POPULATIONS AND RANGE EFFECTS OF RODENTS ON THE SAND SAGEBRUSH GRASSLANDS OF WESTERN OKLAHOMA

By

CLAY YOUNG McCULLOCH, JR.

Bachelor of Science
Colorado State College of
Agriculture and Mechanic Arts
Fort Collins, Colorado
1948

Master of Science
University of Idaho
Moscow, Idaho
1953

Submitted to the faculty of the Graduate School of
the Oklahoma State University
in partial fulfillment of the requirements
for the degree of
DOCTOR OF PHILOSOPHY
August, 1959

POPULATIONS AND RANGE EFFECTS OF RODENTS

ON THE SAND SAGEBRUSH GRASSLANDS

OF WESTERN OKLAHOMA

Thesis Approved:

Thesis Adviser

Dean of the Graduate School

ACKNOWLEDGMENTS

This study was supported in part by the Oklahoma Cooperative Wildlife Research Unit, with Oklahoma Department of Wildlife Conservation, Oklahoma State University, U. S. Fish and Wildlife Service, and Wildlife Management Institute cooperating; and in part as a special project by the Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, Branch of Wildlife Research, U. S. Department of Interior. Office, laboratory, bunkhouse, and field facilities were provided by the Southern Great Plains Field Station, Agricultural Research Service, U. S. Department of Agriculture.

This project was carried out under the direction of my major advisor, Dr. A. M. Stebler, whose help is much appreciated. For advice and criticism in the preparation of this thesis, I also thank the other members of my graduate committee, who were Dr. F. M. Baumgartner, Dr. W. W. Hansen, Dr. J. R. Harlan, and Dr. G. A. Moore.

I am grateful to E. H. McIlvain, Superintendent, and members of the staff of the Southern Great Plains Field Station for providing me with unpublished records and other information pertinent to this study, for help in identifying range plants, and for much other assistance.

Helpful advice was also given by J. E. Engelman and Earl Nance of the U. S. Soil Conservation Service, by J. M. Inglis of Texas A. and M. College, and by Dr. B. P. Glass of Oklahoma State University.

For permission to work on their lands, thanks are due Arley Hudson and W. A. Vloedman. My wife, Pat Graber McCulloch, assisted in preparing this manuscript and in many other ways.

The scientific names of mammals mentioned here were taken from the list of Miller and Kellogg (1955). Scientific names of plants were from the catalogue of Waterfall (1952).

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

INTRODUCTION

Objectives of the present study were to determine comparative densities of rodent species populations on range lands of the sand sagebrush grassland type; to learn how these populations were related with stages of plant succession; to determine effects of rodents on the range lands, and to attempt to ascertain times and places in which rodent species populations may require control.

Data were collected from June, 1956, to November, 1958. The field work was done on sand sagebrush grasslands of mixed prairie type on the Southern Great Plains.

Estimates were made of densities of rodent species populations on three ten-acre live-trap plots located in pastures having, respectively, light, moderate, and heavy intensities of yearlong grazing by cattle. Relative densities of rodent species populations were compared by kill-trapping on two selected pairs of grazed and ungrazed areas. Annual and seasonal population fluctuations on other grazed and ungrazed areas were sampled by live-trapping or kill-trapping periodically.

Some rodent effects on vegetation were determined by examination of contents of rodent stomachs, cheek pouches, and burrows. Soil movements and other effects on soil were observed.

Among ranchers in this region it seemed a matter of common opinion that rodents are constant and serious forage competitors of cattle, and that rodent controls are needed for the good of the ranching business. That feeling has been partly the stimulus for this as well as earlier studies.

The places of greatest potential competition between rodents and cattle appeared to be the heavily grazed pastures. The time of greatest potential competition, all pastures considered, seemed to be during a population irruption of one species, the cotton rat.

Attempted methods of estimating competition in absolute quantities were unsatisfactory, due to complexities of rodents' diets, to other use of forage materials, and to factors other than rodents which may cause forage disappearance.

Several factors having the effect of natural regulation of populations were observed. Precipitation, topography, density and distribution of plant cover, and spatial behavior of the rodent species seemed important influences affecting densities of rodent populations. Some of these natural regulatory factors were to some extent controllable by the rancher through grazing practices. Observations suggested many and complex ecologic roles of rodents which need consideration as part of any proposed control operations.

METHODS

Most of the summer of 1956 was spent on field work, as was the period from June, 1957, to September, 1958. During the last 12 months of full-time field and laboratory work, the writer resided in Woodward, Oklahoma. Briefer periods were spent in the field during the 1956-1957 and 1958-1959 academic years.

All observations reported in this study were made in sand sagebrush grassland vegetation type in Harper and Woodward counties, Oklahoma, within five miles of the town of Fort Supply. Most of the field work was done on the Southern Plains Experimental Range. Rodent population data from areas ungrazed since 1939 were obtained from the Fort Supply Dam area, reserved by the U. S. Army Corps of Engineers. Other rodent studies were made on two privately owned ranches adjacent to the reserved lands of the Dam.

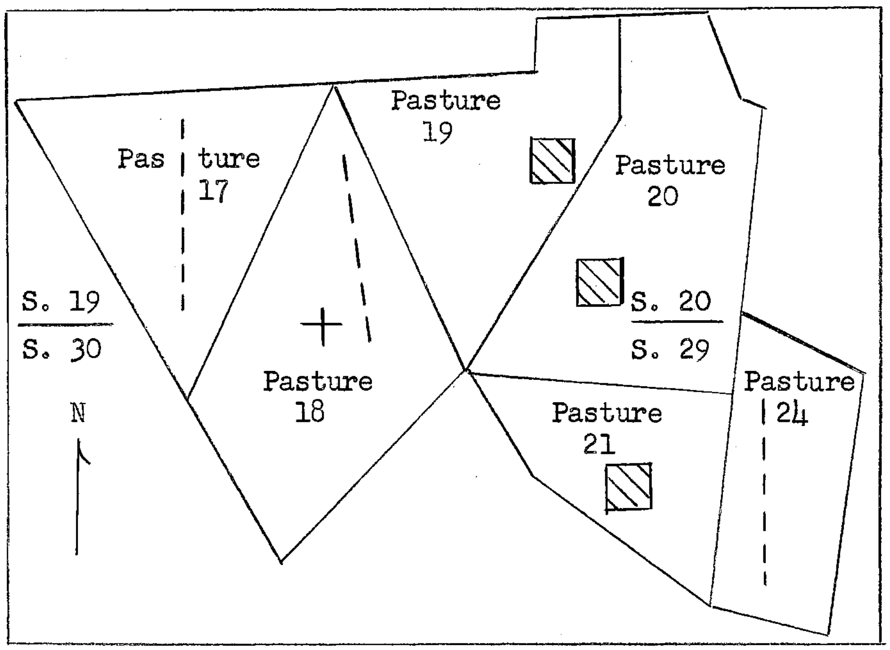
Live-trapping methods were used to get information on movements and for estimates of population trends and densities of rodent species. The animals were captured in part by use of small metal live-traps of the Havahart and the National brands. They were effective for taking native rodent species of all sizes, from silky pocket mice to wood rats, except pocket gophers. Live-trapped individuals were marked, released, and periodically recaptured. A total of 9500 live-trap-nights resulted in 3562 captures among 1183 individuals.

Live-traps were operated on three plots of 100 Havahart traps each. Trap stations on each plot were 66 feet apart in a grid pattern which covered 8.1 acres. The effective size of the grids was greater to an extent depending upon the cruising radii of the rodent species in question and the season. The plots were arbitrarily located in pastures grazed yearlong by cattle on the Southern Plains Experimental Range.

One live-trap plot was in lightly grazed pasture 20; another was in moderately grazed pasture 19, and the third was in heavily grazed pasture 21 (Figure 1). Traps on the plot in pasture 19 were operated from August, 1956, to September, 1958. During the periods of field work, each plot was operated for one to seven nights per month, usually not on consecutive nights on a given plot. For the last six nights' operation of the plot in the heavily grazed pasture, a National live-trap was added at alternate trap stations. This 50 per cent increase in numbers of traps was meant to increase the rate of recapture on that densely populated plot.

A half-cylinder shelter of heavy tar-paper covered each live-trap but did not prevent deaths of some rodents resulting from too long exposure to heat or to cold. Placing non-absorbent cotton nest material and excess food in each trap also failed to prevent some deaths in the traps during cold weather. Live-traps were tended throughout the night during the second winter of the study in an effort to reduce death losses. Only during periods of mild temperatures, mostly in spring and fall, were live-traps left open for 24 hours per day.

In other seasons, setting of live-traps usually began in late afternoon, and emptying began at daybreak the following morning. It usually took from four to eight or ten hours per plot to empty the traps, depending on trapping success and numbers of unmarked individuals to be handled.



Legend:

Live-trap grid, 8.1 acres

Line of 100 kill-traps

Scale: 1 inch = 2200 feet

Figure 1. Locations of live-trap grids and kill-trap lines on the Southern Plains Experimental Range, Harper County, Oklahoma. T. 25 N., R. 22 W.

In effect, live-traps were available to diurnal species during most of each daylight period.

In 1956, live-traps were baited with whole grains of wheat, oats, and sorghums mixed in peanut butter. The peanut oil matted and reduced the insulating value of the rodents' fur, and the trapsetting process was excessively lengthened by use of the paste bait. For these reasons only whole grain bait was used in live-traps in 1957 and 1958.

All live-trapped rodents were marked by toe-clipping until February, 1957. Beginning in July, 1957, metal ear-tags were added to the marked kangaroo rats. After February and March, 1958, the toe-clip method of marking was abandoned except for use on the less numerous species.

A direct method was used for estimating population densities on the live-trap plots. When most of the individuals on a plot seemed to have been captured and marked, the total number caught during that trapping period was presumed to be approximately the population of the plot. After the third or fourth night of trapping during a given period, additional trapping effort usually took previously uncaptured individuals at a rate which was not more than five to ten per cent of the total catch. In one period the number of previously uncaptured individuals of a species in the nightly catches was greater than ten per cent of the total catch. Population estimates were then made by use of a formula described by Underhill (1941), as reviewed by Stickel (1950).

For estimating species population densities, the effective size of a live-trap plot was assumed to be ten acres. This was the size of plot formed by adding to the grid area a boundary strip of width equal to one-half the distance between traps. The average cruising radius of each species studied was great enough to suggest that the effective size of an 8.1-acre grid was more nearly 11 or 12 acres, or even 16 or 17 acres for some species. Thus the total numbers captured on a grid may have come from an area larger than ten acres, and the estimated densities may be higher than were the actual densities. Cruising radii varied among rodent species, and they also may have fluctuated seasonally for a given species. The constant effective plot size was assumed for the sake of convenience in estimating densities.

The estimates of population densities assumed a random spatial distribution of the species. Actually, most rodent species' distributions appeared clumped in association with certain factors such as vegetation or topography.

"Homestead" refers to an area defined by Dice (1952) as "home range." The former term is used because, as proposed by Stebler (1958), it seems more appropriate for historic and linguistic reasons.

For a given period, the homestead of a recaptured individual was assumed to include all live-trap stations at which he was taken. Lines connecting the outside points of capture of an individual formed a polygon except for cases in which the points all lay in one line. The area could include trap stations at which he was not caught. To the polygon or line was added a boundary strip of one-half the distance between traps, to compensate for lack of traps in the presumed boundary area of the homestead.

For all rodent species here discussed, it is likely that the estimated homestead areas may not have coincided exactly with the individuals' true homesteads. It is not known how much the trapping interfered with normal activities of the animals. It is assumed, as suggested by Stickel (1954), that the homesteads revealed by live-trapping are significantly related to the natural homesteads and are not merely artifacts.

Generally correlated with relative size of homestead was the "cruising radius," which refers to the distance between the most widely separated sites of capture of an individual during a given period. The cruising radius seemed useful for some comparative purposes and was more easily computed than homestead area.

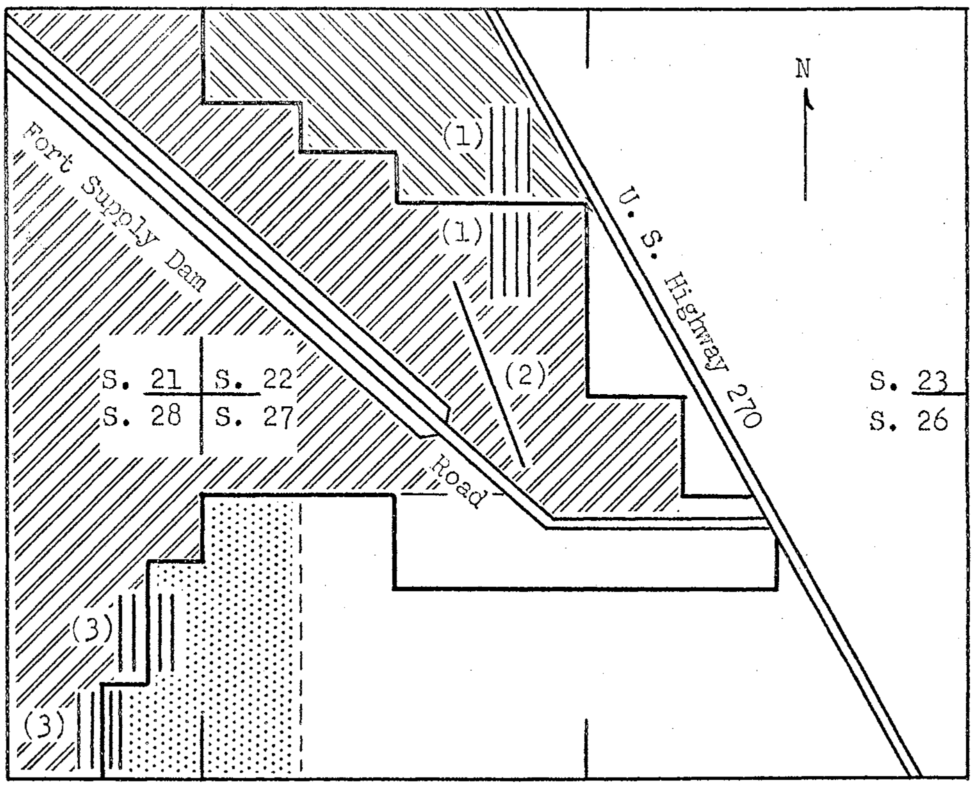
"Dead-trapping" or "kill-trapping" provided information on population trends and relative numbers of species, as well as carcasses for food-use samples and data on age and breeding cycles. Excluding pocket gophers, 5142 kill-trap-nights yielded 1664 rodents.

Dead-trapping methods were not used for estimating absolute numbers of rodents per unit of area because of factors which lead to exaggerated estimates. Dead-trapping makes it difficult to allow for movement of animals into a trapped plot as residents are removed in successive nights of trapping. Dead-trapping also fails to indicate size of the area beyond the grid boundaries which contributes to the catch in the grid. For example, a species with an average nightly cruising radius of 65 feet would cause the effective size of a half-acre kill-trap grid to be more than three times the area enclosed by the grid of traps. Bole (1939), Dice (1941), and Stickel (1946) have demonstrated the unreliability of removal trapping on small plots as a method of estimating actual numbers of rodents on an area.

Except where otherwise noted, dead-trapping was done along 2178-foot lines of 100 trap-stations each, with 22 feet between stations. In July and August, 1957, one Victor rat and one Museum Special trap were set at each station each night. Beginning in October, 1957, a Victor rat trap with bait pedal enlarged to 2-by-2 inches was the only trap set at each station. Museum Special traps tended to catch disproportionate numbers of immature kangaroo rats, presumably because adults often snapped but escaped from these smaller traps. Therefore, Museum Special traps were not used after November, 1957. Rat traps with enlarged triggers seemed effective for all sizes of rodents on the area except silky pocket mice. Museum Special traps also failed to take this small species. Whole grain in peanut butter was used as bait on all snap-traps.

Four kill-trap lines were operated repeatedly at various times from July, 1957, to November, 1958. The starting point and bearing of each 2178-foot line were arbitrarily selected. The lines were located in this way in order to keep them within their pasture boundaries and to avoid permanent cattle-exclosure areas. One line was placed in lightly grazed pasture 18, one in moderately grazed pasture 17, and one in heavily grazed pasture 24 of the Experimental Range (Figure 1). A fourth was located on an ungrazed area near Fort Supply Dam (Figure 2). Each line served chiefly to sample seasonal changes in populations in a given place and also to provide carcasses for studies of age composition, reproduction, and food use.

The single kill-trap lines seemed less satisfactory than grid arrangements of traps for comparing relative densities of a given species on different areas. Single lines seemed seldom to transect equal proportions



Legend:

Area Ungrazed since 1940

Area grazed intermittently

Area grazed yearlong

(1) Lines of 50 kill-traps each, set in April, 1958

(2) Line of 100 kill-traps, set repeatedly, November, 1957-November, 1958

(3) Lines of 50 kill-traps each, set in May, 1958

Scale: 2 inches = 1 mile

Figure 2. Locations of kill-trap lines on ungrazed and grazed areas near Fort Supply Dam, Woodward County, Oklahoma. T. 24 N., R. 22 W.

of each different topographic and vegetational type on the areas where a comparison was desired. By replication, however, a series of trap-lines, forming a grid, appeared to average these proportional differences and presumably allowed a more valid comparison of relative densities of populations on different areas.

Relative numbers of rodents on two privately-owned pastures were compared with rodent numbers on adjacent ungrazed areas. Grids formed by pairs of lines of Victor rat traps were used for each comparison. One line of a pair was on a grazed area, and its counterpart was on an ungrazed area. Each line was 1078 feet long and contained 50 traps spaced 22 feet apart. Each pair of trap-lines was set for one night, both lines of a pair being run the same night.

In one comparison, four such lines formed a grid 1078 by 594 feet, which contained 200 traps. One grid was located on an ungrazed area and the other was on a pasture grazed seasonally and intermittantly, probably at a moderate degree. The trap-lines started at 100 feet, and extended at right angles, from the fence between grazed and ungrazed areas. The total effort was 200 trap-nights on each of a matched pair of 14.7-acre grids, the opposing edges of which were 200 feet apart.

The second comparison also involved four matched pairs of 1078-foot trap-lines, allowing 200 trap-nights on an ungrazed area and 200 on a pasture grazed yearlong and probably moderately. These lines were parallel to the fence which separated grazed from ungrazed land. They formed two matched pairs of kill-trap grids 1078 by 150 feet, or 3.7 acres per grid.

A comparison of average trapping success during the present and earlier studies was based on records for a given type of kill-trap.

Interpretation of this comparison is limited by differences in arrangements of traps and in lengths of trapping periods. The methods used during the years 1940-1942 and 1949 were those described by Trowbridge (1941); they were employed by Trowbridge (1941, 1942), McMurry (1942, 1943, 1947), and Frank (1950) on the Experimental Range.

Studies of foods used by eight rodent species were the chief means of investigating the effects of rodents on the range. Contents of 400 stomachs and 298 pairs of cheek pouches were examined as taken from the various areas and seasons. Virtually all of the cheek-pouch items were identifiable and were tallied according to occurrence frequency. The contents of each collected stomach were placed in Petri dishes and examined under a binocular dissecting microscope. Usually, only a fraction of a per cent of the volume of a stomach sample could be identified as to plant species. The rest of the stomach contents were classed according to such major categories as color and consistency, and their relative volumes were recorded.

Twenty-two kangaroo rat dens were excavated in 1956 and 1957 on the Experimental Range. Their food caches, nest materials, and debris were examined. Materials ejected from three dens by their occupants were sifted from the sand around the entrances and also examined, as was debris sifted from loose sand along 30 feet of tunnels in one burrow system.

The number of rodent burrows per acre was sampled on the three live-trap grids in the summer of 1957. Burrow entrances were counted on one hundred mechanically-spaced circular plots of 0.01 acre each, on each grid. The circular plots were centered at the live-trap stations, which had been located by chain and compass.

Pocket gophers required field work separate from that of the other species population studies. Areas on and off the Experimental Range were systematically searched along grid lines for pocket gopher mounds in the summers of 1956 and 1957 and in the late winter and spring of 1958. In addition, records were kept of pocket gopher workings noted during the course of other field work. Specimens of this species were kill-trapped by the use of pincers-type traps set in the burrows.

A tally of mounds and a census of pocket gophers was made in the 160 acres of moderately grazed pasture 19 from February to April, 1958. Locations of all mound-groups were recorded, all mounds in each group were counted, and the occupants were removed. Trapping was continued until each burrow system seemed void of pocket gophers. The mound-groups were repeatedly checked for signs of renewed activity until November 12, 1958. A complete count was also made of mounds, but not pocket gophers, on 40 acres of ungrazed land near Fort Supply Dam in May, 1958.

Composition of vegetation was sampled by the line interception method on each of three live-trap plots. One hundred mechanically-spaced transect lines were used on each plot. The procedure was essentially as described by Parker and Savage (1944) except that two-meter rather than the customary ten-meter lines were employed. Both lengths had been used and found satisfactory by Southern Great Plains Field Station personnel, who recommended the shorter lines because they could be handled by a single worker. Comparable vegetation data on entire experimental pastures were provided by samples taken by crews of the Southern Great Plains Field Station. These data are used here with the understanding that they are unpublished tabulations which may be subject to correction in the final analyses.

DESCRIPTION OF AREA

Physiography and Soils

Sand sagebrush grassland covers about 20 to 25 million acres of the Southern Great Plains, according to estimates by the Southern Great Plains Field Station. Areas of this vegetation type seldom exceed a dozen miles in width but extend for more than a hundred miles in an east-west direction along the major streams. Elevation is approximately 2000 feet above sea level at the Southern Plains Experimental Range, which appears to be almost directly on two of the four natural boundaries which might be considered the eastern limit of the Great Plains (Great Plains Committee, 1936). One boundary is the eastern edge of the Great Plains Physiographic Province, and the other is the line dividing short grass from tall grass regions. The third suggested boundary is the 20-inch rainfall line, about 75 miles west of the Experimental Range. The fourth is the western boundary of the pedalfers, which is about 75 miles east of the Experimental Range.

Topographically, the area is characterized by dunes, most of which are stabilized to some degree by vegetation. Soils of the Experimental Range are mostly of three categories, according to a soil type map prepared by the U. S. Soil Conservation Service in 1956. They are fine sands, loamy sands, and fine sandy loams. These are subdivided into various classes according to topography and other factors.

The live-trap grid in lightly grazed pasture 20 was entirely of loamy fine sand of 8-12 per cent slopes, according to the Soil Conservation Service map. Within all three live-trap grids there were areas of topographic differences which seemed to affect vegetation, even though such areas were too small to be shown on the soil type map.

Approximately 91 per cent of the area of the live-trap grid in moderately grazed pasture 19 was shown on the map as loamy fine sand of 8-12 per cent slopes. The remaining 9 per cent of the grid area was shown as fine sandy loam of 3-5 per cent slopes.

The area of the live-trap grid in heavily grazed pasture 21 was shown as approximately 90 per cent loamy fine sand of dune topography and 3-8 per cent slopes. The remainder of the grid area was about half loamy fine sand of 0-3 per cent slopes and half fine sand of high dunes with greater than 15 per cent slopes.

Topographic differences seemed to affect vegetation more than did the mapped differences in soil types.

Climate

The present study began during a year of severe drought, 1956, following a year when above-average precipitation was recorded during the growing season at the Experimental Range (Table I) and at the nearby town of Fort Supply (U. S. Dept. of Commerce, 1956, 1957). However, the period 1952-1956 as a whole was one of drought. Annual precipitation at Fort Supply during those five years was less than the 55-year average of 21 inches (U. S. Dept. of Commerce, 1959). The study continued through a year with an extremely wet growing season, 1957, and through another growing season during which precipitation was above average (Table I). Wind velocities and evaporation at the Experimental Range are high (McIlvain et al., 1955). The temperature extremes recorded there since 1940 are 113° F. and minus 28° F. The 200-day average growing season extends from about April 10 to October 27 (McIlvain et al., o. c.).

Vegetation

Vegetation of the sand sagebrush grassland is a mixed prairie type characterized by a shrub, sand sagebrush (*Artemisia filifolia*), which seldom exceeds a height of three or four feet. Tall and short grasses are typical of the herbaceous vegetation. Species composition and percentage of area covered by the vegetation on dunes differ somewhat from those on the relatively low and flat areas between dunes. These topographic differences were associated with important differences in rodent populations which will be discussed later. Sand sagebrush occurs on all areas, regardless of topography or degree of grazing, but tends to be relatively more abundant on dunes than on interdunal sites. Sand sagebrush was only slightly more abundant on the grazed pastures than on the ungrazed areas. For example, crown coverage of that shrub was 44 per cent on the heavily grazed pastures, as compared with 38 per cent on the ungrazed exclosures (Table 2).

