P. gossypinus* and only 49 percent above the minimum value in *Sigmodon* (unpubl. data).

Metabolic data also indicate that the cotton

rat is no more sensitive to low temperatures than *Peromyscus* species found in the same region, which suggests that its reproductive physiology should thus not be any more affected by low temperature than that of the smaller mice, even allowing for a possibly lesser ability of the cotton rat to avoid extreme microclimatic conditions. Some comparative oxygen consumption values at low ambient temperature (5° C.) for *Sigmodon* and two southern species of *Peromyscus* are as follows: *Sigmodon* (mean body weight, 107.5 g), 2.3 ccO<sub>2</sub>/g/hr; *P. gossypinus* (mean weight, 30.6 g), 5.7 ccO<sub>2</sub>/g/hr; and *P. floridanus* (mean weight, 24.5 g), 6.8 ccO<sub>2</sub>/g/hr (unpubl. data).

#### Seasonal Variation in Body Weight

Individual body weight loss during winter appears to be a general phenomenon in cotton rat populations throughout the range and in various habitat types. Chipman (1966) found body weights in March in Texas cotton rats to be less than weights in January even though the March sample presumably had an older age composition. He attributed this to individual weight loss rather than to recruitment of younger animals into the population. In Tennessee, Dunaway and Kaye (1961a) recorded an average winter weight loss of 14.3 percent in seven rats over a period of three months or less. The same authors (1964) reported that during cold weather cotton rats gained weight slowly or actually lost weight and that rapid weight gain commenced in April. Green (1964) and Goertz (1965b) found a similar condition in Oklahoma populations. In the latter study, the average individual weight loss over a mean interval of 34.7 days between October and February was 2.26 grams. Komarek (1937) found lowest mean weight of breeding Georgia cotton rats in March and referred to a "dropping out" of adults in the winter of 1934, which correlated with a "die off" at Shellmound, Tennessee. However, it is possible that individual weight loss accounted, at least in part, for the apparent loss of the adult age class. Odum (1955) noted a general increase in body weight in a Georgia population when numbers were low and a decrease at higher densities. This relationship also could have been due to change in age composition rather than individual weight trends. In Arkansas, Sealander and Walker (1955) found

a decline in adult weights in February and March which accompanied withdrawal of depot fat.

In the present study, some individuals in all age classes exhibited slowing of growth or actual loss of weight in the period between October and April; and, insofar as the data from this and other studies can be compared, winter weight loss in the Florida population was as pronounced as that in more northerly populations.

#### Longevity

Laboratory-raised cotton rats may live up to 400 days (Meyer and Meyer, 1944), and maximum longevity reported in natural populations range from nine weeks to 403 days (Erickson, 1949; Hays, 1958; Dunaway and Kaye, 1961a; Goertz, 1964; Chipman, 1965). Average length of appearance of individuals in field studies is considerably less. Only 28 (16%) of 180 cotton rats handled by Dunaway and Kaye (1961a) were present more than six months. Half of the individuals trapped by Goertz (1964) disappeared by the second month and 98 percent had dropped out by the sixth month. Overall mean longevity was about three months. Although survival was somewhat higher during low population, the monthly disappearance rate was about equal, 40-60 percent of the previous month's total, under both high and low densities. On one study area between October, 1959, and September, 1961, males and females had the same average longevity (2.8 months), while in another study area between July, 1960, and September, 1961, males had a lower mean longevity (4.1 months) than females (5.2 months). Few of the rats studied by Odum (1955) survived longer than six months.

The 14 months of known residence of two individuals in the present study apparently constitutes the maximum recorded longevity of the cotton rat in wild populations. The mean longevity of approximately three months for all age classes and both sexes combined is close to the value reported by Goertz (1964) in Oklahoma. As was the case in Goertz's study, the general trend of the data suggested a reciprocal relationship between longevity and population level, with increased survival during winter months when the population was low. This was especially

true of the adult and subadult age classes. There is no indication in the presently available data of any substantial difference in survival rates of southern and northern cotton rat populations that is clearly attributable to climatic factors.