At the time of this study, the most abundant grasses on dunes of the ungrazed areas appeared to be the clump-forming tall species. Sand lovegrass (*Eragrostis trichodes*) and little bluestem (*Andropogon scoparius*) were especially abundant on ungrazed dunes. Total basal coverage of herbaceous vegetation tended to be less on dunes than on interdunal areas. On the ungrazed interdunal sites, the principal herbaceous species were

Table 1. Annual and Growing-Season Precipitation on the Southern Plains Experimental Range, Harper County, Oklahoma. The 1939 and 1940 records are for Woodward, Oklahoma.

Year	Jan. 1 - Dec. 31 inches	April 1 - Sept. 30 inches
1939	20.24	13.44
1940	18.09	10.53
1941	41.22	24.60
1942	23.59	13.77
1943	20.99	16.43
1944	25.37	15.61
1945	19.33	15.69
1946	21.69	9.69
1947	22.51	16.47
1948	24.89	17.07
1949	32.76	23.70
1950	28.08	27.14
1951	22.25	16.97
1952	12.40	9.44
1953	18.27	10.71
1954	9.97	8.63
1955	19.57	18.67
1956	10.47	9.05
1957	42.64	30.65
1958	22.83	18.85
20-Year Average, 1939-1958	22.86	16.36

Table 2. Vegetation on Three Pairs of Pastures Grazed Yearlong Compared With Vegetation on Live-Trap Grids in Three of Those Pastures and With Areas Ungrazed for 18 Years. Southern Plains Experimental Range, Harper County, Oklahoma. July-August, 1958.

Species	Average Percentage of Line-Intercept Per Species						
	Lt. Grazed		Mod. Grazed		Hv. Grazed		Ungrazed
	Past.	Grid	Past.	Grid	Past.	Grid	Areas
Sporobolus cryptandrus	1.96	2.14	2.12	1.86	2.25	1.45	.45
Bouteloua gracilis	3.20	5.08	1.79	.45	3.20	.17	1.27
Andropogon hallii	.10	.20	.08	.04	.08	.04	.34
Andropogon scoparius	.12	.16	.12	.21	.04	.22	.94
Eragrostis trichodes	.15	.11	.16	.38	.08	.16	.43
Panicum virgatum	.02	.10	.02	.11	.02	.04	.04
Bouteloua curtipendula	.02	0	.04	.08	.04	.02	.14
Poa arachnifera	.02	.12	.01	.04	T	0	.08
Paspalum ciliatifolium	.79	.97	.89	1.42	.81	1.16	.25
Cyperus schweinitzii	1.30	2.24	1.37	1.18	2.06	1.07	1.04
Bouteloua hirsuta	.01	.06	.04	0	.06	0	.01
Miscellaneous grass	.33	.42	.55	.54	.75	.43	.59
Total perennial grass	8.02	11.60	7.19	6.30	9.39	4.77	5.57
Total annual grass	.44	.13	.56	.46	.72	1.32	.10
Total perennial forbs	.32	.58	.24	.58	.08	.17	.17
Total annual forbs	.97	1.21	.90	1.06	.87	.44	1.07
Total herbaceous spp.	9.75	13.52	8.80	8.41	11.06	6.70	6.91
Artemisia filifolia	38.26	33.80	42.11	34.68	44.17	48.14	38.05
Rhus aromatica	2.52	0	.03	0	0	0	0
Miscellaneous shrubs	.01	0	0	0	.01	0	.20

sand bluestem (*Andropogon hallii*), little bluestem, sand dropseed (*Sporobolus cryptandrus*), and blue grama (*Bouteloua gracilis*).

Heavy grazing tended to remove the tall grasses except where they were protected under crowns of sagebrush. On heavily grazed dunes the principal herbaceous species in terms of basal cover were sand dropseed, sand paspalum (*Paspalum ciliatifolium* var. *stramineum*), and annual grasses. Blue grama and sand dropseed tended to be the most abundant herbaceous species on heavily grazed interdunal sites. Heavily grazed areas tended to have much more blue grama on their interdunal sites than there was on the ungrazed interdunal sites.

On lightly and moderately grazed areas, the amounts of the various plant species tended to be intermediate between those on ungrazed and heavily grazed areas. Among the pastures in 1958 there was one notable difference. It was that dense stands of ragweed (*Ambrosia psilostachya*) were present on interdunal areas in lightly and moderately grazed pastures and absent on heavily grazed areas. Tall forbs were not absent from heavily grazed interdunal areas, but the species present there were mostly those which tended to form crown cover less dense than that of ragweed. On all observed areas, the species aspects of tall forb stands were markedly different in different years. For example, *Mentzelia stricta* appeared as one of the most abundant tall forbs on most grazed areas in 1957 but was a comparatively small part of the herbaceous crown cover in 1958. *Croton texensis* and *Eriogonum annuum* were other species whose relative abundance varied greatly from year to year.

The chief difference between grazed and ungrazed areas apparently was that the latter had an estimated two to four times more basal coverage of tall grasses than did areas with any degree of grazing. Ungrazed areas also tended to have less basal coverage of sand dropseed and less of the sod-forming blue grama than any grazed area.

Comparison of vegetation on three live-trap plots and the paired pastures in which they were located is given in Table 2. The sample percentage of ground surface covered by each species is indicated by the average percentage of transect line intercepted by the species. Basal coverage was determined for herbaceous plants, and crown or foliage coverage was recorded for shrubs. In terms of their crown coverage, which was not sampled, forbs were much more conspicuous than they seemed to be in the line transect data. Sedge (Cyperus schweinitzii) is included in the total perennial grass figures.

The data for the three pairs of pastures (Table 2) were provided by the Southern Great Plains Field Station. Standard errors of these samples did not exceed five per cent for the totals of perennial grasses. Field Station crews also sampled the ungrazed areas, which were seven small permanent exclosures of 1.5 acres to 11 acres each, not grazed by cattle for 18 years, that is, since 1940. The two lightly grazed pastures of this set of samples totalled 426 acres in area. The two moderately grazed pastures totalled 320 acres, and the two heavily grazed pastures totalled 214 acres in area. Within one of each pair of pastures was an 8.1-acre live-trap grid on which vegetation samples were taken by me. Standard errors of samples on the live-trap grids ranged from 10 to 11 per cent for total perennial grasses.

In the sample percentage of crown coverage of sand sagebrush, each live-trap grid was similar to its associated pair of pastures. In percentage of basal coverage of herbaceous species in the samples, there were some appreciable differences between two of the live-trap grids and their respective paired pastures.

According to the samples, the lightly grazed live-trap grid had greater percentage cover of blue grama and perennial forbs than did the paired lightly grazed pastures as a whole. The difference in vegetation was probably due mainly to topographic differences. The live-trap grid contained proportionately more of the low flat areas between dunes. Such areas generally support denser stands of herbaceous vegetation than do the dunes, perhaps because more moisture is available for plants in the low areas. Runoff does occur on these sandy soils, and pools of water sometimes accumulate to depths of several inches on the interdunal areas during torrential storms.

The moderately and heavily grazed live-trap grids had proportionately less of the principal interdunal species and more of the dune species than did their respective paired pastures. These differences also seemed due mostly to the differences in proportional areas of dunal and interdunal topography on the grids as compared with their pastures as a whole. These two grids had proportionately less interdunal area than their paired pastures.

In comparing the three live-trap grids with each other, it appeared that the lightly grazed one had more interdunal area than the other two. Accordingly, the lightly grazed live-trap grid had more blue grama coverage than the moderately and heavily grazed ones. The lightly grazed grid, however, had somewhat less tall grass coverage than did the moderately grazed grid. Tall grass and herbaceous coverage on the heavily grazed live-trap grid were much less than on the lightly and moderately grazed grids.

RESULTS

Total Rodent Species Populations

Rodent populations were characterized more by extreme periodic fluctuations in numbers than by any stable or average densities on a given area. During the two years of the present study, live- and dead-trap records indicated changes in rodent numbers. Ten species of rodents were taken during this period, and eight of these were trapped on both ungrazed and grazed areas of sand sagebrush grassland.

For a given season, trapping success with dead-traps paralleled that of live-traps (Table 3). It is not known if the actual differences between dead- and live-trapping success were due to differences in populations on the sampled areas, or to possible differences in effectiveness of the two types of traps. As explained in "Methods" (p. 8), it did not appear feasible to try to convert dead-trap records into estimates of numbers of rodents per unit of area.

The first comparison of different grazed areas was made in the summer of 1957. Compared with those of other periods, total numbers of rodents were extremely low in July and August of 1957 on the four experimental pastures then sampled. In three pastures grazed lightly, moderately, and heavily, respectively, average trapping success varied from three to four rodents per hundred kill-trap stations per night (Table 4). These were the lowest rates of success observed during the

Table 3. Comparison of Trapping Success on Dead-Trap Lines and Live-Trap Grids. Southern Plains Experimental Range, Harper County, Oklahoma

Period	Total Rodent Species Average Catch Per Night Per Hundred Traps					
	Lightly Grazed Pastures		Moderately Grazed Pastures		Heavily Grazed Pastures	
	P.18 Dead-Trap Line	P.20 Live-Trap Grid	P.17 Dead-Trap Line	P. 19 Live-Trap Grid	P. 24 Dead-Trap Line	P. 21 Live-Trap Grid
	no.	no.	no.	no.	no.	no.
July 16 - Sept. 26, 1957	3	8	3	6	3	15
Oct. 8 - Nov. 1, 1957	11	11	6	8	14	24
May 20 - 29, 1958	40	49	39	75	40	63

study. The total-catch estimate of total rodent population density was 35 individuals per ten acres on the moderately grazed live-trap plot in July, 1957.

Throughout late summer, 1957, rodent numbers remained low on all of the grazed areas which were sampled. In September the total-catch estimates of densities were 24, 17, and 48 rodents per ten acres on lightly, moderately, and heavily grazed live-trap plots, respectively (Table 5). The lowest rates of live-trapping success observed during this study occurred in September, 1957 (Table 3).

Table 4. Population Variations Suggested by Trapping Success Along Dead-Trap Lines, Harper and Woodward Counties, Oklahoma

Rodent Species	Average Catch Per Night Per Line of 100 Trap-Stations												
	Ungrazed Area, Fort Supply Dam			Lightly Grazed Pasture 18			Moderately Grazed Pasture 17			Heavily Grazed Pasture 24			
	Nov. 12-14 1957	May 20 1958	Nov. 12 1958	Aug. 4-6 1957	Oct.30-Nov. 1 1957	May 21 1958	July 16-18 1957	Oct. 29-31 1957	May 20 1958	Aug. 4-6 1957	Oct. 29-31 1957	May 22 1958	Nov. 12 1958
	no.	no.	no.	no.	no.	no.	no.	no.	no.	no.	no.	no.	no.
Dipodomys ordii	22.7	32	11	2.0	8.0	18	2.0	6.3	17	1.7	12.3	23	13
Onychomys leucogaster	5.3	7	9	0.7	1.7	14	1.0		14	0.7	1.0	12	17
Sigmodon hispidus	14.3	5	65		0.3	1			1		0.3		50
Citellus spilosoma		2		0.3	1.0	1	0.3		1	0.7	0.7	2	
Citellus tridecemlineatus						2				0.7			
Peromyscus maniculatus	4.7	16	4			4			3			1	3
Perognathus flavus													
Perognathus hispidus									1				
Neotoma micropus	3.0	7							2			2	1
Total	50.0	69	89	3.0	11.0	40	3.3	6.3	39	3.8	14.3	40	84

Table 5. Comparisons of Late Summer Populations of Rodent Species on Three Live-Trap Plots, Southern Plains Experimental Range, Harper County, Oklahoma.

Species	Total-Catch Estimates of Individuals Per Ten Acres						
	1956	1957			1958		
	Mod. Grazed Pasture 19	Lt. Gr. Past. 20	Mod. Gr. Past. 19	Heav. Gr. Past. 21	Lt. Gr. Past. 20	Mod. Gr. Past. 19	Heav. Gr. Past. 21
	no.	no.	no.	no.	no.	no.	no.
Dipodomys ordii	68	18	10	36	50	63	106
Onychomys leucogaster	6		2	3	26	13	28
Sigmodon hispidus					121	105	16
Citellus spilosoma	11	5	5	8	5	6	12
Citellus tridecemlineatus	2	1			2	2	3
Peromyscus maniculatus						2	
Perognathus flavus	4			1	1	1	
Perognathus hispidus					7		2
Total Rodents	91	24	17	48	212	192	167

That first comparison of populations on live-trapped areas suggested that numbers of rodents varied more from season to season on a given area than they did from one area to another during a given season. In September, 1957, the differences in total rodent numbers among the three live-trap plots were considerably less than the differences between Septembers of 1956 and 1957 on the moderately grazed plot (Table 5).

In the latter part of the drought summer of 1956, there had been an estimated 91 rodents per ten acres on the moderately grazed live-trap plot (Table 6). The moderate to high numbers of rodents then present were not sustained through the following winter.

The live-trap records suggested a decline in total rodent numbers, especially among kangaroo rats (Dipodomys ordii richardsoni), during the winter of 1956-1957 (Table 6). The cool and unusually wet spring of 1957 may have contributed to mortality and other causes of the low populations found in the summer of 1957. The greater part of the decline, however, occurred before those rains which began in March. A similar decline was observed by J. M. Inglis (personal communication) during the winter of 1956-1957. His observations pertained to sand sagebrush grassland sites 65 miles southwest of the Southern Plains Experimental Range.

On all of the grazed areas which were sampled, the total rodent densities began to increase during the fall of 1957. Kill-trapping success in November, 1957, was two and three times as great as it had been in July and August (Table 4). On the live-trap plots, the total rodent catch generally continued to increase throughout the winter of 1957-1958 (Tables 6, 7, and 8). The increase at that time seemed mostly

Table 6. Totals of Individuals of Rodent Species Captured on One 8.1-Acre Live-Trap Grid. Moderately Grazed Pasture 19, Southern Plains Experimental Range, Harper County, Oklahoma. (h = hibernation)

Species	Aug.28-Sept.6, 1956	Dec. 24, 1956	Jan. 23, 1957	Feb. 15, 1957	July 6-10, 1957	Sept. 8-12, 1957	Oct. 7-18 1957	Dec. 18, 1957	Jan. 22, 1958	Feb. 21, 1958	March 24, 1958	April 11-22 1958	May 25, 1958	June 20-29 1958	Aug.11 -Sept.5 1958
	no.	no.	no.	no.	no.	no.	no.	no.	no.	no.	no.	no.	no.	no.	no.
Dipodomys ordii	68	28	30	23	21	10	22	27	41	40	52	65	56	53	63
Onychomys leucogaster	6	2	4		3	2	2	4	2	2		5	5	6	13
Sigmodon hispidus							1		1	4	2	8	9	37	105
Citellus spilosoma	11	h	h	h	6	5	1	h	h	h		2		5	6
Citellus tridecemlineatus	2	h	h	h	3			h	h	h		2		1	2
Peromyscus maniculatus								3	8	9	3	8	2	2	
Perognathus flavus	4			1	2		1					1	3	6	2
Neotoma micropus												1			1
Total	91	30	34	24	35	17	27	34	52	55	57	92	75	110	192

due to reproduction of one species, the kangaroo rat.

By April and May, 1958, the total rodent catches were from two to six times as great as they had been in the fall of 1957 on the six experimental pastures (Tables 4, 6, 7, and 8). During the summer of 1958, the total rodent density on each area continued to increase after the end of the 1957-1958 breeding season of kangaroo rats. The summer buildup of total rodent numbers was due mostly to cotton rats, although other species, such as grasshopper mice (Onychomys leucogaster breviauritus), also reproduced abundantly during the spring and summer of 1958.

In the spring of 1958, each of two grazed areas differed little from its ungrazed counterpart in terms of total rodent densities suggested by kill-trapping (Tables 9 and 10), but there were marked differences in species ratios. For example, cotton rats were the most numerous species on the ungrazed areas; kangaroo rats were the most abundant on grazed lands.

Total rodent densities in late summer and fall of 1958 seemed unusually great, judging from total catches on each sampled area during earlier periods of this study (Tables 4, 6, 7, and 8). Average trapping success (Table 11) during the latter part of 1958 also seemed unusually high in comparison with that of studies made in 1940-1942, and 1949, on the Experimental Range. Those studies were reported by Trowbridge (1941, 1942), McMurry (1942, 1943, 1947), and Frank (1950).

Along the single kill-trap lines, the total rodent catches were greater on the ungrazed land than in the pastures in November, 1957 (Table 4). Those first trapping records on the ungrazed area suggested that one species in particular was abundant there in late 1957, when it was notably scarce on the grazed lands (Tables 4, 6, 7, and 8). That species was the cotton rat (Sigmodon hispidus texianus).

Table 7. Totals of Individuals of Rodent Species Captured on One 8.1-Acre Live-Trap Grid. Lightly Grazed Pasture 20, Southern Plains Experimental Range, Harper County, Oklahoma. (h = hibernation)

Species	Sept. 22-26, 1957	Oct. 8-18, 1957	Dec. 22, 1957	Jan. 27, 1958	Feb. 24, 1958	March 26, 1958	April 19-30, 1958	May 27, 1958	Aug. 8-22, 1958
	no.	no.	no.	no.	no.	no.	no.	no.	no.
Dipodomys ordii	18	21	37	29	32	34	39	33	50
Onychomys leucogaster			6	10	1	2	9	2	26
Sigmodon hispidus		1	1	4	1	3	5	8	121
Citellus spilosoma	5	8	h	h	h	1			5
Citellus tridecemlineatus	1	1	h	h	h	1			2
Peromyscus maniculatus			1	1	2	1	5	3	
Perognathus flavus				1	1		3	3	1
Perognathus hispidus									7
Total	24	31	45	45	37	42	61	49	212

Table 8. Totals of Individuals of Rodent Species Captured on One 8.1-Acre Live-Trap Grid. Heavily Grazed Pasture 21, Southern Plains Experimental Range, Harper County, Oklahoma. (h = hibernation)

Species	Sept. 15-19, 1957	Oct. 9-21, 1957	Dec. 26, 1957	Jan. 30, 1958	Feb. 27, 1958	March 21, 1958	April 16-28, 1958	May 29, 1958	July 1-9, 1958	Aug. 12- Sept. 3, 1958
	no.	no.	no.	no.	no.	no.	no.	no.	no.	no.
Dipodomys ordii	36	41	59	66	76	73	100	62	125	106
Onychomys leucogaster	3	2	2		3		1		3	28
Sigmodon hispidus									1	16
Citellus spilosoma	8	9	h	h	h			1	6	12
Citellus tridecemlineatus			h	h	h				5	3
Peromyscus maniculatus							2		1	
Perognathus flavus	1		1			1	1		4	
Perognathus hispidus									2	2
Total	48	52	62	66	79	74	104	63	147	167

Table 9. Comparison of Rodent Species Taken in Paired Dead-Trap Lines on Ungrazed and Intermittently Grazed Areas. Fort Supply Dam and Vicinity, Woodward County, Oklahoma. April, 1958.

Species	Ungrazed Area		Intermittently Grazed Area	
	Number	Percentage of Catch	Number	Percentage of Catch
Dipodomys ordii	11	9	77	58
Onychomys leucogaster	1	1	23	17
Sigmodon hispidus	87	72	17	13
Citellus spilosoma			2	1
Peromyscus maniculatus	21	18	9	7
Neotoma micropus			5	4
Total	120	100	133	100

Table 10. Comparison of Rodent Species Taken in Paired Dead-Trap Lines on Ungrazed and Yearlong Grazed Areas. Fort Supply Dam and Vicinity. Woodward County, Oklahoma. May, 1958.

Species	Ungrazed Area		Yearlong Grazed Area	
	Number	Percentage of Catch	Number	Percentage of Catch
Dipodomys ordii	47	43	75	62
Onychomys leucogaster	7	6	17	14
Sigmodon hispidus	22	20	1	1
Citellus spilosoma	4	4	10	8
Peromyscus maniculatus	25	23	12	10
Perognathus hispidus	3	3	0	0
Neotoma micropus	1	1	6	5
Total	109	100	121	100

Table 11. Comparisons of Relative Densities of Total Rodent Species Populations and of Two of the Most Abundant Species Populations in Various Periods, as Suggested by Average Trapping Success with Victor Rat Traps, 1940-1958. Southern Plains Experimental Range, Harper County, Oklahoma. Averages Represent All Pastures for Which Results were Reported for a Given Period.

Period	Rodents Taken Per Night Per Hundred Traps		
	Total Rodents	*Dipodomys ordii*	*Sigmodon hispidus*
	no.	no.	no.
Nov. 22-Dec. 28, 1940 [Avg. computed from Table 2 of Trowbridge (1942)]	14	12	0
June 12-19, 1941 [Avg. computed from Table 4 of McMurry (1942)]	5	4	0
Nov. 25-Dec. 19, 1941 [Avg. computed from Table 2 of Trowbridge (1942)]	20	16	2
May 22-June 6, 1942 [Avg. computed from Table 1 of McMurry (1943)]	14	9	1
Dec. 10-21, 1942 [Avg. computed from Table 1 of McMurry (1947)]	27	20	4
Oct. 30-Dec. 17, 1949 [Avg. computed from Table 30 of Frank (1950)]	11	7	T
July 16-Aug. 6, 1957 [This study]	3	2	0
Oct. 29-Nov. 1, 1957 [This study]	11	9	T
May 20-22, 1958 [This study]	40	19	1
Nov. 12, 1958 [This study]	84	13	50

Kangaroo Rat Populations

Throughout most of the period of the study, the kangaroo rat (Dipodomys ordii richardsoni) was the most abundant rodent trapped on each of the areas. Some of its population characteristics, therefore, can be described in some detail.

Results of trapping with a grid arrangement of traps suggested that degree of grazing was associated with average densities of kangaroo rats over areas of several acres or larger. Grazing by cattle tended to determine the amount of plant cover on an area, which in turn affected distribution of kangaroo rats. Of the three live-trap plots, the heavily grazed one had the greatest densities of kangaroo rats in the summer of 1958 (Table 5). The total-catch estimates of populations then varied from 50 to 106 individuals per ten acres on the respective plots. The heavily grazed plot was the one with the least herbaceous cover, least tall grass, most annual grass, and the most sand sagebrush (Table 12). In 1949, Frank (1950) had concluded that the denser populations of kangaroo rats were associated with heavy grazing.

Heavy grazing apparently made a greater proportion of a given area usable for kangaroo rats than would light, moderate, or no grazing. Under less than heavy degrees of grazing, dense stands of herbaceous plants taller than blue grama tended to occupy the low flat areas between dunes. Kangaroo rats generally tended to avoid such sites (Table 13) except those which were crossed by roads or cattle trails. These made the dense stands penetrable. In the absence of trails, kangaroo rats had obvious difficulty travelling through dense herbaceous vegetation. It tended to

Table 12. Vegetation Cover and Kangaroo Rat Densities on Three Live-Trap Plots. Southern Plains Experimental Range, Harper County, Oklahoma. August, 1958.

	Plot		
	Lightly Grazed	Moderately Grazed	Heavily Grazed
Kangaroo rats per ten acres (no.)	50	63	106
Percentage basal cover:			
Total herbaceous species	13.52	8.41	6.70
Tall grasses	.57	.74	.46
Blue grama	5.08	.45	.17
Sand dropseed	2.14	1.86	1.46
Annual grasses	.13	.46	1.32
Perennial forbs	.58	.58	.17
Annual forbs	1.21	1.06	.44
Percentage crown cover:			
Sand sagebrush	33.80	34.68	48.14

be much more of a hindering factor to kangaroo rats than did the sand sagebrush, the crown coverage of which was somewhat greater on heavily than on lightly and moderately grazed areas.

The heavily grazed sites with sparse herbaceous cover seemed to be used by a greater number of kangaroo rats per unit of area than were the lightly and moderately grazed areas of sparse cover. On the heavily grazed plot, which as a whole had sparse herbaceous cover, the rate of

Table 13. Comparison of Kangaroo Rat Use of Areas of Dense and Sparse Herbaceous Vegetation on Three 8.1-Acre Live-Trap Grids. Southern Plains Experimental Range, Harper County, Oklahoma. May 25-September 5, 1958.

Type of Area in Which Trap-Stations Were Located	Kangaroo Rat Captures Per 100 Trap-Nights		
	Lightly Grazed Pasture 20	Moderately Grazed Pasture 19	Heavily Grazed Pasture 21
	no.	no.	no.
Dense Herbaceous Cover	12	25	(no dense cover)
Sparse Herbaceous Cover	28	44	51
Plot as a Whole	24	38	51

capture was greater than on those parts of the other two plots where herbaceous cover was sparse (Table 13). Associated with the differences in rate of capture on sparsely covered areas were corresponding differences in population densities for each plot as a whole (Table 5).

The greater densities of kangaroo rats on heavily grazed areas seem contradicted by the greater numbers of kangaroo rats taken along the kill-trap line on the ungrazed area, as compared with similar lines in the experimental pastures (Table 4). The anomaly was probably due to the fact that the line on the ungrazed area had more traps on dunes than did any of the lines on the grazed pastures. Dunes, even though ungrazed, tended to have herbaceous vegetation sparse enough for those areas to be used by kangaroo rats. When topographically similar areas were compared, ungrazed sites yielded fewer kangaroo rats than grazed ones, (Tables 9 and 10).

The differences in rates of capture on sparsely and densely covered parts of live-trap plots were not as definite as the figures suggest (Table 13). Many of the capture sites were on edges of the compared vegetation types, and it was a subjective decision as to whether or not the trap station was in "dense" or "sparse" cover. Presence of roads and trails in some of the cover types further complicated the efforts to make precise comparisons of densely with sparsely covered sites of capture on the areas grazed by cattle.

Patches of dense, tall herbaceous cover were lacking on the heavily grazed live-trap plot in the summer of 1958, and there the captures of kangaroo rats were randomly distributed ($t = 1.53$ and d. f. = 199), according to the chi-square method used by Evans (1942). Likewise, during the drought summer of 1956, when cover was relatively sparse on the interdunal areas, there was random distribution of captures on the moderately grazed plot ($t = 1.12$ and d. f. = 199).

Distribution of burrows also suggested that kangaroo rats made greater use of sparsely covered than of densely covered areas. Rodent burrow entrances, presumably mostly of kangaroo rats, seemed to be more numerous on areas of dune topography and sparser herbaceous cover than on densely covered interdunal areas.

No differences were noted among the various grazed and ungrazed areas with regard to age composition of the kangaroo rat populations. For a given area, however, there were marked differences in breeding success in equivalent seasons of different years. These differences resulted in marked differences in the percentages of adult individuals in the populations in different years (Tables 14 and 15). The estimated

Table 14. Sex and Age Composition of Kangaroo Rat Populations, Southern Plains Experimental Range and Vicinity, Harper and Woodward Counties, Oklahoma. 1956-1957. Age Class was Based on Weight of Dead-Trapped Animals Except as Noted. Rats Weighing Less than 60 Grams were Classed as Immature.

Period	Age Class	Percentages		
		total	males	females
Aug. 16-31, 1956	Adult	100	55	45
(Sample Size, N = 20)	Immature	0	0	0
	Total	100	55	45
Nov. 22-Dec. 24, 1956	Adult	100	40	60
(N = 20)	Immature	0	0	0
	Total	100	40	60
Jan. 23-Feb. 15, 1957	Adult	100	32	68
(N = 19)	Immature	0	0	0
	Total	100	32	68
July 6-Aug. 6, 1957	Adult	100	50	50
(N = 18)	Immature	0	0	0
	Total	100	50	50
Oct. 7-21, 1957	Adult	99	56	43
(N = 84, live-trap records)	Immature	1	0	1
	Total	100	56	44
Oct. 29-Nov. 1, 1957	Adult	80	42	38
(N = 80)	Immature	20	8	12
	Total	100	50	50
Nov. 12-14, 1957	Adult	64	33	31
(N = 66)	Immature	36	15	21
	Total	100	48	52

Table 15. Sex and Age Composition of Kangaroo Rat Populations, Southern Plains Experimental Range and Vicinity, Harper and Woodward Counties, Oklahoma, 1958. Age Class Was Based on Dentition.

Period, 1958	Age Class	Percentages total	males	females
Jan. 15-Feb. 27	Old Adult	37	19	18
	Intermediate Adult	16	3	13
(Sample Size, N = 93)	Young Adult	34	19	15
	Immature	13	10	3
	Total	100	51	49
March 18-April 28	Old Adult	19	8	11
	Intermediate Adult	23	11	42
(N = 120)	Young Adult	39	19	20
	Immature	19	7	12
	Total	100	45	55
May 5-25	Old Adult	15	5	10
	Intermediate Adult	40	17	23
(N = 231)	Young Adult	36	20	16
	Immature	9	6	3
	Total	100	48	52
June 22-23	Old Adult	13	3	10
	Intermediate Adult	46	16	30
(N = 30)	Young Adult	27	7	20
	Immature	14	7	7
	Total	100	33	67
July 28-Aug. 22	Old Adult	19	6	13
	Intermediate Adult	81	34	47
(N = 32)	Young Adult	0	0	0
	Immature	0	0	0
	Total	100	40	60
Oct. 24	Old Adult	33	14	19
	Intermediate Adult	62	38	24
(N = 21)	Young Adult	0	0	0
	Immature	5	0	5
	Total	100	52	48
Nov. 10-12	Old Adult	28	14	14
	Intermediate Adult	65	29	36
(N = 28)	Young Adult	0	0	0
	Immature	7	0	7
	Total	100	43	57

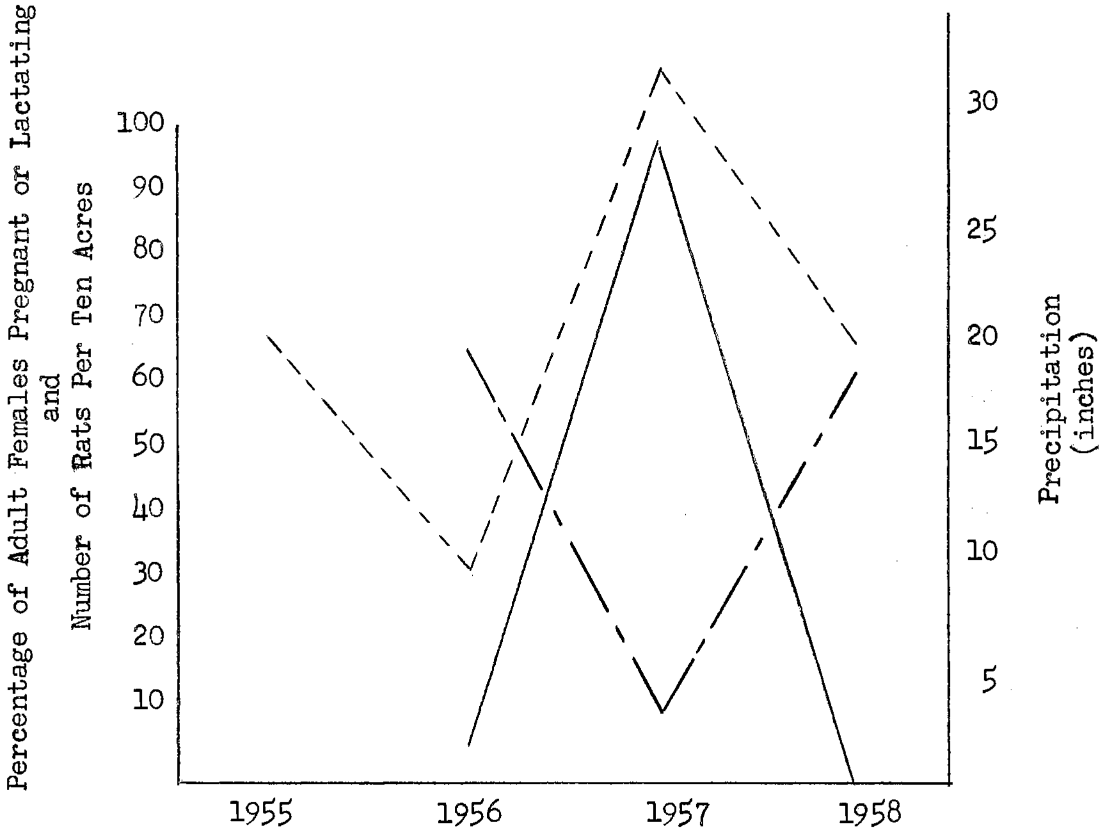
ages were based on weights of the individuals in 1956 and 1957, and on dentition in 1958.

The population fluctuations discussed in the preceding chapter were impressive in that they were not unlimited. For example, the estimated increase in eight months, from a population of 36 to one of 130 kangaroo rats on the heavily grazed plot, was far less than what seemed physiologically possible.

Embryo counts and observed pregnancy rates among sampled kangaroo rats (McCulloch and Inglis, ms.) suggested that the birth rate was very high during the 1957-1958 breeding season. Had there been no losses, that estimated rate could have resulted in populations several times as large as those which appeared on the live-trap plots at the end of that breeding season. For example, it was estimated that a population of 50 male and 50 female adults in September, 1957, could have increased to a population of 670 individuals by April, 1958. The apparent mortality of the young, however, was only one of the factors which tended to keep kangaroo rat populations within bounds.

Precipitation seemed to have important effects on kangaroo rat numbers, yet favorable moisture conditions alone did not result in population increases. It appeared that a summer of drought adversely affected kangaroo rat breeding success the following winter (Figure 3) and perhaps the rate of survival during that winter also. Very low population densities occurred in the summer (1957) which followed a previous summer's (1956) drought.

When kangaroo rat populations were sparse, a high rate of reproduction occurred in the fall-winter season which followed a wet growing



— — — Precipitation, April-September

—·— Estimated number of kangaroo rats per ten acres at start of breeding season (September) on live-trap plot in moderately grazed pasture 19

——— Percentage of adult females pregnant or lactating on all areas sampled with kill-traps in November

Figure 3. Comparisons of growing-season precipitation with kangaroo rat late-summer population densities and late-autumn breeding success. Southern Plains Experimental Range and vicinity, Harper and Woodward counties, Oklahoma.

season (1957). When kangaroo rat densities were high, however, a wetter-than-average plant growing season was not followed by a season of high breeding success. Information in earlier reports suggests that there was a similar parallel between precipitation and the declines and increases of populations in 1940-1942 (Trowbridge, 1942; McMurry, 1942, 1943, 1947).

Precipitation probably affected kangaroo rat populations chiefly through its effects on vegetation, especially with regard to cover and food supply. In Hemphill County, Texas, J. M. Inglis (personal communication) found that a large increase in kangaroo rat populations occurred following the summer of 1955, when there were large amounts of seed available on the soil. He noted a population decline during the summer of 1956, when he found soil-seed availability low.

Kangaroo Rat Spatial Behavior

It appeared that some of the factors which affected the observed limits to increase of kangaroo rat populations were weather, degree of grazing, and topography. Through their effects on vegetation, one or more of these factors seemed associated with kangaroo rat distribution and population density to the extent that the latter were associated with cover conditions and presumably with food supply.

Another major factor in population regulation is the spacing of individuals within the area occupied by their species. The process tends to provide for a more even distribution over the habitat, with a maximum efficiency in utilization of the resources of the ecosystem (Dice, 1952). The majority of the live-trapped kangaroo rats were recaptured individuals (Tables 16 to 19 inclusive). Furthermore, the sites of

Table 16. Numbers of Recaptured Kangaroo Rats and Those Taken Only Once on the 8.1-Acre Live-Trap Grid, Lightly Grazed Pasture 20. Southern Plains Experimental Range, Harper County, Oklahoma.

Trapping Period	Catch Per Period			Trap-Nights Per Period
	Total Individuals	Recaptured Individuals	Individuals Caught Once Only	
	no.	no.	no.	no.
Sept. 22-26, 1957	18	15	3	500
Oct. 8-18, 1957	21	20	1	700
Dec. 22, 1957	37	37	8	100
Jan. 27, 1958	29	26	3	100
Feb. 24, 1958	42	38	4	100
March 26, 1958	34	29	5	100
April 19-30, 1958	39	33	6	200
May 27, 1958	33	30	3	100
Aug. 8-22, 1958	50	41	9	500

capture of each recaptured individual were generally clustered, rather than being widely dispersed over the live-trap grid. These facts suggested the operation of a spacing process for kangaroo rats.

A means of considering the spacing process was to try to ascertain the homestead area, which is the area over which an individual usually travels in pursuit of its daily and seasonal activities.

There are various objections to methods of estimating the area of a homestead from records of recaptures in live-traps arranged in a regularly-spaced grid pattern. Hayne (1949), for example, pointed out that an animal's homestead does not necessarily coincide exactly with the distribution pattern of the traps. Also, the homestead could extend for some distance beyond the traps in which the animal was caught. It was this factor which suggested that the boundary strip be added to the estimated homestead area, as described in "Methods" (p. 6).

Table 17. Numbers of Recaptured Kangaroo Rats and Those Taken Only Once on the 8.1-Acre Live-Trap Grid, Moderately Grazed Pasture 19. Southern Plains Experimental Range, Harper County, Oklahoma.

Trapping Period	Catch Per Period			Trap-Nights Per Period
	Total Individuals	Recaptured Individuals	Individuals Caught Once Only	
	no.	no.	no.	no.
Aug. 28-Sept. 7, 1956	68	39	29	600
Dec. 24, 1956	28	24	4	100
Jan. 23, 1957	30	24	6	100
Feb. 15, 1957	23	17	6	100
July 6-10, 1957	21	15	6	500
Sept. 8-12, 1957	10	9	1	500
Oct. 7-18, 1957	22	16	6	700
Dec. 18, 1957	27	23	4	100
Jan. 22, 1958	41	38	3	100
Feb. 21, 1958	40	40	0	100
March 24, 1958	52	45	7	100
April 11-22, 1958	65	56	9	200
May 25, 1958	56	47	9	100
June 20-29, 1958	53	53	0	200
Aug. 11-Sept. 5, 1958	63	60	3	500

Table 18. Numbers of Recaptured Kangaroo Rats and Those Taken Only Once on the 8.1-Acre Live-Trap Grid, Heavily Grazed Pasture 21. Southern Plains Experimental Range, Harper County, Oklahoma.

Trapping Period	Catch Per Period			Trap-Nights Per Period
	Total Individuals	Recaptured Individuals	Individuals Caught Once Only	
	no.	no.	no.	no.
Sept. 15-19, 1957	36	32	4	500
Oct. 9-21, 1957	41	38	3	700
Dec. 26, 1957	59	53	6	100
Jan. 30, 1958	66	62	4	100
Feb. 27, 1958	76	68	8	100
March 21, 1958	73	65	8	100
April 16-28, 1958	100	84	16	200
May 29, 1958	62	60	2	100
July 1-9, 1958	125	115	10	600
Aug. 12-Sept. 3,1958	106	100	6	600

Other objections are that the apparent area of a homestead depends to some extent on numbers of captures per individual (Hayne, o. c.), as discussed below. The distance between traps was found to affect the computation of apparent size of the homestead area (Hayne, o. c.). Possible intra- and interspecies overlap of homesteads could result in competition for traps, so that individuals could fail to be caught in some of the traps within their homesteads. Development of trap shyness could result in failure of individuals to appear in traps in parts of their homesteads. The trap-visiting habit, on the other hand, may cause some

Table 19. Numbers of Kangaroo Rats by Frequency-of-Capture Classes on Three 8.1-Acre Live-Trap Grids. Southern Plains Experimental Range, Harper County, Oklahoma. August 28, 1956 - September 5, 1958.

Times Captured	Kangaroo Rats: Three Grids, Combined Records	Lightly Grazed Pasture 20	Moderately Grazed Pasture 19	Heavily Grazed Pasture 21
	no.	no.	no.	no.
1X	202	42	93	67
2X	97	25	43	29
3X	57	12	21	24
4X	47	5	16	26
5X	38	8	15	15
6X	34	7	12	15
7X	32	6	13	13
8X	25	5	7	13
9X	24	5	3	16
10X	18	1	7	10
11X-28X	50	6	12	32
Total	624	122	242	260

individuals to be caught repeatedly in certain traps, to the exclusion of other traps in their homesteads.

The mean cruising radius of kangaroo rats was expected to and, in general, did tend to vary directly with the number of times the individuals were captured (Table 20). The tendency has been observed in studies of other species, as discussed by Dice (1952). In restating a concept of

Table 20. Variations in Mean Cruising Radii of Kangaroo Rats According to Number of Captures on Three 8.1-Acre Live-Trap Grids. Southern Plains Experimental Range, Harper County, Oklahoma. September, 1957-September, 1958.

No. Times Captured	Mean Cruising Radii			
	Three Grids, Combined Records	Lightly Grazed Pasture 20	Moderately Grazed Pasture 19	Heavily Grazed Pasture 21
N =	379	80	106	193
	ft.	ft.	ft.	ft.
2X	66	38	59	96
3X	73	106	58	61
4X	88	98	70	95
5X	102	109	97	102
6X	125	139	169	92
7X	95	144	81	82
8X	168	202	137	177
9X	98	123	106	87
10X	162	187	244	119
11X-23X	197	254	276	159
All Groups	110	110	115	107

Hayne (1949), Calhoun and Casby (1958) proposed that "...the longer the period of observation, the more likely will the animal be observed at those distant points which it visits infrequently." This concept may partly explain the tendency for the mean cruising radius of kangaroo rats to increase with number of captures. The latter depended partly upon the number of nights of trapping and, therefore, on the length of the trapping period, or "period of observation."

The above definition of homestead (p. 44) appears compatible with the data in Table 20. The definition also accommodates the view of Harrison (1958), who reported on rats (Rattus spp.) in Malaya. He stated that he had abandoned the concept of "home range" in favor of the idea that an individual has a center of activity surrounded by a series of concentric probability zones within which the rat spends varying proportions of its time. Similarly, Calhoun and Casby (1958) proposed that "...there is actually no boundary or finite limits to the home range." This too is in accord with the definition of homestead used here.

Hypothetical boundaries of homesteads were assigned as described above (p. 6). The apparent homesteads thus ascertained seemed useful for trying to compare ecologic factors which might affect size of the homestead area.

Sexual differences in homestead area were not apparent for kangaroo rats. Mean estimated areas of homesteads were the same for 58 males and 53 females captured five or more times during the summer of 1958, namely, 0.2 acre. As low as the 95 per cent confidence level, F-values indicated that there was no significant difference between cruising radii of 186 males and 193 females recaptured during the year September, 1957-September, 1958. The means were 111 and 109 feet, respectively, for males and females. On the basis of frequency distribution, the records of all recaptured kangaroo rats suggested no appreciable sexual differences in cruising radii (Table 21). It should be noted that the first of the class intervals, 0-49 feet, indicates

Table 21. Comparisons by Frequency Distribution of Cruising Radii of All Recaptured Kangaroo Rats on Three 8.1-Acre Live-Trap Grids. Southern Plains Experimental Range, Harper County, Oklahoma. August, 1956-September, 1958.

Cruising Radius Classes		Percentage Frequencies of Cruising-Radius Classes											
		Three Grids, Combined Records			Lightly Grazed Pasture 20			Moderately Grazed Pasture 19			Heavily Grazed Pasture 21		
	N =	204	218	422	40	40	80	68	81	149	96	97	193
ft.		males	females	both	males	females	both	males	females	both	males	females	both
0-49		25	22	23	23	23	23	26	20	22	24	23	23
50-99		39	43	41	33	45	39	38	42	39	43	43	43
100-149		17	16	16	25	17	21	16	14	15	15	17	16
150-199		4	4	4	2	2	3	3	2	2	5	5	5
200-249		4	8	6	5	5	5	6	11	8	2	6	4
250-299		5	2	4	7	3	5	4	3	4	5	2	3
300-399		2	2	3	0	5	2	1	4	3	4	2	3
400-499		2	2	2	5	0	2	3	2	4	1	2	2
500-plus		2	1	1	0	0	0	3	2	3	1	0	1
Total		100	100	100	100	100	100	100	100	100	100	100	100

individuals which were taken at only one trap station. The distance between traps was 66 feet.

An effort was made to learn if degree of grazing by cattle might affect area of kangaroo rat homesteads. Stebler (1958), for example, proposed that the area of an individual homestead is proportional to carrying capacity of the habitat and to population density. It seemed likely that cattle grazing could affect kangaroo rat food supply or other factors of carrying capacity.

Three types of comparisons suggested that degree of grazing had little or no effect on average homestead area of kangaroo rats. The F-test indicated no significant differences among the mean cruising radii of the three live-trap plots for the one-year period, September, 1957, to September, 1958 (Table 20). The mean estimated area of homesteads was 0.2 acre on each live-trap plot, based on records of all 242 kangaroo rats recaptured during the summer of 1958. In the third comparison, using only the records of animals caught five times or more during the summer of 1958, it also appeared that there were no appreciable differences in the majority of kangaroo rats' cruising radii on the three plots (Table 22). In that frequency distribution, 86 to 92 per cent of the rats had observed cruising radii of less than 100 feet during the summer of 1958.

Next examined were the records of the small group of kangaroo rats which had been captured the greatest number of times over the longest period on all three live-trap plots (Table 23). The group was further restricted to individuals which had been recaptured in each of three selected periods of a year. The records of these 11 individuals indicated a mean homestead of 1.2 acres and a mean cruising radius of 323 feet.

Table 22. Comparisons by Frequency Distribution of the 1958 Summer Cruising Radii of All Kangaroo Rats Captured Five or More Times on Three 8.1-Acre Live-Trap Grids. Southern Plains Experimental Range, Harper County, Oklahoma. May 25 - September 5, 1958.

Cruising Radius	Frequencies of Cruising Radius Classes			
	Three Grids, Combined Records	Lightly Grazed Pasture 20	Moderately Grazed Pasture 19	Heavily Grazed Pasture 21
N =	111	7	33	71
ft.	per cent	per cent	per cent	per cent
0-49	35	29	33	37
50-99	56	57	58	55
100-149	7	14	6	7
150-199	1	0	0	1
200-249	0	0	0	0
250-299	1	0	3	0
300-399	0	0	0	0
400-499	0	0	0	0
500-plus	0	0	0	0
Total	100	100	100	100

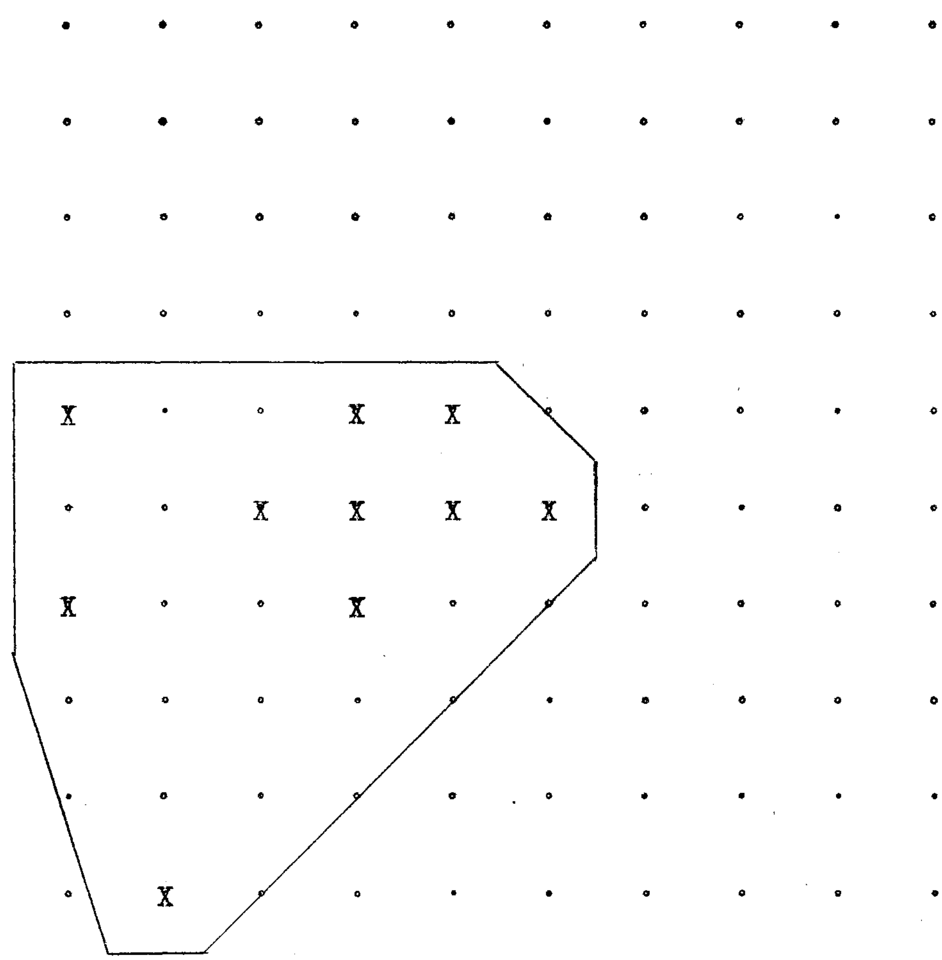
The duration of the trapping records of these individuals varied from 12 to 24 months. The data (Table 23) included no individuals which had been taken only in the outer rows of traps of their grids. The purpose of this omission was to minimize effects of homesteads which may have been mostly outside the grid area.