In none of the field studies to date have losses from the population due to actual mortality and emigration been distinguished, and there is little direct evidence on sources of mortality in cotton rats. Dunaway and Kaye (1961b) observed animals that had apparently died from cold and starvation during an unusually cold winter, and Goertz (1964) also attributed reduction of populations in Oklahoma to abnormally cold weather. Predation is probably a significant mortality factor. However, although a number of putative or known predators on cotton rats have been recorded (Svihla, 1929; Sealander and Walker, 1955; Schnell, 1964, 1968; Wolfe and Rogers, 1969; Jackson, Roberts, and Wright, 1972; present study), little is known about the actual magnitude of predation on specific populations. Under experimental field conditions, Schnell (1968) found that predation accounted for a minimum of 20 percent of mortality in an enclosure. He also (1964) reported a case in which a single mink (*Mustela vison*) eliminated the majority of an introduced cotton rat population in a 1.7-acre field on a small man-made island. Wiegert (1972) on the basis of field enclosure experiments concluded that avian predators had a larger effect on the cotton rat populations than mammalian predators.

Parasites and diseases are also potential mortality agents in cotton rat populations. However, although the cotton rat is host to a wide variety of ectoparasites and endoparasites as well as viral and other disease organisms, there are few data on the relative importance of these agents as mortality factors. Komarek (1937) noted a high internal parasite population in cotton rats at the time of apparent disappearance of adult *Sigmodon* in a Georgia population and recorded cases of severe coccidiosis in another locality after a small population had disappeared. In neither case, however, was there definite evidence that parasitism was causally associated with the population decline. It seems most probable that parasites and disease play an indirect rather than a direct role in cotton rat mortality.

### Causes of Population Fluctuations

Population fluctuations in this study appeared to be more closely linked to natality than mortality. Seasonal trends in density closely followed changes in reproductive activity. Differences in abundance between years also appeared to be correlated with level of reproduction. This relationship was most clearly evident in 1972, when an unusually high late-winter population was associated with a much higher level of breeding in this season than in other years of the study. Although data on yearly variation in mortality were not available, seasonal trends in mortality rate, as indicated by numbers surviving from month to month, were not so closely correlated with population levels as reproductive activity. The major reproductive parameters responsible for variation in population density appeared to be length of breeding season, frequency of litter production, and age at puberty. Limited data on litter size did not suggest any obvious relationship between this parameter and population level.

Circumstantial evidence suggests that temperature and rainfall are the major environmental factors affecting natality. High summer and low winter temperatures may have a direct inhibiting effect on reproductive physiology. However, it seems more likely that temperature and rainfall influence reproduction indirectly through effects on food. Cool temperature and normally low rainfall in winter probably cause a reduction in the amount, kinds, or quality of herbaceous vegetation on which the rats feed with consequent reduction or cessation of breeding and a population decline. In contrast, in warm, wet winters with better food conditions and lower maintenance energy demands, breeding may continue at a high level and numbers remain at the summer or fall level or even build up over winter. The critical nutritional factor relating to breeding intensity may be the amount of green vegetation available. In addition to influencing the level of winter breeding, variation in winter temperatures and rainfall probably also determine the time of onset and cessation of the summer breeding period and thus the extent of recruitment during this season. The amount and distribution of summer rainfall might also conceivably affect reproduction in warm weather, with a hot, dry spell

resulting in reduced breeding activity as a consequence of drying of vegetation.

As in the present study, Odum (1955), Dunaway and Kaye (1961a), and Goertz (1965a) also found a general positive correlation between reproductive activity and density. Cotton rat outbreaks in western United States have also been attributed to increased breeding as a result of better food supply associated with increased rainfall (Negus, Gould, and Chipman, 1961).

There are fewer data available from other studies on the relative influence of natality and mortality on density. Goertz (1964) found less variation in survivorship than reproductive rate in the same population at low and high levels, which supports the idea that natality tends to outweigh mortality in determination of density. It is possible, however, that mortality, particularly in winter, may exert a stronger influence on population levels in northern areas than in the south. Dunaway and Kaye (1961a, 1961b) and Goertz (1964) believed that winter population declines resulted from increased mortality from cold stress and starvation. Cockrum (1952) and Petryszyn and Fleharty (1972) also attributed winter declines in density to direct effects of adverse weather. However, as reproduction also stops or is reduced to a very low level during severe winter conditions, it is difficult to assess the relative contributions of lack of recruitment and mortality to the observed population declines.

On the basis of experimental studies in enclosures, Schnell (1968) postulated that predation, particularly during the nonbreeding season, was a major determinant of population density of cotton rats in southeastern United States. However, Schnell's hypothesis suffers from the fact that he intentionally dealt with nonreproductive populations and thus was not able to compare the relative effects of natality and predation on population size. Furthermore, the enclosures used in his experiments may have produced an abnormal concentration of predators. Thus, although predation and other mortality factors are certainly involved in determining how fast a population may decline and the lower limit to which density in a particular habitat may fall in a given year in the absence of reproduction, the major cause of fluctuation in numbers appears to be the time and intensity of reproductive input.