Table 23. Comparisons of Periodic Differences in Areas of Homesteads Used and in Cruising Radii of 11 Adult Kangaroo Rats, Each of Whose Recapture Record Spans One Reproductive Cycle. Southern Plains Experimental Range, Harper County, Oklahoma.

Identification No. and Sex	Entire Period of Record of Individual			Early Part of Breeding Season (Sept.8-Oct.21,1957)			Latter Part of Breeding Season (Dec. 18, 1957-April 30, 1958)			Between Breeding Seasons (May 25-Sept. 5, 1958)		
	Homestead	Cruis. Radius	Times Caught	Area Used	Cruis. Radius	Times Caught	Area Used	Cruis. Radius	Times Caught	Area Used	Cruis. Radius	Times Caught
	a.	ft.	no.	a.	ft.	no.	a.	ft.	no.	a.	ft.	no.
15 f	2.7	660	28	0.8	209	8	0.2	147	8	0.2	66	7
90 m	2.5	423	22	1.4	360	9	0.8	272	6	0.3	66	6
78 m	1.2	272	15	0.4	147	3	0.7	272	7	0.1	0	5
92 m	1.2	330	12	0.8	238	4	0.4	147	5	0.1	0	3
135 f	1.0	330	16	1.0	330	8	0.2	66	6	0.1	0	2
102 m	0.9	337	11	0.7	209	6	0.6	272	3	0.1	0	2
53 m	0.9	209	26	0.8	209	5	0.7	187	7	0.3	93	7
103 m	0.9	417	14	0.8	417	4	0.3	93	5	0.1	0	5
81 m	0.8	187	21	0.4	147	6	0.6	147	6	0.4	93	9
91 f	0.7	238	18	0.6	209	6	0.5	238	8	0.2	66	4
101 f	0.5	147	16	0.3	93	6	0.4	147	8	0.2	66	2
Mean	1.2	323	18.1	0.7	233	5.9	0.5	181	6.3	0.2	41	4.7

The largest estimated homestead of a kangaroo rat, 2.7 acres, was that of a female whose record extended over a period of 24 months. It appeared that, as an adult, during the first four months of her trapping record, she moved from one part and became established in another part of the live-trap grid. During the last 20 months of her record, the estimated area used by her was only 1.1 acres. Movements of the other kangaroo rats (Table 23) did not seem to be those of immigrating, emigrating, or dispersing individuals. In most cases, however, the actual nature of an individual's movements was difficult to classify. The estimated homestead of a male with a relatively extensive trapping record is shown in Figure 4.

The fact that one kangaroo rat seemed to have moved more or less permanently from one area to another would suggest that others also did this occasionally. This is also suggested by the disappearance of some individuals from and the appearance of others on a live-trap plot during a season when no young were added to the population. For example, ten recaptured kangaroo rats apparently disappeared from the live-trap plot after July, 1957, and 11 new individuals, subsequently recaptured, appeared there by October, 1957, in moderately grazed pasture 19. Other evidence of attrition in the populations is suggested by Table 19. Only a relatively small number of individuals seemed to remain on the plots long enough to be recaptured the maximum number of times. How much of this apparent loss (Table 19) was due to emigration, and how much to mortality, was not determined.



"X" indicates capture site

Dots represent live-trap stations 66 feet apart

Figure 4. Homestead area (2.5 acres) of an adult male kangaroo rat (no. 90) captured 22 times during a period of 12 months on the 8.1-acre live-trap grid in heavily grazed pasture 21. Southern Plains Experimental Range, Harper County, Oklahoma. September 16, 1957-September 5, 1958.

Means of the cruising radii of individuals captured during some periods differed greatly from mean cruising radii of individuals captured during other periods (Table 24). However, the number of captures per individual varied considerably from period to period, and, therefore, the mean cruising radii in that table may not be reliable indicators of differences in the areas of homesteads used in the different seasons.

Another comparison of mean cruising radii of individuals taken in different seasons (Table 25) made use of records of the kangaroo rats which were recaptured the greatest number of times. This comparison also suggested a seasonal change in mean cruising radius.

A third, and probably the most valid, comparison of seasons employed the estimated areas of use and the cruising radii of each individual which had been recaptured during three different periods of a year (Table 23). The seasonal area of use and the cruising radius of each of those 11 kangaroo rats were smaller in the summer of 1958 than previously.

These three comparisons (Tables 23, 24, and 25) suggested that individuals' areas of use during the early summer and midsummer period of 1958 were smaller than the areas used during the preceding late summer, fall, and winter. For the summers of 1956 and 1957, also, the portion of the homestead used by individual kangaroo rats may have been smaller than in fall and winter periods, although the samples (Tables 26 and 27) were not adequate for satisfactory comparisons.

Associations of conditions with and as possible causes of these seasonal differences in areas used by kangaroo rats were not clear in most cases. It was thought that crowding might tend to restrict the

Table 24. Seasonal Variations in Mean Cruising Radii of Kangaroo Rats on Three 8.1-Acre Live-Trap Grids, Computed for All Individuals Recaptured During Each Period. Southern Plains Experimental Range, Harper County, Oklahoma

Period	Mean Cruising Radii			
	Three Grids, Average	Lightly Grazed Pasture 20	Moderately Grazed Pasture 19	Heavily Grazed Pasture 21
	ft.	ft.	ft.	ft.
Aug. 28-Sept. 7, 1956	40		40	
Dec. 24,1956-Feb.15, 1957	111		111	
July 6-10, 1957	93		93	
Sept. 8-Oct. 21,1957	158	181	137	158
Dec. 18,1957-April 30,1958	115	107	135	107
May 25-Sept. 5, 1958	52	40	49	57

areas used by individuals. However, these areas appeared relatively large during a period of low population density as well as during one of high density; namely, September and October, 1957, compared with December, 1957 to April, 1958 (Table 23). The large areas used by individuals during the winter, when densities were high, suggest that food was abundant, and that there was no apparent intraspecific competition to satisfy vital needs.

There was no suggestion that dense herbaceous cover tended to restrict areas used by individuals, although dense vegetation did hinder their movements except along established trails. The estimated areas of use were comparatively large during a season of relatively dense herbaceous cover and also when much of that cover had become dead and sparse. For

Table 25. Comparisons of Winter and Summer Mean Areas of Use and Cruising Radii of 39 Kangaroo Rats Captured 11 or More Times on Three 8.1-Acre Live-Trap Grids. Southern Plains Experimental Range, Harper County, Oklahoma.

Period	Mean Area of Use	Mean Cruising Radius
	a.	ft.
Dec. 18, 1957-April 30, 1958	0.4	138
May 25-Sept. 5, 1958	0.2	61

example, this is shown in the comparison of September and October, 1957, with December, 1957 to April, 1958 (Table 23).

Relative availability of food may have been associated with the size of the area used by an individual, although the seasons of greatest and least availability of kangaroo rat foods were not known. An individual might have been able to satisfy his food requirements in a relatively small area when there was a large amount of unharvested food per unit of area. Presumably, unharvested food was most abundant in late summer and autumn and least during winter and early spring. If this was correct, kangaroo rats used large areas in a period of food abundance as well as during one of food scarcity; for example, September and October, 1957, compared with December, 1957 to April, 1958.

The periods during which individuals used relatively large areas did coincide with the kangaroo rat breeding season, which lasted approximately from early September, 1957, through March, 1958. This was also a period in which large numbers of young were added to the population and

Table 26. Late Summer Areas of Use and Cruising Radii of Nine Adult Kangaroo Rats Captured Three or Four Times, August 28 - September 7, 1956, on the 8.1-Acre Live-Trap Grid, Moderately Grazed Pasture 19, Southern Plains Experimental Range, Harper County, Oklahoma.

Sex	Area of Use	Cruising Radius	Times Caught
	a.	ft.	no.
f	0.4	198	3
m	0.3	93	4
f	0.2	93	4
f	0.2	66	4
m	0.2	66	3
m	0.2	66	3
m	0.1	0	3
m	0.1	0	3
f	0.1	0	3
Average	0.2	65	3

were establishing new homesteads among those of the older rats. A period in which individuals used small areas occurred during the non-breeding season, which included the summer of 1958 (Table 23).

Mean cruising radii of all kangaroo rats recaptured during the respective periods suggested that individuals also used small areas during non-breeding seasons in the summers of 1956 and 1957 (Table 24). The means in that table, however, may have been affected by variables other

Table 27. Comparisons of the 1957 Midsummer With Late Summer Areas of Use and Cruising Radii of Five Adult Kangaroo Rats on the 8.1-Acre Live-Trap Grid, Moderately Grazed Pasture 19. Southern Plains Experimental Range, Harper County, Oklahoma.

Sex	Area of Use	Cruising Radius	Times Caught	Area of Use	Cruising Radius	Times Caught
	July 6-10, 1957			Sept. 8-12, 1957		
	a.	ft.	no.	a.	ft.	no.
m	0.4	132	4	0.4	132	5
m	0.4	132	4	0.4	187	3
f	0.3	132	2	0.6	147	4
f	0.2	93	2	0.3	147	2
f	0.1	0	2	0.3	147	3
Average	0.3	98	2.8	0.4	152	3

than phases of the reproductive cycle, such as variations in numbers of captures per individual.

The kangaroo rats caught the greatest number of times in the summer of 1956 (Table 26) were not taken often enough in the following winter to allow a comparison of the 1956 summer with 1956-1957 winter homesteads. In 1957, a few individuals were caught several times in both the midsummer and late summer periods, respectively, before and after start of the breeding season (Table 27). At that time, herbaceous vegetation appeared at least as dense as it had been during the midsummer period. However, the differences between means of the 1957 midsummer and late summer homesteads and cruising radii were not significant according to F-tests.

It appeared that during a given night the movements of a kangaroo rat were extensive enough to allow it to cruise over the greater part of its homestead area. During the winter of 1957-1958, live-traps were emptied throughout all or parts of some nights. Traps containing no rodents at the time of the first check each night were left open, allowing a few individuals to be caught twice in one night. This work indicated that the mean of the distances between sites of capture during one night was more than half the average cruising radius for those same individuals during the entire periods of their live-trap records (Table 28).

Other aspects of the one-night records of recaptures suggested that kangaroo rat homestead areas were not sharply separated, and they also supported the idea that individuals made sorties outside the smaller areas in which they spent most of their time. Although 83 per cent of the individuals had one-night moves of less than 150 feet, three males' exceeded 300 feet, and one female's was 532 feet. Apparently, none of these large one-night movements were those of either emigrating or dispersing individuals. Their previous and subsequent capture sites indicated that these long movements were not one-way. Records of the total of 422 kangaroo rats recaptured during the present study parallel the one-night observations in this respect. Twenty of the 422 cruising radii exceeded 300 feet, but only six of the 20 appeared as one-way moves.

The frequency of overlap in areas used by adult kangaroo rats seemed fairly great on all three live-trap plots. The frequency was estimated by tallying the number of recaptured individuals which had capture sites in common with other "recaptures" during a given period (Table 29).

Table 28. Means of Distances Between Sites of Capture of Kangaroo Rats During One Night, Compared With Mean Cruising Radii of the Same Individuals During Their Entire Periods of Record on Three 8.1-Acre Live-Trap Grids. Southern Plains Experimental Range, Harper County, Oklahoma. 1957-1958.

Period	Three Grids, Average	Lightly Grazed Pasture 20	Moderately Grazed Pasture 19	Heavily Grazed Pasture 21
N =	41	10	15	16
	ft.	ft.	ft.	ft.
One night (eight hours or less)	129	126	108	151
Entire live-trap record	242	269	244	222

Percentages of these individuals which shared trap-sites were great in a period of low population density (September and October, 1957), as well as in a time of high density (May to September, 1958). The percentages were also great when areas used by individuals were small, between breeding seasons, as well as when the areas were enlarged, which was during the breeding season.

The proportion of recaptured kangaroo rats which shared sites of capture tended to vary directly with the number of trap-nights employed, and, therefore, with the average number of captures per individual. This correlation with number of times captured parallels the situation reported for cruising radii (Table 20).

By itself, a high frequency of overlap in sites of capture does not necessarily indicate a great extent of overlap of homesteads in terms of

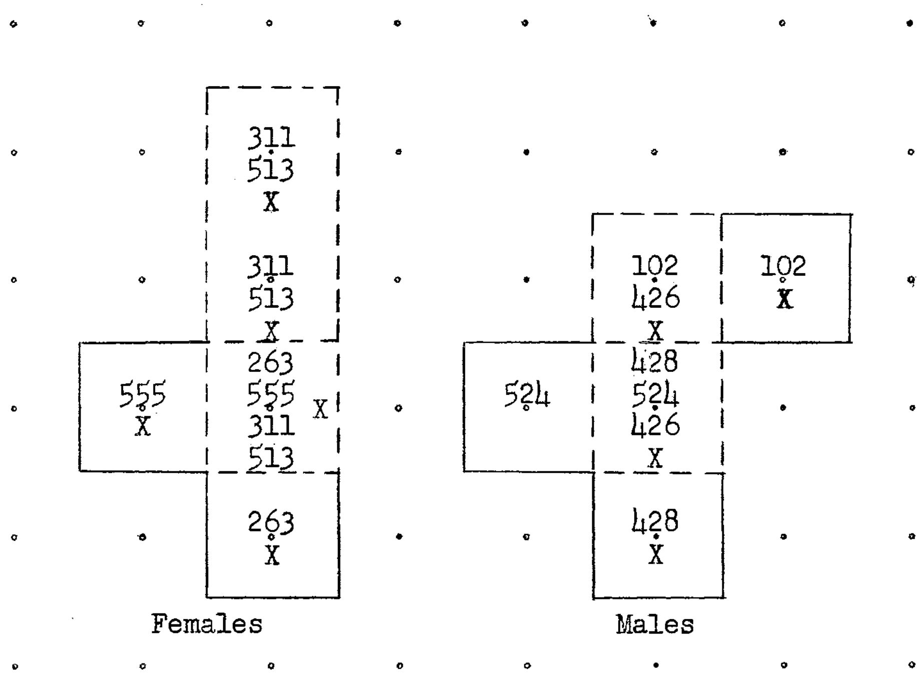
Table 29. Percentages of Recaptured Adult Kangaroo Rats Which Had Sites of Capture in Common, Compared With Population Density and Number of Captures Per Individual. Southern Plains Experimental Range, Harper County, Oklahoma.

Location of Live-Trap Grid and Period of Comparisons	Estimated Population	Both Sexes		Males		Females		Trap-Nights Employed
		Per Cent Which Shared Sites	No. of Captures Per Rat	Per Cent Which Shared Sites	No. of Captures Per Rat	Per Cent Which Shared Sites	No. of Captures Per Rat	
	rats/10 a.		avg.		avg.		avg.	no.
Lightly Grazed Pasture 20								
Sept.22-Oct.18,1957	21	85	5	83	5	12	4	1200
May 27-Aug.22,1958	50	40	4	29	3	28	4	600
Moderately Grazed Pasture 19								
Aug.28-Sept.7,1956	68	33	2	0	2	17	2	600
July 6-10,1957	21	27	3	0	3	22	2	500
Sept.8-Oct.18,1957	22	78	9	40	8	50	10	1200
May 25-Sept.5,1958	63	74	4	37	4	46	4	800
Heavily Grazed Pasture 21								
Sept.15-Oct.21,1957	41	88	5	86	5	30	4	1200
May 29-Sept.3,1958	125	89	5	70	5	68	5	1300

area. Most of the shared sites of capture could be on the peripheries of the individual homesteads.

There was, however, some suggestion of considerable extent of overlap among homesteads, according to estimates of populations and average homestead areas. In July, 1958, for example, there were estimated 125 kangaroo rats on the 10-acre plot in heavily grazed pasture 21. The total of 125 rats times the average homestead of 0.2 acre equals 25 acres. Since the 125 homesteads were apparently contained within 10 acres instead of 25, this suggested that 100 per cent of the average rat's homestead was overlapped by those of some of his neighbors. That product, 25 acres, would of course require but little overlap within each sex. It is not known if kangaroo rats occupied homesteads as mated pairs, but the above estimates apply to the non-breeding season. It seems unlikely that the sexes were especially tolerant of each other at that time. The species is apparently not noted for lasting pairing between adult males and females, even in the breeding season (Allan, 1944; Rosasco, 1955). Examples of overlapping homesteads during the non-breeding season are those in Figure 5.

The average winter homestead, multiplied by estimated population densities, suggested that there was much overlap of homestead areas within each sex, especially during the latter part of the breeding season, namely, December, 1957 to April, 1958, when population density had become great. Observations of kangaroo rats which entered burrows also suggested much overlap of homesteads within each sex, as in the example (Figure 6).



Individuals' homestead areas are shown by blocks containing each rat's identification number

Solid lines bound parts of individuals' homesteads which were not overlapped by another's of the same sex

Broken lines bound areas of overlapping homesteads of individuals of the same sex

"X" indicates homestead areas shared with one or more individuals of the opposite sex

Dots represent live-trap stations 66 feet apart

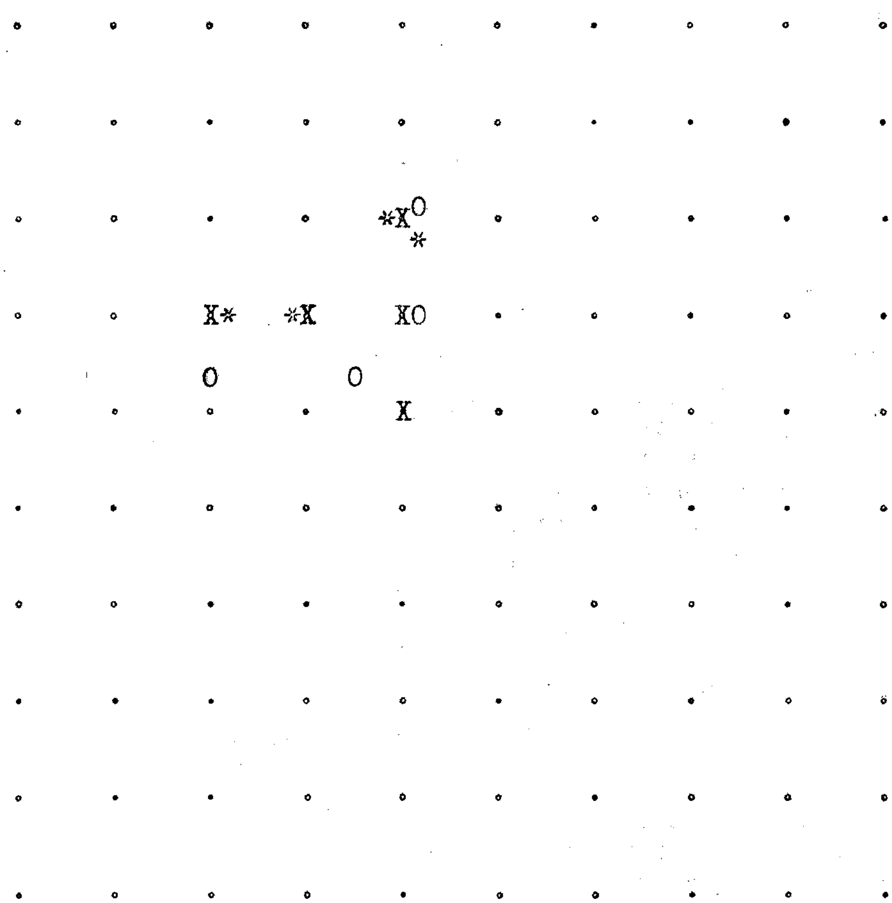
Figure 5. Examples of overlapping homestead areas of four male and four female adult kangaroo rats during a summer of high population density, May 29 - September 3, 1958. The entire Figure represents a 3.5-acre portion of the 8.1-acre live-trap grid in heavily grazed pasture 21, Southern Plains Experimental Range, Harper County, Oklahoma.

The large frequency and extent of overlap of kangaroo rat homesteads do not necessarily indicate that use of all parts of each homestead was completely mutual. Within any group of overlapping homesteads, there probably were areas used more frequently by one individual than by any of his neighbors. Thus a certain amount of spacing apparently was maintained between individuals.

Another factor which may have affected the spacing process was the presence in kangaroo rat homesteads of a certain type of niche which seemed to be defended. This was the burrow, which served for shelter, for food storage, and as a place where females could raise young.

It appeared that each recaptured kangaroo rat used several burrows and usually entered the nearest of them when pursued. The distance from the capture site to the burrow entered on a given date was less than fifty feet in 89 per cent of the 209 observed cases. Individuals fled more than 100 feet from their site of capture to the burrow presumably of their choice in less than three per cent of these observed cases. There were 15 rats which were observed entering burrows as often as four times. These 15 individuals seemed to have burrows acceptable to them in places as widely scattered as their sites of capture, as suggested in the example (Figure 6).

It is not known how many, if any, of the burrows might have been the exclusive property of the pursued individual. It appeared that many of the pursued rats found brief refuge in certain burrows, perhaps only a few inches inside, and that they left soon after the observer walked away. It was not uncommon to see a rat emerge when the pursuer stood motionless nearby.



X Capture site of female kangaroo rat no. 15

O Burrow entered by female kangaroo rat no. 15

* Burrow entered by one of four other recaptured female kangaroo rats

Figure 6. Distribution of capture sites and burrows entered by an adult female kangaroo rat (no. 15) on the 8.1-acre live-trap grid in moderately grazed pasture 19. Southern Plains Experimental Range, Harper County, Oklahoma. October 16, 1957 - September 2, 1958.

Territorialism associated with kangaroo rat burrows was suggested by individuals' marked avoidance of certain burrows. Although each pursued rat usually entered a burrow near its capture site on a given date, that burrow was not necessarily the one nearest the site of capture. As stated above, the burrow entered did seem to be the nearest of the several which were used by that individual. Several burrow entrances were often passed over en route to a particular one. In some cases it was impossible physically to force rats into certain burrows. It was assumed that such burrows were defended territory of another individual.

Review of the observations on spatial behavior of kangaroo rats suggests a large degree of sharing of areas on which individuals could gather food. Burrow-entry observations suggest that there may have been defense or territorialism at places where their food was stored. It is not known how far that possibly defended territory extended around each burrow; the trap-spacing of these grids was too broad to detect such behavior.

The observations on recaptures (Tables 16 to 19 inclusive), homesteads (Tables 20 to 28 inclusive), and burrow entries by kangaroo rats are consistent in suggesting a restricted use of area by individuals of this species. This further suggests that individual kangaroo rats were spaced in accordance with some pattern. Other observations suggest that reproduction greatly diminished (Tables 14 and 15; Figure 3) when populations reached high densities (Tables 6, 7, and 8). At the beginning of that season of the reduced rate of reproduction—namely, the fall of 1958--the greatest estimated average density was about 13 individuals per acre (Table 8). This population estimate applied to the plot with the greatest amount of area used by kangaroo rats (Table 13) in a year (1958) when the food supply was presumably abundant.

There seemed to be a pattern of distribution of individual kangaroo rats. It appeared that there was also an approach to a "saturation point" for the population, as suggested above. The relationship between the two phenomena, if any, is not known.

Populations and Spatial Behavior of Other Rodent Species

Grasshopper Mice

The grasshopper mouse (Onychomys leucogaster breviauritus) appeared to be the second most abundant rodent on the grazed areas in some seasons. Estimated densities varied from zero to 28 individuals per ten acres (Table 5). Grasshopper mice never exceeded 22 per cent of the total catch on live-trap plots or 38 per cent on kill-trap lines. Earlier studies on the Experimental Range also found that grasshopper mice on most of the sampled areas ranked next to kangaroo rats, numerically, in 1940-1942 and 1949 (Trowbridge, 1941, 1942; McMurry, 1942, 1943, 1947; Frank, 1950).

For grasshopper mice, there seemed to be no clear differences in population density according to degree of grazing during most periods of trapping (Tables 5 to 8 inclusive). There were not enough captures to suggest a correlation with dense or sparse cover within the grazed plots during the summer of 1958. Chi-square analysis suggested that the catches were randomly distributed over the respective live-trap grids then. Ungrazed areas, however, seemed to support sparser populations than grazed ones

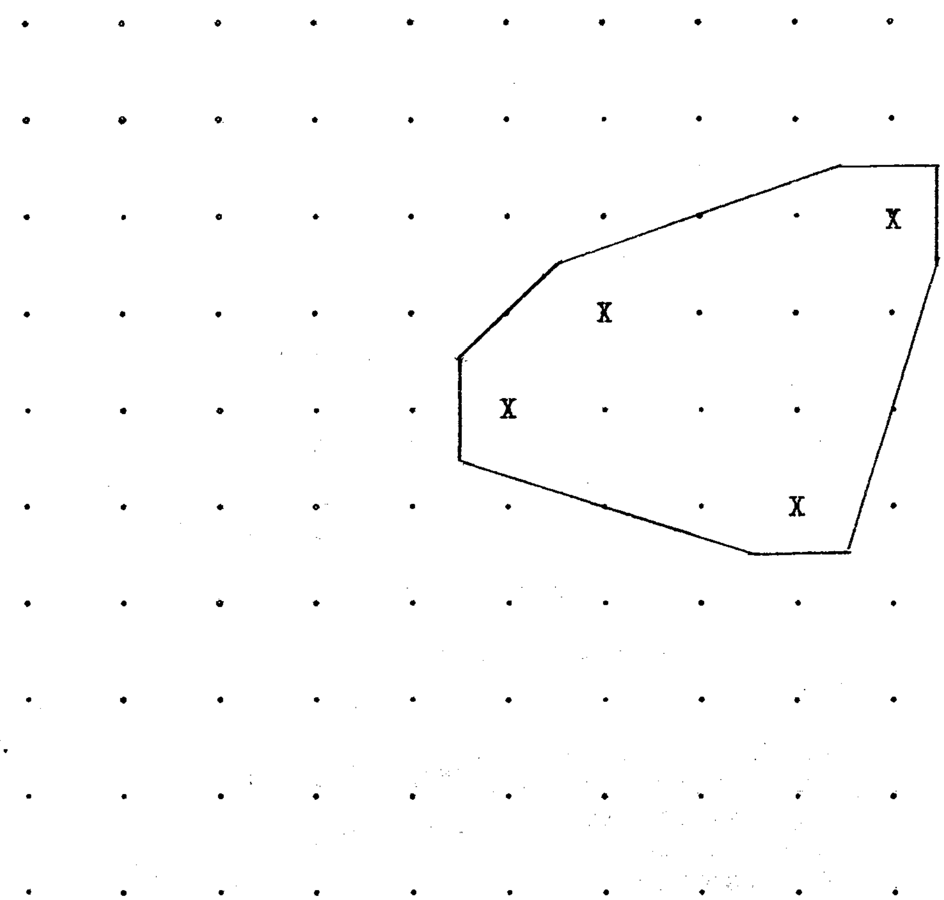
(Tables 9 and 10). Annual population fluctuations of grasshopper mice seemed to parallel those of kangaroo rats, with the lowest estimated densities occurring during the year after the 1956 drought (Tables 4 to 8 inclusive). Pregnant female grasshopper mice were found in all seasons except winter, and the period of greatest reproduction was the spring of 1958.

A tendency for individuals to remain within a limited area seemed typical of grasshopper mice. Forty per cent of the 114 individuals taken on the live-trap plots were recaptured at least once. Individuals of both sexes were observed within areas of one to two acres for as long as 8 to 13 months (Table 30). The homestead of an adult male is outlined in Figure 7. One male moved 1500 feet, from one plot to another, during a 36-day period. This individual was captured only two times and was presumed not to have an established homestead at these times. The largest cruising radii of individuals with apparent homesteads were less than 550 feet. Homestead data were not adequate for comparisons of different pastures. The same is probably true of an attempt to compare differences in homestead areas of sexes, although the averages (Table 30) suggest that male homesteads were slightly larger than females'.

The degree of social and spatial tolerance among adult grasshopper mice of the same sex is not known. Male and female adults were sometimes taken together in live-traps. Individuals which were followed upon release usually entered burrows, the entrances of some of which were of diameters which would admit animals no larger than grasshopper mice. It is not known if they dug their own burrows, but males as well as females

Table 30. Homestead Areas and Cruising Radii of 23 Adult Grasshopper Mice Captured 3 to 8 Times on One of Three Live-Trap Plots. Southern Plains Experimental Range, Harper County, Oklahoma. 1957-1958.

Males					Females				
Pasture Number	Homestead	Cruis. Radius	Duration of Record	Times Caught	Pasture Number	Homestead	Cruis. Radius	Duration of Record	Times Caught
	a.	ft.	mo.	no.		a.	ft.	mo.	no.
21	1.9	515	3	4	21	2.5	544	12	8
21	1.8	544	1	4	21	0.6	264	3	5
19	1.4	295	13	6	21	0.5	272	2	5
20	1.3	442	8	5	20	0.5	264	7	5
19	1.1	564	4	3	20	0.5	238	7	3
20	1.1	360	8	4	20	0.5	209	1	3
19	0.8	238	2	5	21	0.5	198	3	3
19	0.7	402	8	3	21	0.4	187	1	3
21	0.7	337	2	4	20	0.4	147	7	3
21	0.7	264	2	3	21	0.4	147	2	3
20	0.4	187	1	3	20	0.3	132	4	3
21	0.2	93	1	3	Average	0.6	236	4	4
Average	1.0	353	4	4					
					Average, Both Sexes	0.8	298	4	4



"X" indicates capture site

Dots represent live-trap stations 66 feet apart

Figure 7. Homestead area (1.4 acre) of an adult male grasshopper mouse (no. 3) captured six times during a period of 13 months on the 8.1-acre live-trap grid in moderately grazed pasture 19. Southern Plains Experimental Range, Harper County, Oklahoma. July 6, 1957-August 11, 1958.

displayed a characteristic burrow-plugging defense action when pursued. It appeared that behavior of individuals was oriented to the use of certain particular burrows as well as areas.

Cotton Rats

The cotton rat (*Sigmodon hispidus texianus*) was one of the rarest rodent species taken on all of the grazed areas sampled during most of the two-year period of this study. It is a species noted for phenomenally high populations, which have been observed about once every ten years in parts of its geographic range (Davis, 1958). The peak populations probably represent what have been called irruptions (Leopold, 1933). An outbreak occurred in 1958 in many parts of a large area extending from southern Texas to southern Kansas. Prior to that irruption, cotton rats did not appear during this study in any of the live- or kill-traps on any of the grazed pastures throughout the latter half of the drought year of 1956 and until October, 1957.

The favorable plant-growing conditions of 1957 seemed to result in small increases in cotton rat numbers during the 1957 summer and fall. A few young were born during the winter of 1957-1958, although the rate of reproduction was quite low, at least on uncultivated sand sagebrush grassland, as suggested by size classes in the populations (Table 31). The fact that there was year-round reproductive activity at this time may have been indicative of the population irruption which followed. Early in the spring of 1958 there were sharp increases in the rate of pregnancy and average number of embryos per pregnant female (Table 32).

Table 31. Sex and Age Composition of Cotton Rat Population, Southern Plains Experimental Range and Vicinity, 1957-1958. Harper and Woodward Counties, Oklahoma. Weight was presumed to Indicate Relative Age.

Period	Weight Class grams	Percentages total	males	females
Oct. 31-Nov. 19, 1957	180 or more	2	0	2
	120-179	27	21	6
(N = 51)	60-119	43	16	27
	0- 59	28	14	14
	Total	100	51	49
Feb. 18-March 19, 1958	180 or more	0	0	0
	120-179	30	26	4
(N = 47)	60-119	70	38	32
	0- 59	0	0	0
	Total	100	64	36
April 7-24, 1958	180 or more	0	0	0
	120-179	21	17	4
(N = 97)	60-119	78	45	33
	0- 59	1	0	1
	Total	100	62	38
May 5-20, 1958	180 or more	12	9	3
	120-179	56	28	28
(N = 35)	60-119	18	9	9
	0- 59	14	11	3
	Total	100	57	43
Aug. 18-22, 1958	180 or more	10	6	4
	120-179	29	11	18
(N = 105)	60-119	41	30	11
	0- 59	20	8	12
	Total	100	55	45
Oct. 24-Nov. 12, 1958	180 or more	2	1	1
	120-179	20	10	10
(N = 130)	60-119	66	36	30
	0-59	12	7	5
	Total	100	54	46

Table 32. Pregnancy Rates and Average Numbers of Embryos in Female Cotton Rats of Adult Size (60 grams or more) Before and During the Population Irruption of 1958. Harper and Woodward Counties, Oklahoma.

Period	Adult Females Examined	Per Cent Pregnant	Embryos Per Pregnant Female
	no.		no.
Oct. 31-Nov. 19, 1957	18	22	4.75
Feb. 18-March 19, 1958	17	6	2.00
April 7-24, 1958	37	40	4.40
May 5-20, 1958	14	86	7.33
Aug. 18-22, 1958	38	82	6.52
Oct. 24-Nov. 12, 1958	53	0	0

By midsummer of 1958, cotton rats appeared about as numerous as kangaroo rats on the lightly and moderately grazed live-trap plots (Tables 6 and 7) and were continuing to reproduce at a great rate, as suggested in Tables 31 and 32. The increase due to local reproduction may have been abetted by ingress from nearby fields, cattle exclosures within the pastures, and adjacent highway rights-of-way. These areas had dense stands of herbaceous vegetation. One or more such areas lay near enough to all of the sites sampled during this study that the distances could have been covered in a few weeks by successive generations of dispersing cotton rats. For example, the distance from an ungrazed exclosure to any of the live-trap plots was not more than ten feet in excess of the average cruising radius (Table 33) of male cotton rats.

Table 33. Homestead Areas and Cruising Radii of 16 Adult Cotton Rats Captured 4 to 7 Times on One of Two Live-Trap Plots. Southern Plains Experimental Range, Harper County, Oklahoma. 1958.

Sex	Pasture Number	Homestead	Cruising Radius	Duration of Record	Times Caught
		a.	ft.	mo.	no.
m	19	2.4	423	3	4
m	19	2.2	660	6	4
m	19	2.0	385	6	6
m	20	1.9	476	4	4
m	19	1.0	337	3	7
m	19	1.0	295	1	4
m	19	0.7	295	2	5
m	19	0.7	272	1	4
m	19	0.7	238	1	5
m	19	0.6	264	2	7
m	19	0.4	132	2	4
m	19	0.3	93	2	5
	Average, Males	1.2	322	3	5
f	20	1.5	396	7	7
f	19	0.4	198	2	4
f	19	0.3	93	2	7
f	19	0.3	93	4	5
	Average, Females	0.6	195	4	6

When cotton rats first began to be taken in traps in the experimental pastures, in late 1957 and early 1958, the capture sites were usually in the interdunal areas, where herbaceous cover was most dense. As the populations built up, however, cotton rats were more commonly taken in all parts of the trapped areas.

Heavily grazed pastures were among the last areas to be occupied by large numbers of cotton rats in 1958. This species was still in the minority among rodents on the heavily grazed live-trap plot as late as the first week of September, 1958 (Table 8). By early November, however, the catch along the kill-trap line (Table 4) suggested that cotton rats outnumbered kangaroo rats even in a heavily grazed pasture.

The great increase in cotton rat numbers in 1958 involved nearby croplands as well as the sand sagebrush pastures. There apparently were large numbers of cotton rats in nearby wheat fields two months or more before the rodents became abundant on the grazed lands.

By May, 1958, appreciable damage, presumably by cotton rats, was observed in wheat fields adjacent to the grasslands, although cotton rats were still relatively few on grazed areas. The wheat had grown to stands of dense vegetative cover several weeks earlier than had the native grasses.

In personal conversations with the writer, farmers reported that the amount of rodent damage to wheat in the fields,as compared with that of other years, was unusually great in Woodward County in May, 1958. Some of the interviewed persons estimated that as much as ten per cent of the stand of wheat in some fields had been cut by rodents at least a month before the time of harvest. Some of the farmers had concluded that the damage was that of cotton rats, known locally as "field rats." Others did not attempt to assign the damage to a given species.

In fields observed by the writer, adjacent to and within 35 miles of the Experimental Range, there seemed to be not a square yard which did not contain some cut stalks of wheat. Occasional areas five to ten feet in diameter had an estimated three-fourths of the wheat stalks cut down and cut into sections several inches long. Part of the unripe grain was eaten from the seed heads of these cut stalks. That this was mostly the work of cotton rats was suggested by the writer's observations of the abundance of fecal pellets resembling those of cotton rats, and by the large numbers of cotton rats which farmers reported seeing in the fields, especially during the June harvest season.

It is not known how the population densities compared on the three live-trap plots at the actual end of the period of the cotton rat build-up. By a Lincoln Index method--namely, the formula of Underhill (1941)--the estimated density of cotton rats was 73 individuals per ten acres on the lightly grazed plot on August 8, 1958. The total catch on that plot was 121 cotton rats during the period August 8 to 22, 1958. The Lincoln Index estimate was 60 individuals per ten acres on the moderately grazed plot on August 11, 1958, as compared with the total catch of 105 individuals on the plot during the period August 11 to September 5, 1958.

The total-catch estimate of population was only 16 cotton rats per ten acres on the heavily grazed plot for the period August 12 to September 3, 1958. No Lincoln Index estimate was attempted for that small population. For the final live-trapping period on all plots, the estimated densities of cotton rats may have been considerably greater than the actual densities. The large cruising radii of cotton rats, especially males', made the effective size of a live-trap plot more nearly 16 or 17 acres, instead of only the estimated ten acres.

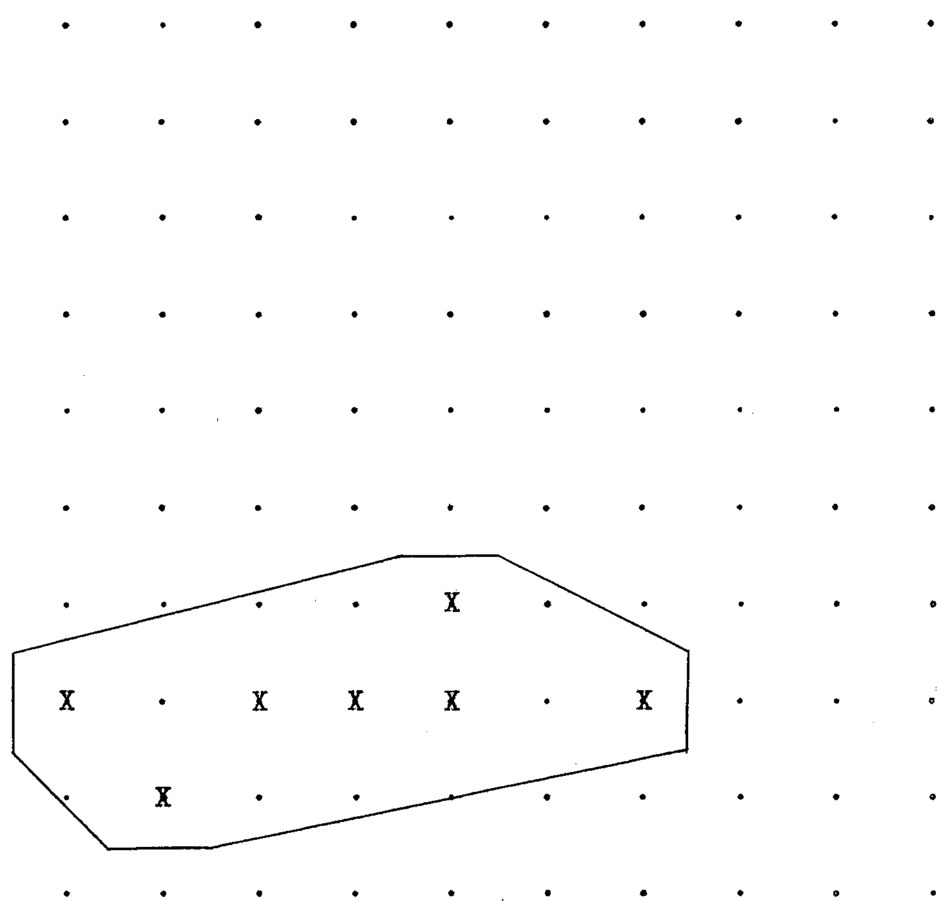
After the final live-trapping period, local reproduction may have increased densities until about the end of September, 1958, as suggested by the data on age composition and breeding success (Tables 31 and 32). The cotton rat population apparently did continue to increase for a few weeks after the period of August and early September. This was suggested by the fact that cotton rats had become abundant on heavily grazed areas by November and also by the great apparent increase in the amount of cut vegetation during the fall of 1958.

Reproduction of cotton rats seemed to halt abruptly (Table 32) as the population neared its greatest density in late summer or fall of 1958 (Tables 4 to 8 inclusive). Pregnant females were absent from catches on ungrazed and grazed areas in October and November, 1958, where pregnant females had been common in October and November of the preceding year. Associated with the female cotton rats' apparent failure to conceive were conditions similar to those observed in natural populations of voles (Clethrionomys spp.) by Kalela (1957), as reported by Christian (1959). Kalela (o. c.) found that prevalence of pregnancy among fecund females was high in a year when population density was low, whereas prevalence of pregnancy was low when population density became high. Similarly, Christian (o. c.) reported decreased fertility among house mice (Mus spp.) and Norway rats (Rattus spp.) when population density increased.

The cotton rat population of 1958 was apparently one of unusually high densities on grazed areas of sand sagebrush grassland. The present study found cotton rats scarce on grazed land in 1956 and 1957 (Tables 4 to 8 inclusive). They seem to have been a numerically minor species also in 1940-1942 and 1949, when cotton rats made up less than five per cent of the total catches (Table 11) on the Southern Plains Experimental Range. During 1956 and until termination of his field work in the summer of 1957, J. M. Inglis (personal communication) reported that cotton rats were less than ten per cent of the total catches on upland plots of ungrazed sand sagebrush grassland near Canadian, Texas.

As with other rodent species, there seemed to be a spacing of individual cotton rats within their habitat. As late as August and early September, 1958, when the population was at or near its peak or plateau, about half of the live-trapped individuals apparently maintained homesteads. At least they were recaptured within relatively restricted areas. Some of these recaptures had been observed in their homesteads for as long as four to seven months (Table 33). The homestead of one female cotton rat (Figure 8) exemplifies the apparent tendency of some individuals to remain within a limited area for a period of several months.

During the final month of studies on the live-trap plots, approximately half of the cotton rats taken on the plots were individuals which were captured only one time. For the last night of live-trapping, the



"X" indicates capture site

Dots represent live-trap stations 66 feet apart

Figure 8. Homestead area (1.5 acres) of an adult female cotton rat (no. 5) captured seven times during a period of seven months on the 8.1-acre live-trap grid in lightly grazed pasture 20. Southern Plains Experimental Range, Harper County, Oklahoma. January 27-August 20, 1958.

average ratio of recaptured to other cotton rats was 41 to 44 on the lightly and moderately grazed plots. It was, therefore, suggested that a large proportion of the population did not have established homesteads during the period of rapid increase in numbers, as population density was becoming unusually great.

During late summer and the fall of 1958, it was common to find adult cotton rats, especially males, with what appeared to be bite-wounds on their legs, tails, feet, and other parts of their bodies. Absence of such injuries among other species at that time suggested that this was not evidence of interspecific strife. The possibility of interspecific strife is not ruled out, of course, but it is suggested that there may have been some social stress among cotton rats themselves as the population neared its greatest observed densities.

Spotted Ground Squirrels

Spotted ground squirrels (*Citellus spilosoma marginatus*) were a numerically minor species present on ungrazed as well as grazed areas. Kill-trap records suggested that the squirrels were more numerous on grazed than on ungrazed sites (Tables 9 and 10). Populations were probably denser on heavily than on lightly grazed areas, but the live-trap data did not strongly suggest this (Tables 5 to 8 inclusive). The species may have been slightly more abundant during the drought year, 1956, than in 1957 and 1958, although this also was not strongly suggested. Earlier rodent studies found spotted ground squirrels relatively scarce on the Experimental Range. They made up only five to seven per cent of the total rodent catches reported in the early summers of 1941 and 1942 (McMurry, 1942, 1943).

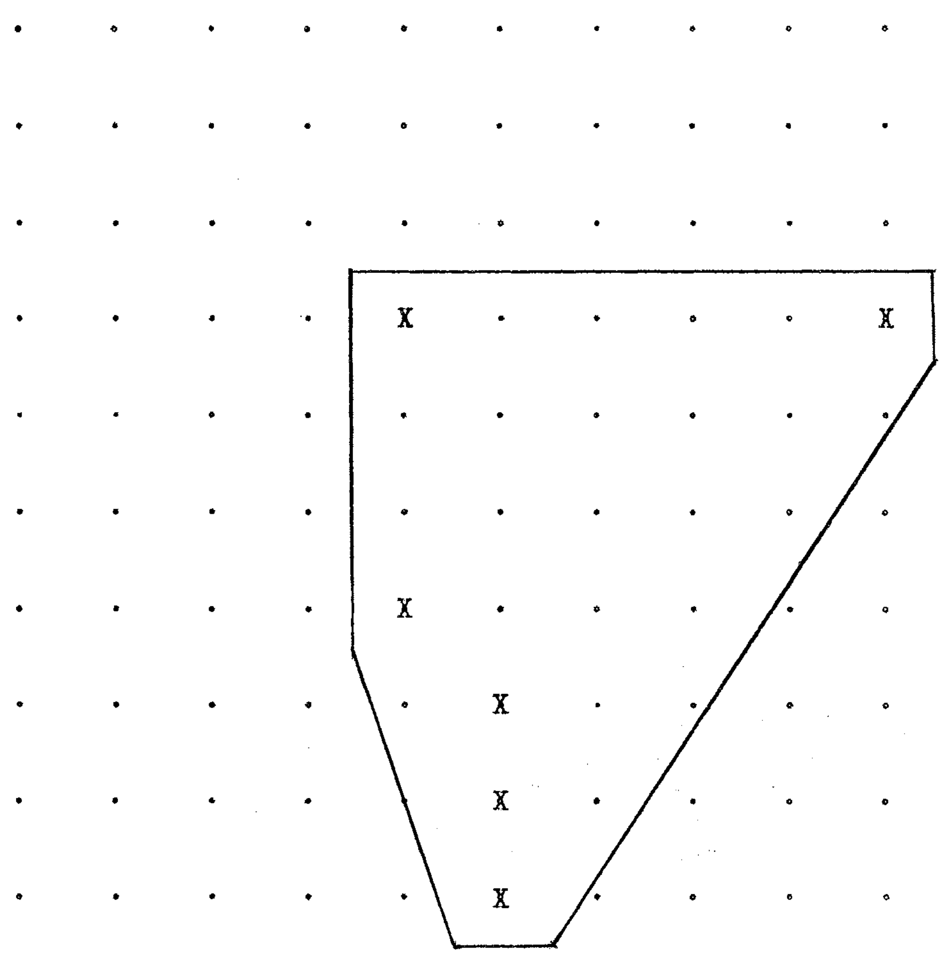
During some of the trapping periods, such as the summer of 1956, spotted ground squirrels did slightly outnumber grasshopper mice on one or more of the live-trap plots (Tables 6, 7, and 8). The estimated differences in numbers of the two species, however, were not more than seven individuals per ten acres at any time. Grasshopper mice were approximately twice as numerous as ground squirrels on the basis of total numbers taken on the live-trap plots during the study period as a whole. In 1958, spotted ground squirrels were an especially small proportion of the total catches, in comparison with kangaroo rats, grasshopper mice, and cotton rats (Tables 4 to 10 inclusive).

The greatest estimated density of spotted ground squirrels was 12 per ten acres (Table 5), after the appearance of young of the current breeding season. The relative abundance of spotted ground squirrels ranged from zero to 29 per cent of the total catch on live-trap plots in various periods. The species hibernated from late October or early November until middle or late March. Pregnant females were taken only during the month of May, and populations reached their seasonal peaks in middle and late summer.

The mean estimated homestead of spotted ground squirrels was 0.8 acre(Table 34), and the average cruising radius was 280 feet. One female was captured within an estimated area of 2.7 acres during a period of 14 months (Figure 9). Forty-seven per cent of the 70 individuals taken on live-trap plots were recaptured at least one time each.