In summary, the tentative conclusion reached here on the basis of empirical evidence is that variation in natality resulting principally from the influence of weather conditions on food supply is the primary cause of population fluctuations in the cotton rat, with mortality operating mainly to modulate reproductive input and determine the rate of decline and lower limit of the population during lulls in reproductive activity. This does not imply that other factors such as aggressive behavior, endocrine responses to stress, and parasites and diseases are not significantly involved through their effects on natality or mortality (including emigration), or both. In fact, under some conditions these factors may actually assume a major role in population regulation.

### Movements

Because of the many differences in methods used to measure spatial activity in various studies, overall comparison between populations in different regions and habitats is not possible. Movement data in terms of greatest distance between captures presented by Stickel and Stickel (1949), Dunaway and Kaye (1961a), and Goertz (1964) are comparable to maximum range length values of the present study. Mean maximum range lengths in the Tennessee population studied by Dunaway and Kaye (1961a) were  $573 \pm 76$  feet for males and  $236 \pm 17$  feet for females from May to October and  $276 \pm 32$  feet for males and  $175 \pm 33$  feet for females from November to April. MRL in Goertz's (1964) study was nearly always less than 300 feet in the period October to February but often exceeded 300 feet from July through September. Mean distance moved by males was greater than that of females. Stickel and Stickel (1949) believed that the mean maximum range length, based on nine nights of trappings was probably 200 feet or less in males and 100 feet or less in females. In the present study, average MRL of animals first taken as adults, subadults, and juveniles was 358, 248, and 347 feet, respectively. In each group except juveniles, males exceeded females in mean MRL.

Erickson (1949), in coastal Georgia, utilized mean distance between captures as an index of mobility. The method of calculation probably

corresponds most closely to the measure Mean Distance Between all Captures ( $AvD_T$ ) used in this study. Average distance between captures in Erickson's study was 67 feet for males and 56 feet for females and for immature and adult rats 71.7 and 59 feet, respectively. Comparable estimates for the flatwoods population considerably exceed these values,  $AvD_T$  of all animals regardless of age at first capture being approximately 129 feet.

Using the inclusive boundary zone method (Stickel, 1954), Goertz (1964) calculated home range areas on two grids in Oklahoma. During high populations home range ranged from 0.31 to 0.72 acres for males and 0.30 to 1.20 acres for females and during low populations from 0.55 to 9.90 acres for males and 0.80 to 3.30 acres for females. Mean home ranges based on the inclusive method reported by Howell (1954) in Tennessee were  $0.85 \pm 0.13$  acres for males and  $0.44 \pm 0.07$  acres for females. Calculated by the exclusive boundary zone method (Stickel, 1954), seasonal home ranges of cotton rats studied by Fleharty and Mares (1973) in a habitat with dense understory and protective overstory in Texas were 0.96 acres in males and 0.54 in females. Cotton rat home ranges in this population were smaller when numbers were high. Fitch (1958) gave mean minimum home range areas in a Kansas study area as 0.65 acres for adult males, 0.45 acres for adult females, 0.26 acres for young males, and 0.22 acres for young females. Average minimum home range areas in an old field habitat in Alabama were 0.18 acres for males and 0.14 acres for females based on recapture data and 0.19 acres for males and 0.20 acres for females based on radio-tracking (Roper, 1971). In comparison, average minimum home range areas obtained in the present study for animals that were adult, subadult, or juvenile at time of first capture were 0.87, 0.55, and 0.86 acres, respectively. Except in the case of juveniles, males had larger average home ranges than females.

Howell (1954) and Dunaway and Kaye (1961a) found little overlap of female home ranges but considerable overlap among males. The results of the present study suggest a similar relationship in the Florida population.

In summary, available data on movement patterns of cotton rats suggest at least three general

trends: (1) males tend to have larger home ranges than females, at least in some seasons of the year; (2) female home ranges overlap less than males; and (3) seasonal and/or density related changes in extent of movements occur, with largest home range size being associated with warmer times of the year and greater density. The last relationship tends to be more pronounced in males. Beyond these generalizations, which appear to apply to populations in widely separated regions and different habitats, there seems to be no obvious regional or habitat trend in actual size of home ranges insofar as the data from different studies can be compared. Spatial activity is highly responsive to local environmental conditions and thus may vary considerably within the same population. Given such lability in movement patterns in a given population, it would take a substantial amount of carefully gathered and analyzed data to conclusively demonstrate either broad geographic trends in home range size or basic differences in home range size between major habitat types in the same region.

#### ACKNOWLEDGMENTS

It is a pleasure to express my gratitude to Dr. Andrew Arata, Dr. Dale E. Birkenholz, Miss Lueta Carlson, Mr. Peter Cone, Dr. Robert MacFarlane, and Mr. Chet E. Winegarner for their help in the field at various times and to Mrs. Katherine Carter Ewell and Miss Dolores Smoleny for their assistance in analyzing the data. Mr. Cecil Grady kindly permitted the use of his property for the study. I also thank Mr. Robert H. Thomason for preparation of the graphs; Mrs. Charlotte Lohrer for typing the manuscript; and Drs. J. M. Kinsella, L. M. Ehrhart, and J. L. Wolfe, and Mr. C. E. Winegarner for critically reading and commenting on the manuscript. This research was aided by a grant-in-aid from Cornell University while I was on the faculty of that institution and Archbold Expeditions of the American Museum of Natural History.

#### SUMMARY

Observations of small mammals of a mixed longleaf pine-slash pine flatwoods habitat in north-central Florida were made during 1960 to

1972. A permanent study plot was sampled by livetrapping each month from June, 1960, through May, 1961, and in May and August, 1962, March, 1963, and February, 1972. A portion of the study area burned in December, 1960, provided an opportunity to document the effects of fire on the vegetation and small mammals.

Three hundred seventy-nine individuals of seven species were livetrapped a total of 1792 times from 1960 through 1963. The species trapped and percentages of total original and recaptures, respectively, represented by each were: opossum (*Didelphis virginiana*) 0.3/0; least shrew (*Cryptotis parva*) 11.6/1.5; rice rat (*Oryzomys palustris*) 0.3/0; harvest mouse (*Reithrodontomys humulis*) 1.8/0.8; cotton mouse (*Peromyscus gossypinus*) 7.9/2.4; cotton rat (*Sigmodon hispidus*) 77.0/95.2; and black rat (*Rattus rattus*) 1.0/0. In addition to the species appearing in traps, the seminoe bat (*Lasiurus seminolus*), eastern mole (*Scalopus aquaticus*), cottontail rabbit (*Sylvilagus floridanus*), raccoon (*Procyon lotor*), and pocket gopher (*Geomys pinetis*) were recorded.

Data on trappability, populations, body weight, sex ratio, reproduction, longevity, and movements are given for the four species (*Cryptotis parva*, *Reithrodontomys humulis*, *Peromyscus gossypinus*, *Sigmodon hispidus*) considered resident on the study plot.

On the basis of this and previous studies, 25 species of small mammals are known to occur in various types of flatwoods habitat in Florida. The most common species are the cotton rat, cotton mouse, and least shrew. Only the cotton rat is recorded in all studies. Among a wide variety of Florida habitats for which data are available, flatwoods are intermediate in both number of species and abundance of small mammals.

All resident species living on the burned study area were affected by the fire. Except for one shrew trapped in January, least shrews, harvest mice, and cotton rats disappeared from the burned area for several months after the fire. Shrews were not trapped in the burned area after January, and harvest mice and cotton rats did not reappear until March and April, respectively. There was no evidence of direct mortality from the fire, and the failure of animals from the

burned area to settle in the unburned area and an increased loss of residents from the unburned area appear to be attributable to social pressure. Cotton rats were relatively more abundant on the burned area in 1962 and 1963, but prior to the fire and in 1972 were more prevalent on the unburned area. This suggests that the unburned area provided generally superior habitat, but that for a period following the fire the burned area was more favorable. Cotton mice differed from other species in their response to fire, becoming more abundant on the burned area after the fire than before.

A review of the literature on population levels and fluctuations; reproduction, including sex ratio, age at puberty, litter size and frequency, and breeding season; seasonal variation in body weight; longevity; and movements of *Sigmodon hispidus* reveals considerable flexibility in its life history and ecology. The absence of well-marked geographic trends in the parameters examined suggests that local environmental conditions, mainly habitat type, may be as important an influence on the life history and ecology of this species as major climatic factors.

In the present study, natality appeared to be relatively more important in determination of population level than mortality. Variation in natality appears to be correlated primarily with temperature and rainfall. Although these physical environmental factors may affect natality directly, it is suspected that their principal influence is indirect through an effect on food quality.

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