Table 34. Homestead Areas and Cruising Radii of 14 Adult Spotted Ground Squirrels Captured 3 to 8 Times on One of Two Live-Trap Plots. Southern Plains Experimental Range, Harper County, Oklahoma. 1956-1958.

Sex	Pasture Number	Homestead	Cruising Radius	Duration of Record	Times Caught
		a.	ft.	mo.	no.
m	21	0.7	280	1	8
m	19	0.7	272	1	5
m	21	0.6	272	1	5
m	21	0.3	238	10	3
	Average, Males	0.6	266	3	5
f	19	2.7	476	14	6
f	21	1.7	515	1	6
f	19	1.3	330	1	6
f	21	0.9	402	11	6
f	21	0.8	238	9	4
f	21	0.7	272	11	4
f	19	0.6	272	1	5
f	19	0.6	147	12	5
f	19	0.3	147	1	4
f	21	0.2	66	1	3
	Average, Females	1.0	286	6	5
	Avg., Both Sexes	0.8	280	9	5



"X" indicates capture site

Dots represent live-trap stations 66 feet apart

Figure 9. Homestead area (2.7 acres) of an adult female spotted ground squirrel (no. 4) captured six times during a period of 14 months on the 8.1-acre live-trap grid in moderately grazed pasture 19. Southern Plains Experimental Range, Harper County, Oklahoma. July 10, 1957-September 5, 1958.

The data did not permit satisfactory comparisons of homesteads on areas under different degrees of grazing or of males' with females', although there was some suggestion that male homesteads were smaller than females'.

Thirteen-Lined Ground Squirrels

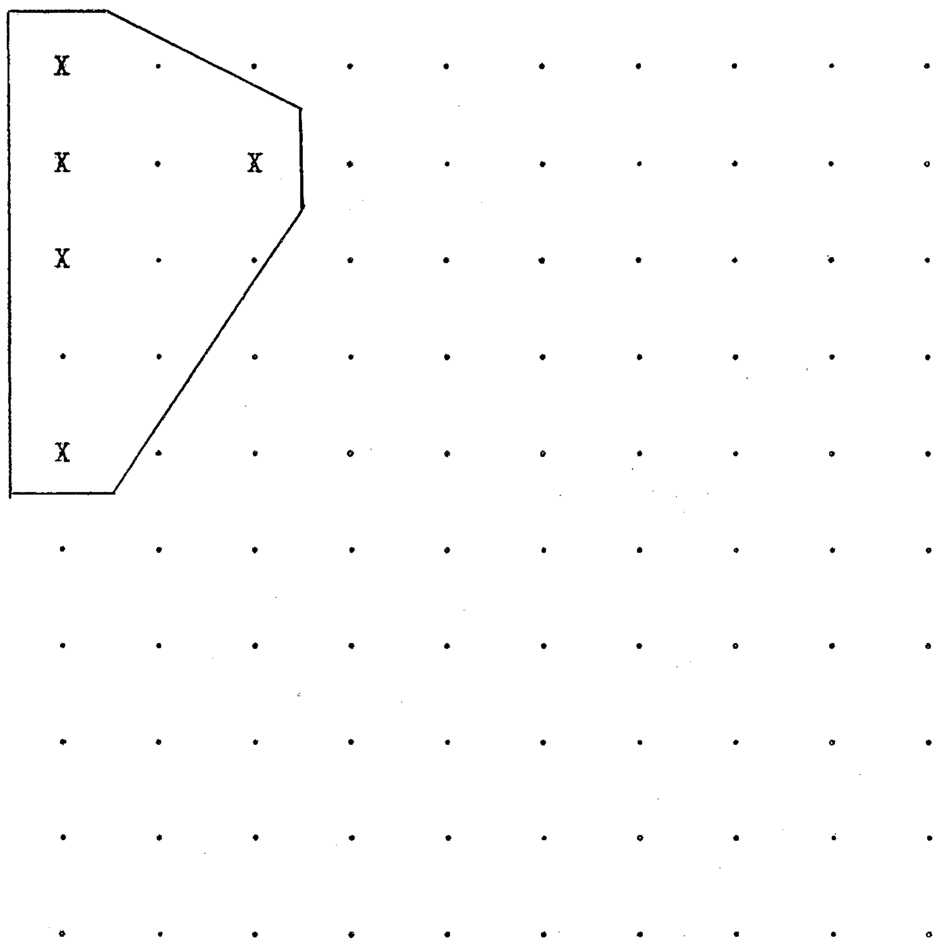
Thirteen-lined ground squirrels (Citellus tridecemlineatus arenicola) were among the least common rodent species trapped on grazed sand sagebrush grasslands (Tables 4 to 10 inclusive). This species was not taken on ungrazed areas. The maximum estimated density was five individuals per assumed ten-acre plot and pertained to the live-trap grid in heavily grazed pasture 21 in July of 1958.

Thirteen-lined ground squirrels were found on dunes as well as on interdunal sites, but the majority of individuals were associated with the low flat areas and with less sandy soils. This species also appeared scarce on the Experimental Range in 1941 and 1942 (McMurry, o. c.).

The largest estimated homestead was 1.9 acres for thirteen-lined ground squirrels, and the longest cruising radius was 396 feet (Table 35). The estimated homestead of the individual whose live-trapping record extended over the greatest period is shown in Figure 10. This species of ground squirrel also hibernated from November to March, and females were found pregnant only in May. Fifty-six per cent of the 16 live-trapped individuals were recaptured at least once.

Table 35. Homestead Areas and Cruising Radii of Nine Adult Thirteen-Lined Ground Squirrels Captured 2 to 6 Times on One of Three Live-Trap Plots. Southern Plains Experimental Range, Harper County, Oklahoma. 1956-1958.

Sex	Live-Trap Plot Location	Homestead	Cruising Radius	Duration of Live-Trap Record	No. Times Caught
	pasture no.	a.	ft.	mo.	
m	20	1.9	396	1	6
f	19	1.0	264	12	5
m	21	0.6	360	1	2
m	21	0.6	295	1	2
m	19	0.4	147	1	4
f	21	0.4	147	1	3
m	20	0.3	147	1	2
m	19	0.2	93	9	2
m	21	0.2	66	1	2
Average		0.6	213	3	3



"X" indicates capture site

Dots represent live-trap stations 66 feet apart

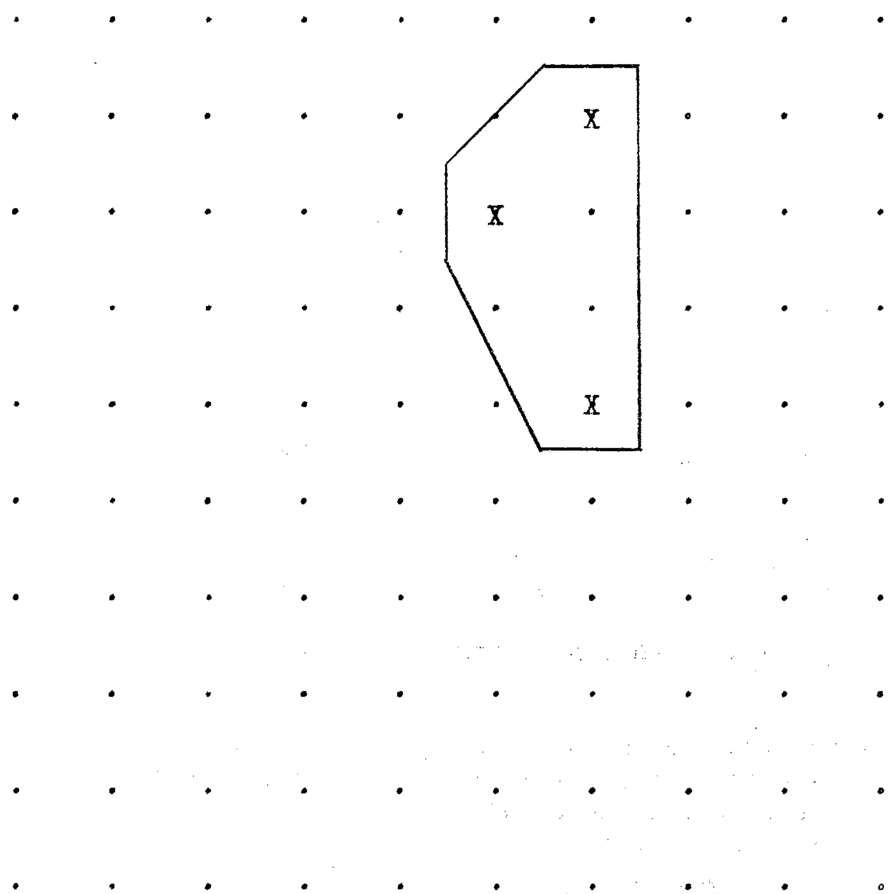
Figure 10. Homestead area (1.0 acre) of an adult female thirteen-lined ground squirrel (no. 4) captured five times during a period of 12 months on the 8.1-acre live-trap grid in moderately grazed pasture 19. Southern Plains Experimental Range, Harper County, Oklahoma. July 10, 1957-June 29, 1958.

Deer Mice

Dense stands of tall grasses seemed to support the greatest numbers of deer mice (Peromyscus maniculatus nebrascensis). They were more numerous on ungrazed than on grazed areas and seemed more abundant in the spring of 1958 than at any other time during the present study (Tables 4 to 10 inclusive). So few were taken on the live-trap plots that no comparison of densities seemed feasible on areas under different degrees of grazing. Thirty per cent of the 37 live-trapped individuals were recaptured at least once. Estimated homesteads and cruising radii of deer mice (Table 36 and Figure 11) were somewhat smaller than those of larger species, such as the kangaroo rat(Table 23 and Figure 4). Three captures, however, seem a scant basis for estimating the extent of an area used by an individual. It is likely that the estimated homesteads of deer mice would appear larger if more data were available.

Table 36. Homestead Areas and Cruising Radii of 11 Adult Deer Mice Captured 2 or 3 Times on One of Two Live-Trap Plots. Southern Plains Experimental Range, Harper County, Oklahoma. 1957-1958.

Sex	Live-Trap Plot Location	Homestead	Cruising Radius	Duration of Live-Trap Record	No. Times Caught
	pasture no.	a.	ft.	mo.	
m	20	1.2	360	2	3
m	19	0.6	209	5	3
m	19	0.7	198	3	3
m	20	0.3	198	3	2
m	20	0.2	93	1	2
m	19	0.1	0	3	3
m	19	0.1	0	2	2
	Average, Males	0.5	151	3	3
f	20	0.5	330	3	3
f	19	0.4	238	1	2
f	19	0.1	0	1	2
f	19	0.1	0	1	2
	Average, Females	0.3	142	1	2.5
	Average, Both Sexes	0.4	148	2	2



"X" indicates capture site

Dots represent live-trap stations 66 feet apart

Figure 11. Homestead area (0.7 acre) of an adult male deer mouse (no. 8) captured three times during a period of three months on the 8.1-acre live-trap grid in moderately grazed pasture 19. Southern Plains Experimental Range, Harper County, Oklahoma. January 22-April 22, 1958.

Pocket Mice

Pocket mice (*Perognathus* spp.) were rarely taken on any sites during the present study. They seem to have been equally uncommon during all other rodent studies on the Southern Plains Experimental Range (Trowbridge, 1941, 1942; McMurry, 1942, 1943, 1947; Frank, 1950). Pocket mice were also rare during a study by J. M. Inglis (personal communication) near Canadian, Texas.

Silky pocket mice (*P. flavus bunkeri*) apparently did not occur in large numbers on sand sagebrush grasslands under any degree of grazing or non-grazing by cattle. On the live-trap plots, the frequencies of capture were too few to suggest any difference or lack of difference in populations on dune sites and interdunal sites.

Silky pocket mice may have been less numerous on the lightly grazed live-trap plot than on the moderately and heavily grazed ones, although this was not strongly indicated (Tables 6, 7, and 8). The greatest estimated density was six silky pocket mice per ten acres. This species was not taken on ungrazed areas, where most of the trapping was done with Victor rat traps.

The large kill-traps may have been less effective than other traps for taking such small animals, but 100 trap-nights with the smaller Museum Special traps also caught no silky pocket mice on an ungrazed area in November, 1957. This species was not taken in 1400 Museum Special trap-nights on six different pastures of the Experimental Range in 1956 and 1957.

Among the traps which were used, the live-traps seemed to be the most effective type for silky pocket mice, and the live-trap records

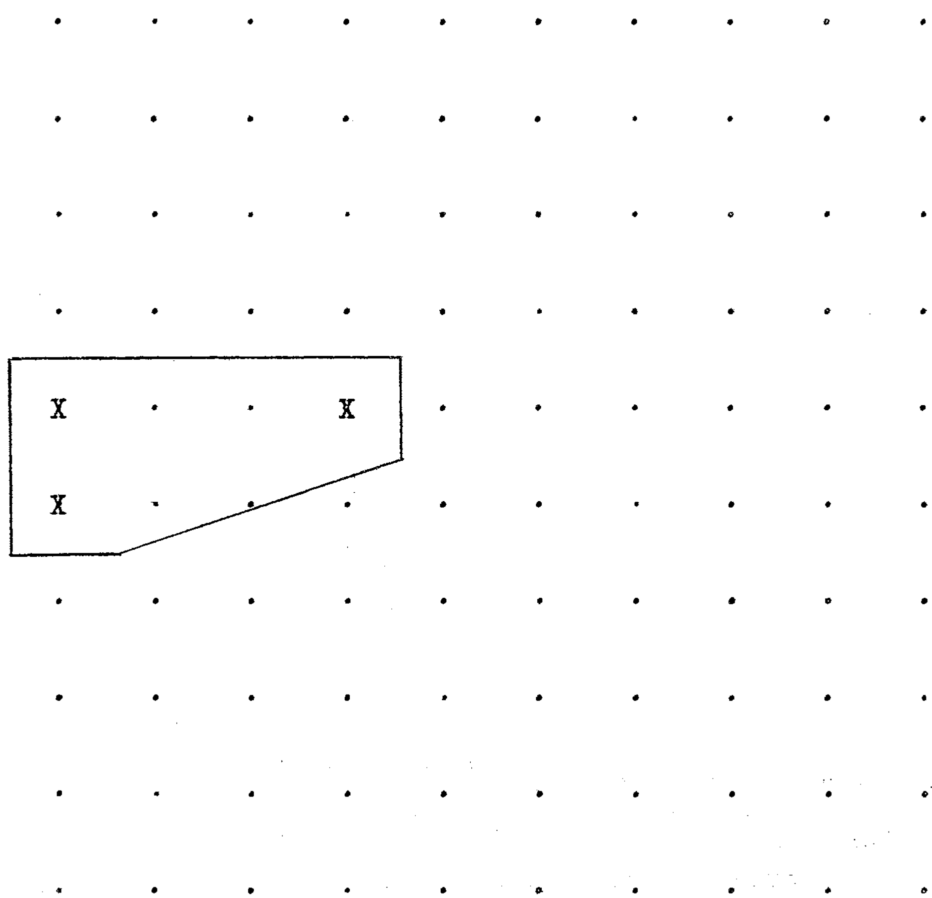
(Tables 5 to 8 inclusive) support the observation that this species was generally scarce. A total of 40 individuals was taken on live-trap plots, and 19 per cent of these were recaptured at least once.

Population fluctuations of silky pocket mice seemed to parallel those of kangaroo rats, with the low occurring in 1957, following the drought of 1956. Average homestead areas were probably larger than the 0.4 acre shown in Table 37, for which the number of recaptures was rather limited. The example of one individual's homestead (Figure 12) was estimated from comparatively few recaptures.

Hispid pocket mice (P. hispidus paradoxus) seemed even more uncommon than the silky pocket mice. None of the former appeared on any of the areas until the spring of 1958, when they were taken on ungrazed areas and on areas under three degrees of grazing (Tables 4, 5, 7, 8, and 10). The numbers recaptured on live-trap plots (Tables 7 and 8) were insufficient to allow estimates of homestead size. For the same reason no comparison of densities seems feasible for different areas.

Table 37. Homestead Areas and Cruising Radii of Six Adult Silky Pocket Mice Captured 2 or 3 Times on One of Three Live-Trap Plots. Southern Plains Experimental Range, Harper County, Oklahoma. 1958.

Sex	Live-Trap Plot Location	Homestead	Cruising Radius	Duration of Live-Trap Record	No. Times Caught
	pasture no.	a.	ft.	mo.	
m	21	0.8	330	1	2
m	21	0.6	209	5	3
f	20	0.4	147	4	3
m	19	0.3	132	2	2
m	19	0.2	66	3	3
m	20	0.2	66	1	2
Average		0.4	158	3	3



"X" indicates capture site

Dots represent live-trap stations 66 feet apart

Figure 12. Homestead area (0.6 acre) of an adult male silky pocket mouse (no. 18) captured three times during a period of five months on the 8.1-acre live-trap grid in heavily grazed pasture 21. Southern Plains Experimental Range, Harper County, Oklahoma. March 21-August 17, 1958.

Wood Rats

Most of the wood rats (*Neotoma micropus micropus*) which were captured were taken in or near clumps of sand plum (*Prunus angustifolia*) or skunkbush (*Rhus aromatica*), and they were common in sheds and other range buildings. Like most of the other rodent species, wood rats seemed to increase in numbers in 1958. Wood rats, nevertheless, appeared relatively scarce on all areas which were sampled by trapping (Tables 4 to 10 inclusive).

Pocket Gophers

It appeared that pocket gophers (*Geomys bursarius major*) made up only a fraction of one per cent of the total rodent numbers on grazed pastures and ungrazed areas, except on certain small areas. Distribution was very much clumped. A census was made in late winter and early spring of 1958, when mounds of pocket gophers appeared more abundant than at any other time during the 1956-1958 study period.

Removal trapping in the burrow systems in the 160 acres of moderately grazed pasture 19 suggested an average population density of one pocket gopher per 12.5 acres during February, March, and April, 1958. Relative abundance of mounds suggested that average populations of pocket gophers were not greatly different on any of the other grazed and ungrazed areas. Remarks in the reports of earlier studies (Trowbridge, 1941, 1942; McMurry, 1942, 1943, 1947) suggest that pocket gophers and their mounds were localized in their distribution and scarce over the experimental pastures as a whole in 1940-1942. These authors did not attempt directly to trap pocket gophers or otherwise systematically to estimate populations or to count mounds. Frank (1950) reported that he conducted no studies on populations or habits of pocket gophers in late 1949. At that time, Frank (o. c.) estimated that the pocket gopher "...was a common rodent on the range as evidenced from mounds, although no indications of excessively high populations were observed."

An interdunal area where water stood during the heavy rains of 1957, a highway borrow-pit, and a corner where cattle tended to gather in the lee of a plum thicket were examples of sites with unusually large numbers of pocket gopher mounds. Large forbs such as mentzelia (Mentzelia stricta) and ragweed (Ambrosia psilostachya) had been abundant there in the summer of 1957. Pocket gopher mounds were not restricted to such sites, however. A typical group of mounds was a meandering line, or a cluster of such lines, totalling as much as a thousand feet in length, and containing as few as a dozen to 600 or more mounds. In some groups, three or four lines diverged from a central cluster of mounds. In some of the clusters there were two or three hundred mounds per acre, but the areas were limited to two or three acres at most. These observations were in accord with those of Phillips (1936), who reported that groups of mounds tended to occur in patches of forbs, among stands of grasses in central Oklahoma.

A large number of mounds in a group did not necessarily indicate a large number of pocket gophers. An average of 182 mounds cast per pocket gopher per winter was estimated for the 13 individuals removed from five groups of mounds during the period, February 3 to April 12, 1958, on the Experimental Range. In a three-week period, 85 mounds were added in an area 45 by 90 feet, apparently by the one young female which was taken from the burrow system in that area.

Harvest Mice

The harvest mouse (Reithrodontomys montanus griseus) apparently was extremely rare during the 1956-1958 period of study, on grazed and ungrazed areas as well. It was not taken in any of the types of traps on any of the sampled areas. J. M. Inglis (personal communication) took only one specimen during two years of field work, 1955-1957, on sand sagebrush grassland in Hemphill County, Texas. Harvest mice were also rare on sand sagebrush grasslands during the 1940's, judging from reports of earlier studies (Trowbridge, o.c.; McMurry, o. c.; Frank, o. c.) on the Experimental Range. Frank (o. c.) indicated that he took harvest mice mostly in or near dense stands of tall grasses, especially near the cattle exclosures. A report by Blair (1954) suggested that harvest mice were generally rare and local in distribution in the Mesquite Plains district of the Southern Great Plains. The same is perhaps true of the harvest mice on sand sagebrush grasslands.

Plants Used By Kangaroo Rats

Observable ways in which range rodents affect vegetation are in their uses of plants for food and nests and removal for development of runways. They may dispose of parts of plants by eating them, by storing them in nests and food caches, and by cutting and leaving parts on the ground as litter.

Food-use studies showed that rodents did not haphazardly devour whatever materials occurred in their habitats. Some of the rodent species seemed to have preferences for certain major classes of foods, such as seeds, herbage, and animals.

Like other members of their genus, kangaroo rats of western Oklahoma showed strong preferences for seeds. Finely chewed endosperm and pericarp made up 80 to 90 per cent of the average volume of stomach contents. Seeds and fragments of seeds were by far the most frequently identified items in stomachs of kangaroo rats (Table 38). Items other than seeds were but a minor part of the contents of cheek pouches, on bases of number, volume, and occurrence frequency (Tables 39 and 40).

It appeared that relative abundance of most kinds of seeds in kangaroo rat cheek pouches was determined chiefly by availability of the seeds at a particular time and place, although there were no actual measures of seed availability. If any plant species could be termed dietary staples of kangaroo rats during this study, they were probably sand dropseed (<u>Sporobolus cryptandrus</u>), purple sandgrass (<u>Triplasis purpurea</u>), and flatsedge (<u>Cyperus schweinitzii</u>), at least on the grazed areas (Table 39).

Table 38. Percentage Occurrence of Items in Stomachs of 171 Kangaroo Rats. Harper and Woodward Counties, Oklahoma.

Items, in Order of Decreasing Frequency	Areas Grazed by Cattle						Ungrazed Area		
	1956		1957			1958	1957		1958
	Sum	Win	Sum	Aut	Win	Spr	Aut	Win	Spr
N =	11	14	17	63	5	15	30	5	11
Endosperm, seedcoat	100	100	100	97	100	100	100	100	100
Green material spp.	3	38	29	56	60	47	40	60	64
Arthropod fragments		7	47	11	20	13	30	20	36
Grasshopper eggs				2					9
Seed fragments:									
<u>Sporobolus cryptandrus</u>	100	93	29	14		40			9
<u>Linaria canadensis</u>						93			9
<u>Triplasis purpurea</u>				48			33		
<u>Eriogonum annuum</u>				2	40		17		9
<u>Lepidium densiflorum</u>						40			18
<u>Cycloloma atriplicifolium</u>			10			33			9
<u>Portulaca oleracea</u>			29						
<u>Helianthus annuus</u>							27		9
<u>Mentzelia stricta</u>			5		20				
<u>Silene antirrhina</u>						13			
Grasses spp.	1			8		7			
<u>Amaranthus</u> spp.				5			3		
<u>Cyperus schweinitzii</u>			5						
<u>Croton</u> spp.				2					
<u>Euphorbia</u> spp.				2					
<u>Oenothera</u> spp.				2					

Table 39. Percentage Occurrence of Seeds in Cheek Pouches of 294 Kangaroo Rats. Harper and Woodward Counties, Oklahoma.

Items, in Order of Decreasing Frequency	Areas Grazed by Cattle						Ungrazed Area		
	1956	1957			1958		1957		1958
	Win	Sum	Aut	Win	Spr	Sum	Aut	Win	Spr
N =	3	8	98	35	28	21	77	9	15
Triplasis purpurea			73	26	7		53	22	7
Sporobolus cryptandrus	67	38	19	3					
Cyperus schweinitzii		62	11	23	39	57	3	33	27
Helianthus annuus							61	56	20
Cassia fasciculata			2	20	4		35		53
Linaria canadensis					46				7
Commelina erecta		38	8	11	14		8	44	20
Rhus aromatica			1			43	1	44	
Artemisia filifolia				6		5	1	44	
Euphorbia spp.			1	43		5	1	11	
Croton texensis		12	41	26	14	24	6	22	
Cycloloma atriplicifolium			16	34	4	33	10	22	
Strophostyles leiosperma			17	9	7		1		33
Paspalum ciliatifolium			7	31		5	3	11	
Eriogonum annuum			2	6		5	12	22	
Plantago purshii				6		19			20
Lepidium densiflorum			1	14					
Mentzelia stricta			12	3					
Argemone intermedia			10	9				11	7
Cristatella jamesii							1	11	
Salsola kali							1	11	

Table 39. (Continued)

Items, in Order of Decreasing Frequency	Areas Grazed by Cattle						Ungrazed Area		
	1956	1957			1958		1957		1958
	Win	Sum	Aut	Win	Spr	Sum	Aut	Win	Spr
Salvia azurea								11	
Cenchrus pauciflorus			3	9					
Descurainia pinnata					7				7
Festuca octoflora					7				
Specularia biflora									7
Bouteloua spp.				6					
Croton glandulosus				6					
Tradescantia occidentalis				6					
Lithospermum incisum			1		4	5	1		
Tephrosia virginiana			1				5		
Silene antirrhina					4				
Viola kitaibeliana					4				
Amaranthus spp.			2	3					
Lespedeza spp.							3		
Machaeranthera pinnata				3					
Polygonum convolvulus			3						
Vicia villosa			3						
Calamovilfa gigantea			1						
Chenopodium spp.							1		
Chloris verticillata			1						
Froelichia floridana			1				1		
Panicum virgatum			1						
Portulaca oleracea							1		
Setaria glauca			1						

Table 40. Percentage Occurrence of Non-Seed Items in Cheek Pouches of 294 Kangaroo Rats. Harper and Woodward Counties, Oklahoma.

Items, in Order of Decreasing Frequency	Areas Grazed by Cattle						Ungrazed Area		
	1956	1957			1958		1957		1958
	Win	Sum	Aut	Win	Spr	Sum	Aut	Win	Spr
N =	3	8	98	35	28	21	77	9	15
Grass leaves, stems spp.	100		5		7			11	
Sporobolus cryptandrus									
leaves, stems	67	25	8	3					
Cow Manure			12	6	4				
Triplasis purpurea									
leaves, stems			11	11			6		
Arthropod parts			11			5		11	
Plantago purshii									
seedlings				9					
Rodent feces			1			5	8		
Forb stems, leaves spp.			3	6			4		
Artemisia filifolia									
leaves			1	3					
Descurainia pinnata									
seedlings				3					
Grass roots spp.			1						

Except for the absence of tall grasses in the samples, there seemed to be no pronounced scarcity of particular species among the seeds gathered by kangaroo rats. Half of the seed species listed in Table 39 were major components of the contents of cheek pouches in one season or another. The number of major items would probably be much greater if rats had been collected in all weeks of each year of this study. Generally, species which were major food items in 1956-1958 were also the major items in 1940-1942, judging from reports of earlier studies on the Experimental Range (Trowbridge, 1941, 1942; McMurry, 1942, 1943, 1947).

The efficiency with which food species could be harvested probably determined their abundance in kangaroo rat diets. Very small seeds were seldom found in cheek pouches unless they were seeds which could be gathered in aggregates, as in seed pods or ensheathed panicles.

Scarcity of tall grasses in cheek pouches and stomachs may have been due to factors other than palatability. Smallness of seeds such as sand lovegrass (*Eragrostis trichodes*) may have resulted in few of them being gathered from the soil surface. Also, tall grasses tend to grow in bunches or in clumps of sagebrush, as in the case of *Eragrostis trichodes*. This perhaps makes them difficult for approach by a kangaroo rat, as compared with stems of *Sporobolus cryptandrus* and *Cyperus schweinitzii*. Finally, during the periods of these collections, most of the tall grasses, especially bluestems (*Andropogon* spp.), seemed not to produce seed as prolifically as some of the others.

Seeds of tall grasses were also scarce among seeds used by kangaroo rats on an ungrazed area of sand sagebrush grassland near Canadian, Texas, according to J. M. Inglis (personal communication). He reported that fewer than one per cent of the cheek pouches contained seeds of Andropogon hallii and Eragrostis trichodes.

There were seasonal differences in foods used by kangaroo rats, as well as differences between grazed and ungrazed areas. Important summer and fall foods were Sporobolus cryptandrus, Cyperus schweinitzii, Triplasis purpurea, and several species of forbs on the grazed areas. The same species were commonly taken in winter, except that Sporobolus cryptandrus had apparently become scarce. By spring the most abundant foods in the pouches were seeds of short-lived spring annuals plus Cyperus schweinitzii. There were not marked differences among pastures under different degrees of grazing.

The chief difference between grazed and ungrazed areas was that Sporobolus cryptandrus seeds were absent and forb seeds were considerably more abundant in cheek pouches of kangaroo rats on the ungrazed land. These differences in kangaroo rat diets on grazed and ungrazed areas seemed merely to reflect differences in relative abundance of the plant species growing on the areas. Triplasis purpurea and Cyperus schweinitzii were major items on both grazed and ungrazed areas.

It was not learned if there were differences in total amounts of seed available to kangaroo rats on the different areas. Vegetation studies indicated differences in relative abundance of some of the major food plants of kangaroo rats on the various grazed and ungrazed sites. However, the abundance of seeds of certain species on one area may have tended to compensate for relative scarcity of other seed species on that area.

Although they seemed seldom to use tall grasses, kangaroo rats did cut stems of short grasses, such as Bouteloua gracilis, when they were in seed. The usual method of kangaroo rats' harvesting seed of *Sporobolus cryptandrus* seemed to be by cutting the ensheathed panicles with attached leaf and culm sections. Axillary seeds of *Triplasis purpurea* were frequently taken by cutting the leaf and culm sections of this abundant annual grass. Kangaroo rats also cut off fruiting parts of spring annuals such as *Linaria canadensis*, *Silene antirrhina*, and *Festuca octoflora*.

It is possible that kangaroo rats had both negative and positive effects on plant propagation, but these were difficult to ascertain. Kangaroo rats seemed to gather seed industriously in all seasons, but this did not seriously restrict propagation of at least the small-seeded species, judging from the abundance of plants such as *Sporobolus cryptandrus* and *Linaria canadensis* in the pastures. The rats spilled great numbers of such small seeds from the pods and panicles as they were harvested. Apparently, not all large seeds were removed from the soil, for the pouches of some of the rats collected in May, 1958, had in them seeds such as *Croton texensis* and *Helianthus annuus*, which were produced the previous summer. *Sporobolus*-size seeds were almost never gathered from the soil, except when they stuck to large seeds such as *Croton* spp.

Plant-propagating effects of surface caches of kangaroo rats were not observed. The smallest seeds sometimes reached kangaroo rat stomachs in whole form, but it was not learned whether or not viable seeds appeared in the feces. The effect of droppings in the process of plant propagation, therefore, was not known.

Little is known of effects of kangaroo rats on newly sprouted seeds on untilled sand sagebrush grasslands. Seedlings and cotyledons were not commonly found in cheek pouches in late winter and spring of 1958, although seedlings and cotyledons seemed comparatively abundant on the study area at that time.

Arthropods were a small part of the kangaroo rat diet, ranging from a trace to ten per cent of the average volume of the stomach contents. Some of the items were the rats' own ectoparasites, namely, fleas. Some of the arthropod material in kangaroo rat stomachs seemed to be carrion. Arthropod fragments were relatively frequent in kangaroo rat stomachs during cold weather, when bodies of presumably winter-killed grasshoppers were commonly seen on the ground. Sources of the arthropod fragments in stomachs in warm weather were not clearly suggested. The insect eggs and larvae in the stomachs do suggest that kangaroo rats preyed upon insects of those life stages.

Very small amounts of green or cured grass or other forage leaves and stems seemed to be eaten by kangaroo rats. Most of the green material in the stomachs was not identifiable as to species. Fragments thought to be grass and forb leaves or stems were found in some stomachs, but the average volume of all yellowish-fibrous or green material, identifiable or otherwise, was less than ten per cent of the stomach contents in most periods. Most of the identifiable items of that green material appeared to be seed husks, seed capsules, or finely chewed green seeds. The prevalence of seeds in the diet of the local subspecies of kangaroo rat indicates similarity to the observed kinds of food used by other members of the genus Dipodomys, as reported by Fitch (1948), Fitch and Bentley (1949), Grinnell (1932), Hawbecker (1940), Monson and Kessler (1940), Monson (1943), Reynolds (1950, 1958), Shaw (1934), Tappe (1941), and Vorhies and Taylor (1922).

Apparently, there was not much plant material stored in burrows in the drought summer of 1956, when there was a moderately high population of kangaroo rats and food appeared to be scarce. The nests or caches found in four of 17 burrows in July, 1956, were old, partly decomposed stems and leaves of undetermined species of grasses.

Plant materials weighing from 126 to 225 grams per burrow were collected from five kangaroo rat burrows in the winter of 1956-1957. The collections were nests, food caches, and ejected debris, composed mostly of leaves and cut fruitstalk sections of Sporobolus cryptandrus, with some Artemisia filifolia seeds and twigs. The weights were somewhat exaggerated by some sand and droppings which could be neither sifted nor washed out conveniently. No stored plant materials were found in the three kangaroo rat burrows which were excavated in August, 1957.

Plants Used by Other Rodent Species

Animals, probably insects, were the chief dietary items of grasshopper mice in all seasons and areas. Arthropod exoskeletons and attached or associated flesh particles occurred in all 79 stomachs of grasshopper mice, and by volume they were the majority of those stomachs' contents in all seasons (Table 41). It is not known what part of this arthropod material was prey and what part was carrion.

Seeds seemed to be a minor item in diets of grasshopper mice. Virtually all of the non-animal matter in the stomachs seemed to be bait, chiefly peanut butter, but one stomach from an ungrazed area contained 20 per cent by volume of Helianthus annuus seed fragments. Four other seeds appeared as trace items in four stomachs, at the rate of one species per stomach (Table 41).

Table 41. Percentage Occurrence of Items in Stomachs of 79 Grasshopper Mice. Harper and Woodward Counties, Oklahoma.

Items in Order of Decreasing Frequency	Areas Grazed by Cattle						Ungrazed Area	
	1956		1957			1958	1957	1958
	Sum	Win	Sum	Aut	Win	Spr	Aut	Spr
N =	9	3	7	23	2	15	15	5
Arthropod parts	100	100	100	100	100	100	100	100
Green material spp.				4				
Identifiable seeds:								
<u>Hoffmanseggia densiflora</u>					50			
<u>Helianthus annuus</u>							40	
<u>Sporobolus cryptandrus</u>		33						
<u>Paspalum ciliatifolium</u>			14					
<u>Linaria canadensis</u>						7		

Unidentifiable green material, arthropods, and seeds were the main items in 54 cotton rat stomachs taken on an ungrazed area (Table 42). Cotton rats apparently ate parts of many of the other trap victims before they themselves were caught. Therefore, much of the material in cotton rat stomachs may have been eaten from stomachs of other rodents. Bait seemed to be a large part of what was classed as endosperm and seedcoat material in cotton rats. In addition to the vegetation which they consumed, cotton rats were presumably responsible for much of the cut vegetation observed in late summer and early fall of 1958, when cotton rat numbers were at a peak.

Table 42. Average Volume and Occurrence Percentages of Items in Stomachs of 54 Cotton Rats. Woodward County, Oklahoma.

Items in Order of Decreasing Volume	Ungrazed Area 1957 Autumn N = 39 Vol.	Occ.	Ungrazed Area 1957 Winter N = 5 Vol.	Occ.	Ungrazed Area 1958 Spring N = 10 Vol.	Occ.
Green material spp.	26	74	65	100	72	90
Endosperm, seedcoat spp.	64	95	13	80	6	30
Parasitic roundworms	4	31	19	100	4	30
Arthropod parts	3	51	tr.	40	18	90
Other animal flesh spp.	3	10	2	20		
Forb leaves, stems spp.	tr.	3			tr.	50
Insect eggs, larvae	tr.	10				
Grass leaves, stems spp.					tr.	30
Total identifiable seeds:	tr.	--	tr.	--	tr.	--
Helianthus annuus		38		40		
Panicum virgatum		18				
Physalis subglabrata		13				
Cycloloma atriplicifolium		10				
Rhus aromatica						10
Amaranthus spp.		8				

Arthropods appeared as the major item in stomachs of spotted ground squirrels in most seasons (Table 43). Endosperm and seedcoat particles, presumed to be mostly bait, were abundant in one sample group. Unidentifiable green material was a major part of the contents in the spring of 1958, when annual forb seeds were apparently being eaten in large quantities. Their green seed pods may have made up most of this unidentifiable green material. Seed of Sporobolus cryptandrus seemed an important food in the drought summer of 1956. The frequency of what seemed to be grass particles suggested that grasses as well as invertebrates were rather important items in diets of spotted ground squirrels.

Foods used by thirteen-lined ground squirrels (Table 44) appeared similar to those of spotted ground squirrels.

Arthropods and seeds, including unknown amounts of bait, were the main dietary items of deer mice (Table 45). Of the seeds, annual forbs and Sporobolus cryptandrus appeared to be the main species used. Unidentifiable green material was abundant in a winter group of stomach samples collected in 1957.

Stomachs of wood rats generally contained greater volumes of unidentifiable green material than of any other item (Table 46). Some of this was forb and some was grass, judging from the occasional identifiable fragments among the masses of finely chewed contents. Endosperm and seedcoat, probably including bait, was also a major dietary item. Most of the identifiable seed material was that of forb species of little or no value as cattle forage.

The six examined stomachs of pocket gophers contained no materials which were identified as to species. Materials were found in cheek pouches

Table 43. Average Volume and Occurrence Percentages of Items in Stomachs of 24 Spotted Ground Squirrels. Harper and Woodward Counties, Oklahoma.

Items in Order of Decreasing Volume	Grazed and Ungrazed Areas							
	1956		1957				1958	
	Summer		Summer		Autumn		Summer	
N =	3		4		5		12	
	Vol.	Occ.	Vol.	Occ.	Vol.	Occ.	Vol.	Occ.
Arthropod parts	63	100	25	100	82	100	28	100
Green material spp.	10	67	5	50	10	40	66	92
Endosperm, seedcoat spp.	27	67	70	100	7	60	3	25
Parasitic roundworms	tr.	33	tr.	50	tr.	20	3	92
Insect eggs, larvae					1	60		
Grass leaves, stems spp.	tr.	33	tr.	25			tr.	25
Forb leaves, stems							tr.	17
Total identifiable seeds:	tr.	--	--	--	tr.	--	tr.	--
<u>Sporobolus cryptandrus</u>	tr.	67			tr.	20		
<u>Linaria canadensis</u>							tr.	17
<u>Silene antirrhina</u>							tr.	17
<u>Lepidium densiflorum</u>							tr.	8

of only four of the 16 individuals collected in late winter and early spring of 1958. Pouches of two of these animals contained sections of culm and upper root parts of unidentified grass species, apparently perennials. One pair of pouches contained corms of <u>Cyperus schweinitzii</u>, and the fourth contained moldy seeds of <u>Strophostyles leiosperma</u> which had apparently been stored for a long time.

Table 44. Average Volume and Occurrence Percentages of Items in Stomachs of Six Thirteen-Lined Ground Squirrels. Harper County, Oklahoma.

Items in Order of Decreasing Volume	Grazed Areas					
	1956 Summer		1957 Summer		1958 Spring	
N =	2		2		2	
	Vol.	Occ.	Vol.	Occ.	Vol.	Occ.
Arthropod parts	85	100	55	100	30	100
Green material spp.	8	50			45	50
Endosperm, seedcoat spp.	5	50	45	50		
Insect eggs, larvae					25	50
Grass leaves, stems spp.	2	50				
Parasitic roundworms			tr.	50		
Total identifiable seeds:	tr.	--	--	--	tr.	--
Linaria canadensis					tr.	100
Silene antirrhina					tr.	50
Sporobolus cryptandrus	tr.	50				

Table 45. Average Volume and Occurrence Percentages of Items in Stomachs of 38 Deer Mice. Harper and Woodward Counties, Oklahoma.

Items in Order of Decreasing Volume	Ungrazed Areas						Grazed Areas	
	1957				1958		1958	
	Autumn		Winter		Spring		Spring	
N =	23		5		5		5	
	Vol.	Occ.	Vol.	Occ.	Vol.	Occ.	Vol.	Occ.
Endosperm, seedcoat spp.	76	100	32	60	32	100	43	60
Arthropod parts	14	78	32	100	68	100	49	100
Green material spp.	10	30	36	80			8	20
Insect eggs, larvae					tr.	20	tr.	20
Total identifiable seeds:	tr.	--	tr.	--	--	--	tr.	--
Helianthus annuus	tr.	65						
Linaria canadensis							tr.	40
Sporobolus cryptandrus							tr.	20
Amaranthus spp.	tr.	8	tr.	20				
Lepidium densiflorum							tr.	20
Mentzelia stricta	tr.	16						
Physalis subglabrata	tr.	8						

Table 46. Average Volume and Occurrence Percentages of Items in Stomachs of 20 Wood Rats. Harper and Woodward Counties, Oklahoma.

Items in Order of Decreasing Volume	Ungrazed Areas						Grazed Areas	
	1957				1958		1958	
	Autumn		Winter		Spring		Spring	
N =	9		2		5		4	
	Vol.	Occ.	Vol.	Occ.	Vol.	Occ.	Vol.	Occ.
Green material, spp.	53	89	35	100	98	100	98	100
Endosperm, seedcoat spp.	8	56	55	100	tr.	20		
Bait	8	56	tr.	50	tr.	20		
Forb leaves, stems spp.	7	44	tr.	50	tr.	80	tr.	100
Arthropod parts	1	22	10	100	2	40	tr.	50
Other animal flesh spp.	tr.	33					2	25
Artemisia filifolia leaves			tr.	100				
Grass leaves, stems spp.			tr.	50			tr.	50
Parasitic roundworms			tr.	50				
Total identifiable seeds:	23	--	tr.	--	tr.	--	tr.	--
Physalis subglabrata	17	78						
Cassia fasciculata	3	67						
Helianthus annuus	2	56	tr.	100				
Mentzelia stricta	1	22			tr.	20		
Lepidium densiflorum							tr.	50
Rhus aromatica					tr.	20		
Triplasis purpurea	tr.	11						

Vegetation Cut and Left on the Ground by Rodents

In addition to what they ate or carried to their burrows, rodents cut and left some plant material as litter on the soil surface. A "spot check" of the amount of vegetation cut and left on the ground was attempted in midsummer of 1958. All visible pieces of plants presumably cut off by rodents were picked up from two circular 0.01-acre plots (diameter 23.6 feet) arbitrarily located where cuttings seemed most abundant, on July 20 and August 1, 1958. Both plots were on dunes where kangaroo rats were abundant. Although the cut material seemed dry when picked up in the pastures, the collections were placed in an oven for 24 hours at 70° C. before they were weighed. This was the standard drying treatment for materials collected in forage inventories by the Southern Great Plains Field Station.

On a pounds-per-acre basis, the 62.5 grams of material from the 0.01-acre plot in moderately grazed pasture 19 represented 1.5 per cent of the average estimated production of grass forage during the period May 15 to August 15, 1958. The other sample weighed 72.7 grams and was from lightly grazed pasture 18, for which there were no estimates of forage production. Both collections of cut material consisted almost wholly of _Sporobolus cryptandrus_. It was not known which rodent species had done the cutting, but location of the cut material and the observed harvesting techniques of kangaroo rats suggested that they may have been mostly responsible for those particular collections.

The material from a pair of hundredth-acre plots was not intended as a statistical sample of rodent destruction of vegetation in two large pastures. The data are presented because they seemed representative of the type of material cut and left on the soil during the early part of the 1958 growing season. The two samples may or may not give some idea as to amount of plant use by rodents under the described conditions. Regardless of the number of plots, of course, a sample of only one part of a growing season would not be a very complete basis for estimating net annual amount of plants cut by rodents. Such harvesting did continue beyond the period covered by the two samples.

By late fall of each year of this study, there was lying on the ground enough cut plant material to attract attention of an observer. On October 24, at the end of the 1958 growing season, the amount of cut material in the experimental pastures appeared several times greater than it had been in midsummer, when the above samples were taken. It seemed much greater than the amount on the ground at any other time during the present study.

Much of the plant cutting observed in the fall of 1958 was probably done by cotton rats, which are largely herbivorous. In late summer or early fall of that year, they became very numerous on all pastures. Destruction of range vegetation by cotton rats was also reported in other parts of the region in which the 1958 irruption occurred.

Rodent Populations in Relation to Forage Disappearance

It appears unsafe to assume that rodents removed most of the forage which disappeared due to factors other than cattle. On the moderately grazed pasture, estimates of total rodent numbers tended to vary not directly, but inversely, with estimated weights of forage which disappeared due to factors other than consumption by cattle (Table 47). The forage disappearance in the pasture was greatest during the summer of 1957, when the total rodent population on the live-trap plot was the least among those of the three years of comparison. On two other pastures, the annual differences in forage disappearance were proportionally much less than the annual differences in total rodent numbers on the live-trap plots (Table 47).

The approximate densities of total rodent populations in the three years shown in Table 47 seemed not unique on those particular live-trap plots but were similar to densities on large areas of sand sagebrush grassland. This was suggested by comparable rates of trapping success on areas other than those live-trap plots (Table 3) and by partly concurrent studies of rodent populations near Canadian, Texas (J. M. Inglis, personal communication).

Table 47. Forage Disappearance During Growing Seasons, Compared With Densities of Total Rodent Populations in Late Summer. Southern Plains Experimental Range, Harper County, Oklahoma.

Year and Location	Total Forage Produced	Estimated Forage Disappearance Due to Factors Other Than Cattle, Average for Pasture		Estimated Total Rodent Population on the Live-Trap Plot in Each Pasture	
			Difference From Previous Year		Difference From Previous Year
	lbs./a.	lbs./a.	per cent	no./10 a.	per cent
Moderately Grazed Pasture 19					
1956	977	295		91	
1957	1668	537	+82	17	-81
1958	1626	498	-7	192	+1029
Lightly Grazed Pasture 20					
1957	1822	448		24	
1958	1830	567	+27	212	+783
Heavily Grazed Pasture 21					
1957	1235	205		48	
1958	1400	249	+21	167	+248

Rodent Burrows

Some of the readily observed effects of rodents on their habitat are the tunnels and mounds of earth made by them. The mixing, manuring, and channeling of soil by animals presumably have important effects on soil formation (Jacot, 1940) and fertility.

Counts of burrow entrances in the summer of 1957 suggested that heavily grazed areas had more rodent burrows per acre than did lightly or moderately grazed ones. The sample average of burrow entrances was 22 per acre on the lightly grazed live-trap grid, 21 per acre on the moderately grazed grid, and 42 per acre on the heavily grazed grid. Dunes generally seemed to have more burrow entrances per acre than did interdunal sites. The majority of these burrows presumably had been used by kangaroo rats, but the species of a burrow's excavator or of its user at that time, if any, was not known. On entire pastures, samples based on plots which were not spaced systematically suggested that frequencies and distributions of burrow entrances on the pastures as a whole were similar to those on the live-trap grids.

An average of 14 pocket gopher mounds per acre was counted on the 160 acres of moderately grazed pasture 19 in the spring of 1958. The average mound covered about 1.6 square feet, suggesting that 0.05 per cent of the pasture was covered by fresh mounds during the 1957-1958 winter. On forty acres of ungrazed land, the average mound-count was 21 per acre, and an estimated 0.08 per cent of that area was covered with new mounds during the same winter period. As discussed in the "Pocket Gophers" section, the spatial distribution of this species and of its mounds was very much clumped. The above averages apply to large areas such as whole pastures,not to conditions in small areas of concentration of pocket gopher activity.

These observed kinds of soil movement by rodents tended to incorporate organic matter in the soil, as in the case of litter and other material covered by pocket gopher mounds. Litter and feces were abundantly scattered throughout kangaroo rat tunnels, most of which lay within 18 to 24 inches of the soil surface. Debris from the burrows was also added to the surface soil as kangaroo rats periodically ejected such material from their dens. It was particularly noticeable in winter, perhaps as new occupants cleaned out abandoned burrows, or as burrows were enlarged.

CONCLUSIONS

Rodent Species Populations In Relation to Vegetation Association

The successional stages of communities in the sand sagebrush grassland were not determined during this study. Rodent species populations are, therefore, discussed as related to associations of plants, rather than to stages of succession.

It was assumed that the areas ungrazed for 18 years represented the most stable associations of vegetation. On the basis of the information in Table 2, the ungrazed areas had relatively more tall grasses and less annual grasses than the grazed pastures. The heavily grazed land was presumed to represent the least stable associations of vegetation. Annual grasses were more abundant there, and perennial forbs and tall grasses were less abundant than on the ungrazed and lightly and moderately grazed areas.

On the ungrazed areas and on each of the grazed areas, there were, in the broad sense, two principal associations of plants. These were the vegetation of the dune sites and that of the interdunal sites. The low, flat areas between dunes tended to have more perennial and annual forbs and more of the sod-forming short grasses than did the dunes. The latter tended to have more of the tall grasses and more sand sagebrush than the interdunal areas. The total density of tall herbaceous cover, including forbs and grasses, was generally greater between dunes than on them.

The relative permanence of these two kinds of communities, which were associated with topographic differences, was not determined.

As compared with ungrazed lands, the grazed areas supported greater average densities of kangaroo rats (Tables 9 and 10). This species tended not to use areas where tall herbaceous cover was relatively dense, as on ungrazed interdunal sites. On lightly and moderately grazed interdunal sites, but not on heavily grazed ones, tall herbaceous cover was also dense enough to restrict use of those flat areas by kangaroo rats during wet years such as 1958 (Table 13). During drought, however, the cover on moderately grazed interdunal sites was relatively sparse, and kangaroo rats then used those areas. Of the grazed pastures, the heavily grazed ones seemed to have the greatest average densities of kangaroo rats at all times of comparison during the present study (Tables 5 to 8 inclusive). Even during a period of moist conditions (1958), kangaroo rats used all parts, dunal and interdunal, of the live-trap plot in a heavily grazed pasture (Table 13).

The fact that drought tended to make greater proportions of moderately grazed pasture usable to kangaroo rats did not mean that drought ultimately increased populations there. Instead, the drought was followed by a decline in kangaroo rat numbers (Table 6). The decrease in population was perhaps associated with a decrease in food supply, possibly caused by drought.

During a moist period, and also on ungrazed areas, cotton rats were more numerous than they were in a dry period and on the grazed areas (Tables 4 to 10 inclusive). Cotton rats were scarce on all of the observed areas during the 1956 drought and the first summer, fall, and winter following that drought (Tables 4 to 8 inclusive). Relative densities of cotton rats on ungrazed areas during the drought were not observed. However, J. M. Inglis (personal communication) indicated that cotton rats were generally scarce in 1956 on the ungrazed areas studied by him.

By the fall of the wet year of 1957, cotton rats were present in relatively large numbers on the ungrazed area (Table 4), where they seemed mostly restricted to the interdunal areas. That species became even more numerous on the ungrazed area, and individuals were taken there on dunes as well as interdunal sites during the second wet year, 1958. Cotton rats also became very numerous on all of the other observed areas--namely, the grazed pastures--during the second wet year (Tables 4 to 8 inclusive). There was a lag in the time of development of the highest densities of populations on the grazed areas. The lag was associated with degree of grazing. The peak of estimated density occurred later on the heavily grazed land (Tables 4 to 8 inclusive) than on the other pastures.

The most systematic comparisons of rodent species populations of ungrazed with those of grazed areas (Tables 9 and 10) were made during the spring of 1958, when cotton rat numbers were rapidly building up to what appeared to be unusual densities. At that time the density of rodents as a whole seemed to be relatively similar on grazed and ungrazed areas, even though there were great differences in relative populations of the respective species. Unfortunately, such a comparison was not made during the drought, when cotton rat densities on the ungrazed areas may have been much less than they were in 1958.

In the cases of kangaroo rats and cotton rats, the most apparent association of population densities was with density of tall herbaceous cover on the various sites and under the different conditions of precipitation. Presumably, the food supply for both species was better in wet than in dry years. However, there was no clear suggestion as to whether or not food supply might also be correlated with a particular association of plants and with degree of grazing, at least in the case of kangaroo rats.

Considering habitat suitability from the standpoint of cover, the above observations on cotton rats seem in agreement with the suggestions of Naumov (1936), as reviewed by Evans (1942). It was proposed that when a population was at its lowest density, it occupied only the most favorable habitats; as density increased, individuals were forced into less favorable habitat situations until a maximum density was reached, when all possible habitats were occupied (Evans, o. c.). For cotton rats, the dense cover was presumably the most favorable habitat.

Grasshopper mice were next to kangaroo rats in numbers taken on grazed lands during most trapping periods. The notable exception was in the latter part of 1958, during the cotton rat irruption (Tables 4 to 8 inclusive).

Grasshopper mice seemed to occur in greater numbers on the grazed pastures (Tables 9 and 10) than on areas where the vegetation was not grazed. It was not known if population densities tended also to vary according to degree of grazing or according to dunal and interdunal sites. As with kangaroo rats, the drought of 1956 was followed by a decline in densities of grasshopper mice, and a population increase occurred during the second of the two wet years which followed the drought.

Deer mice were rare on grazed land but common on ungrazed land (Tables 4 to 10 inclusive). Dense stands of tall grasses on interdunal ungrazed areas seemed to be the most preferred habitat of deer mice.

Spotted ground squirrels were more numerous on the grazed than ungrazed lands (Tables 9 and 10). This species may have been most numerous where there was the least amount of tall cover, although this was not clearly suggested. The relatively small numbers of captures (Tables 4 to 10 inclusive) made it difficult to compare relative densities of spotted ground squirrels of different areas or periods. The same was true of the other numerically minor species discussed below.

Apparently, the sand sagebrush grasslands were not suitable for dense populations of thirteen-lined ground squirrels under any of the conditions of grazing or non-grazing observed during this study (Tables 4 to 10 inclusive). Population differences were not apparent for dunal and interdunal sites.

Grazing may have tended to improve habitat for silky pocket mice, but these tiny mammals did not occur in large numbers under any of the observed conditions (Tables 4 to 10 inclusive). Populations seemed sparsest during the year following the 1956 drought and most dense in the second wet year, 1958. Blair (1954) found this species more common on tight soils and in the buffalo-grass (Buchloe dactyloides) association than on sandy areas.

Hispid pocket mice were so rarely captured that no comparison of populations was attempted on different areas. Their greatest populations apparently occurred in 1958 (Tables 4 to 10 inclusive).

Another uncommon species was the wood rat (Tables 4 to 10 inclusive). Its numbers seemed affected more by the presence of brush thickets than by degree of grazing or non-grazing. Wood rats, like most of the other species, seemed to increase during the second wet year after the 1956 drought.

Pocket gophers were very localized in distribution. They were not wholly restricted to disturbed sites, but their mounds appeared most numerous on areas where large forbs were abundant. Over large areas, for example, 40 acres or more, the average densities of pocket gopher populations represented a very small percentage of the estimated total rodent population. No marked differences in the apparent abundance of mounds and, therefore, of gophers appeared among areas grazed or ungrazed. Signs of the presence of a few pocket gophers seem much more spectacular than evidence which would be left by an equal number of most of the other rodent species of this study area.

No harvest mice were taken during this study. The species was presumably rare, and its relations to the vegetation associated with degrees of grazing are not known.

Some rodent species appeared in such small numbers as to suggest that sand sagebrush grassland is marginal habitat for them. In this category might be the thirteen-lined ground squirrels, silky pocket mouse, hispid pocket mouse, and harvest mouse.

Total Rodent Species Use of Plants

At present, it seems unreasonable to attempt more than comparative and qualitative estimates of foods consumed by the total rodent population.

A quantitative estimate would require knowledge not now available. For example, it would be possible to assign average weights to each rodent species in Table 5, and from that the total weight of rodents per acre might be estimated. That weight per acre might in turn be used to estimate the amount of food consumed by rodents if there were some way of assigning an average rate of food consumption per pound of each rodent species. Such an estimate is not feasible at present because rates of food utilization for the species and conditions involved are not known.

A major difficulty in any attempt to estimate total food consumption by rodents lies in the fact that the total rodent diet consists of mixtures of seeds, animal flesh, and herbage. Concentrations of available nutrients in these three classes of foods are probably quite different. Additional complications are involved in an attempt to estimate only the net effect of plant consumption by rodents with regard to total forage production. One such difficulty would be the need to allow for reduced consumption of herbage which may result from rodents' consumption of plant-eating invertebrates.

As a unit, the rodents do not represent a single trophic level in the sand sagebrush grassland, as shown by the largely contrasting diets of kangaroo rats and grasshopper mice, for example (Tables 38 to 41 inclusive). Diets of given species, such as those of the ground squirrels (Tables 43 and 44), represented several different levels of energy conversion. In short, knowledge of rodent population densities is by itself not an adequate basis for estimating actual amounts of forage eaten by rodents.

Solving the above difficulties in estimating amounts of food consumption by rodents would not answer the question as to total amount of plant material used by rodents. In addition to what they ate, rodents cut and left some vegetation as litter on the soil surface, and some was carried to nests and food caches. The relative amounts of plant parts disposed of by rodents in these various ways were not determined.

A degree of competition presumed between rodents and cattle is a matter of considerable interest to ranchers in this region. The present study suggested some comparative estimates of possible cattle-rodent competition for forage, although no quantitative estimates were attempted.

On the bases of their relative numbers among the rodent species and of their observed uses of plants, kangaroo rats appeared as the chief potential competitors of cattle during most of this study. As noted in the population discussion, kangaroo rats were by far the most numerous rodent species on grazed lands for at least the period from June, 1956, to May, 1958 (Tables 4 to 10 inclusive). And during the latter half of 1958, kangaroo rats were one of the two most abundant rodent species.

The principal observed species of plants disposed of in the various ways by kangaroo rats were the perennial midgrass, sand dropseed, the summer annual, purple sandgrass, flatsedge, and short-lived spring annual grasses and forbs. Not much used by kangaroo rats were the seeds and other parts of tall grasses, namely, sand lovegrass, the bluestems, and switchgrass. Seed-bearing stalks of the principal short grass were frequently cut, presumably by kangaroo rats, when blue grama produced seed, as it did in the summer of 1958.

It was not observed that kangaroo rats cut off the stems or leaves of forbs such as legumes which are of presumed high value as forage for cattle. The rats did, however, gather from the soil appreciable numbers of seeds of forbs such as partridge-pea (Cassia fasciculata) (Table 39). It is not known what effect this may have had on the propagation and relative abundance of forb species. In terms of basal coverage (Table 2), forbs in general were a small part of the total vegetation, in comparison with grasses.

Potential competition between cattle and kangaroo rats appeared considerably less on lightly and moderately than on heavily grazed areas. Of the plant species most often clipped by kangaroo rats, only the sand dropseed was one of the major forage plants for cattle. Other plant species which were frequently used by kangaroo rats (Tables 38, 39, and 40) seemed to be of small importance as cattle forage. For example, flatsedge and purple sandgrass were considered to be of doubtful palatability or of low nutritive value (Savage and Heller, 1947). Other species often used by kangaroo rats, such as the spring annual forb, Linaria canadensis, appeared to be a very small part of the total forage produced and, even if palatable, were presumably of minor importance as forage for cattle.

Tall grasses were relatively abundant on the lightly and moderately grazed pastures (Table 2), and the tall grass species are important as forage for cattle. Disposal of sand dropseed by kangaroo rats where tall grasses were abundant, therefore, seemed of minor importance as a factor in potential competition of kangaroo rats with cattle. In contrast, tall grasses were scarce on heavily grazed areas, and kangaroo rats' destruction of sand dropseed there appeared to be of potentially greater importance to a rancher.

During drought on all pastures, the use of sand dropseed by kangaroo rats may be more important than it is in wet years. Sand dropseed tended to be much more important from the standpoint of total forage produced in all pastures, regardless of degree of grazing, during the dry year of 1956 when tall grasses did not produce much growth.

To whatever extent their relative numbers might be an index of potential competition with cattle, other rodent species generally seemed of minor importance in comparison with kangaroo rats. Cotton rats were an exception. During the latter half of 1958, they became one of the most numerous rodent species on grazed areas (Tables 4 to 8 inclusive). Their apparent frequency of consumption and destruction of range plants (species not known) suggests that cotton rats were perhaps on a par with kangaroo rats as potentially important competitors with cattle at that particular time.

Grasshopper mice appeared numerically second to kangaroo rats on the pastures during most of the study (Tables 4 to 8 inclusive), but there was scant suggestion that these mice consumed vegetation, except for relatively small amounts of seed (Table 41). It seemed unlikely, therefore, that grasshopper mice would compete seriously with cattle. If anything, the amounts of invertebrates eaten by grasshopper mice suggested that these rodents might tend to increase forage for cattle, possibly by destroying some of the cattle's arthropod competitors for forage.

The ground squirrels were suspected of less total use of range plants than were kangaroo rats. Both species of Citellus were considerably less numerous than kangaroo rats (Tables 4 to 10 inclusive). Furthermore, in contrast to kangaroo rats, which were active year-round, the ground squirrels hibernated for approximately one-third of the year. The spotted and the thirteen-lined ground squirrels (Tables 43 and 44) ate some plant species, including grasses, and appeared as potential competitors of cattle. Ground squirrels also took relatively large amounts of arthropods in their diets. It seems especially risky to try to use data from studies of populations and food-uses as the basis for estimating net effects of ground squirrels as competitors of cattle.

On grazed areas, deer mice, pocket mice, harvest mice, and pocket gophers were so few in comparison with the other rodents that it seemed very unlikely that the minority species used economically important amounts of vegetation. There were no suggestions that any of the less numerous rodent species tended to concentrate their use on uncommon but presumably valuable forage species for cattle--such as the so-called "conditioners," prairie clovers (Dalea spp.)--the destruction of which could make those rodents important competitors despite their small numbers.

Ecologic Roles of Rodents

Their apparent length of occupancy of grassland suggests that some members of the rodent order are integral elements of that extensive community. No community can consume its resources faster than they are produced without ultimate disaster (Dice, 1952). In natural communities which endure over a long period, it may be presumed that there is in general a fairly efficient organization and that the available resources are being used to a reasonably satisfactory extent (Dice, o. c.).

The fossil record of rodents of the sand sagebrush grassland specifically is not known, but there seems little reason to suspect that the vegetation there existed for long without rodents in it. Some of the rodent forms now found there were known to be present in other parts of the grassland region at an early time. For example, unconsolidated lower Pliocene sands of Nebraska contain fossils of rather specialized hopping forms of Dipodomyinae (Wood, 1935), suggesting that the kangaroo rat subfamily inhabited sandy lands of the Great Plains perhaps twelve million years before the bison arrived from Eurasia. Dipodomyinae have also been found in Pliocene deposits of California, Nevada, Arizona (Wood, o. c.), Kansas, and Oklahoma (Hibbard, 1954a, 1954b). Some other rodent genera reported from Pliocene sites of the Great Plains are *Onychomys*, *Sigmodon*, *Citellus*, *Perognathus*, *Peromyscus*, and *Geomys* (Hibbard, 1941).

Of the ways in which the various rodent species function in their ecosystem, only a few can be listed as observed during the present study. The section which discussed use of plants by rodents indicated that rodents were active in clipping various parts of plants and in transporting parts of plants, including seeds, to places where they might not occur without the rodents.

The presence of arthropods among foods eaten by some of the rodents (Tables 38 to 47 inclusive) suggested that these rodent species may exert some degree of damping upon the increase of populations such as those of grasshoppers.

Rodent effects in pedogenesis were suggested by the soil movements described above (p. 120). Rodents transported subsurface material to the soil surface and incorporated organic material with the mineral parts of the soil. In a period as short as that of the present study, the visible effects of rodents on soil may seem unimpressive. But in terms of the time involved in the cycle of soil formations, the cumulative chemical and physical effects of rodents on the soil are perhaps important. Soil scientists have called attention to the need for greater appreciation and study of soil fauna (Murphy, 1955), including rodents (Kuhnelt, 1955).

The meager state of our knowledge concerning prairie rodents and their ecologic roles suggests the need for studies in addition to those of rodents as part of the soil fauna. In contrast to short-term studies such as the present one, long-term studies of other aspects of the functions of rodents seem in order, as a step toward more intelligent use of these grasslands.

Regulation of Numbers

Some of the factors which were associated with the apparent limiting of rodent populations were precipitation, topography, and degree of grazing by cattle. These factors affected habitat type, particularly the kinds, amounts, and distribution of vegetation. Habitat type in turn was associated with the occurrence and distribution and, therefore, average densities of rodent species such as kangaroo rats and cotton rats.

Although the abundance of it was not determined by sampling during this study, the food supply, when deficient, was presumably an important limiting factor. Precipitation, through its effects on vegetation, seemed greatly to affect food supply. Limiting effects of other factors, such as disease and predators, also were not determined.

Another factor which may have been associated with relative densities of different rodent species was their comparative social behavior. Species in which individuals seem to tolerate each others' presence fairly well, such as cotton rats, may tend toward greater densities of populations than species whose individuals tend to be solitary, such as the pocket gophers. As noted above (p. 82), even cotton rats at times attained population densities at which social behavior possibly tended to limit their numbers.

The process of spacing, or the pattern of distribution, of individuals was a possible limiting factor presumably related to social behavior. Some evidence of a density-dependent limiting factor was suggested by the data on age composition, population density, and reproduction of kangaroo rats and cotton rats (Tables 4 to 10 inclusive, 14, 15, 31, and 32, and Figure 1). These data appear in accord with the evidence reviewed by Lack (1954), to the effect that rate of reproduction tends to be inversely proportional to population density.

Among kangaroo rats and cotton rats, decreased prevalence of pregnancy and number of embryos per female were associated with high densities of populations (Tables 4 to 8 inclusive and 32 and Figure 1). Although the present study yielded no original information on the subject, it is possible that the decreased fertility may have resulted from increased pituitary-adrenal activity. Christian (1959) has postulated that the latter tends to result from social stress acting through psychological mechanisms which affect endocrine function. Several experiments by Christian (o. c.) suggested that social competition was the major factor inducing a decline in rate of reproduction of house mice and Norway rats for which food, water, nesting material, and nest space were abundant. It is possible that social competition within a species could act in similar ways to regulate numbers of kangaroo rats and cotton rats. There was some suggestion of social competition among cotton rats when population density was high.

Interspecies competition also appeared as a possible regulating factor. Competition for food was one of the observed possibilities, as suggested by overlap in kinds of food eaten by kangaroo rats and ground squirrels, for example (Tables 38, 39, 40, 43, and 44). Individuals of different species may also compete for space, homesites, shelter, and other necessities. The actual occurrence and effects of competition for these things were not observed.

Animal husbandry practices may sometimes serve to regulate numbers of rodent species. For instance, restriction as to the parts of pastures used by kangaroo rats was associated with light and moderate grazing. Those two degrees of grazing were thus associated with the average number of kangaroo rats present per unit of area during the wet year, 1958, when herbage was abundant.

Regulation of grazing, on the other hand, did not prevent an irruptive increase of another species, the cotton rat. Heavy grazing, however, did seem to postpone for a few weeks the development of the great population increases which took place (Tables 4 to 8 inclusive). That irruptions of cotton rats have been infrequent was suggested by the observations in seven years during which rodent populations were sampled on the area of the present study (Table 11).

None of the three degrees of grazing seemed associated with marked differences in populations of rodent species other than kangaroo rats and cotton rats (Tables 5 to 8 inclusive). Effects which different degrees of grazing had upon rodent species' food supplies were not known. Relatively large amounts of sand dropseed, a food much used by kangaroo rats, occurred in pastures representing all three degrees of grazing (Table 2). The line intercept data, however, do not indicate the relative amounts of available seed, and it was the seed which was the important part of the plant, as far as the food supply of kangaroo rats was concerned. Different degrees of grazing did not seem to be associated with extent of the homestead areas of kangaroo rats, although the homesteads were the areas on which individuals gathered their food supplies. However, the comparison of homestead areas in different pastures did not include the drought year, 1956, when food was probably scarce.

Effects of other range management practices were not observed, but sagebrush control and the artificial seeding of pastures are two which perhaps should be considered for their possible effects on rodent populations. To the extent that those practices may tend to reduce the floristic richness of the community of sand sagebrush grassland, it is possible that they may make pastures more susceptible to increases of some rodent species, such as the cotton rat. McIlvain et al. (1955) recommended that attempts at sagebrush control should avoid complete eradication of that plant in pastures. Retention of some of the brush may also be desirable from the standpoint of control of rodent species.

Population outbreaks are characteristic of the simpler ecosystems or "monocultures," whereas species of the more complex communities tend to exert a damping effect on each others' rates of increase, according to Elton (1958). He cited as examples the tropical rain forests, which are communities made up of large numbers of species, and in which insect populations tend to be relatively stable. In contrast, he pointed out that the frequencies and magnitudes of insect outbreaks tend to be relatively great in communities such as cultivated fields, where there are relatively few kinds of organisms. This principle may be presumed to apply not only to insects but to range rodents as well.

Population outbreaks of voles (Microtus spp.) on croplands have been reported at different times in several western states (Jellison et al., 1958; Piper, 1909; Spencer, 1958). Microtine cycles in Germany were reported as typical of large, monotonous, open, uniform biotopes, such as lands extensively cultivated or pastured (Frank, 1957). Species of Microtus were also noted for their outbreaks on the croplands and steppe pastures of Russia and Central Asia (Elton, 1942). The literature is mindful of conditions in which occurred the 1958 outbreak of cotton rats in western Oklahoma.

The grazed, uncultivated pastures of sand sagebrush grassland did not escape some effects of the 1958 outbreak of cotton rats. The irruption, however, seemed not to develop so readily in the pastures as elsewhere.

Large numbers of cotton rats in 1958 first occurred in the wheat fields and on the ungrazed sand sagebrush lands, rather than in the pastures. It is not known how the relative magnitudes of the outbreak compared in terms of population density on the ungrazed areas and croplands.

Rodent Control

It is not known if grazing and the various factors of natural regulation may limit rodent numbers to a degree that is financially desirable on sand sagebrush grasslands. It is a common assumption that it may be advisable there to control rodents by direct artificial reduction of numbers. In this sense, the term "control" is somewhat ambiguous, for the level of reduction is not specified. It might mean only the suppression of numbers by periodic destruction of some of the individuals in a population. Or it might imply the complete eradication of a species on an area.

Another ambiguity concerning rodent control lies in thinking of the possible need for control without regard to species. The lumping of all species in the term "rodents" tends to ignore what may be important differences in species' effects on the range community. The collective term also minimizes the possible importance of differences in population densities of different species, some of which may need artificial control and some of which may not.

The subject of need is also a matter of some vagueness. Decisions are required as to when and where and as to what criteria shall be the basis for determining the need. Commercial, civic, esthetic, and perhaps moral questions may be concerned.

A decision as to economic need for rodent control may involve the degree of acceptance of collectivist political philosophy. For example, should the cost of the operations be borne by public or private funds? Tax-supported destruction of rodent species might be more desirable to an individual rancher than would the same operation if paid for by the rancher alone. The benefits of artificial control, if any, might be proportionally greater for the rancher than for the public at large.

The attempt to ascertain economic need for rodent control should also consider the natural bio-economy of the region. The decision as to need would require knowledge of the extent to which reduction or removal of rodent species would ultimately affect soil, vegetation, and populations of other animal species.

Moral judgment as to need for rodent control may depend on the society and the period for which the judgment is attempted. Rodent control in the United States might not expect to encounter as much public opposition as did the anti-monkey campaign of the government of India, for example. Yet there is some public feeling that eradication of any species is morally questionable.

Answers to some of the above questions concerning the need for rodent control did not appear from this study of populations and range effects of rodents. It did seem, however, that conditional and comparative conclusions could be attempted as to possible need, time, and place for artificial reduction of rodent species populations, from a limited economic or financial point of view.

If it were assumed that artificial suppression of certain rodent species might at times be financially desirable on the observed pastures, it appeared that the other nine species needed control much less than did kangaroo rats and cotton rats. The presumed relative need was judged on the basis of numbers of the species (Tables 4 to 10 inclusive) which used plants of value as cattle forage (Tables 38 to 47 inclusive).

The possible need for reduction of numbers of kangaroo rats or cotton rats seemed less during the 1957 growing season than at any other time during the study. The lowest estimated densities occurred during the summer of 1957.

The possible need for reduction of kangaroo rat populations may have been relatively great during the 1956 growing season and during the winter of 1956-1957. Cattle forage was scarce at those times, in comparison with amounts of forage during other periods of this study. The amount of forage used by moderately dense populations of kangaroo rats may have tended to be critical to a ranching operation during the drought.

During late 1957, the then low densities of kangaroo rats began to increase following a favorable growing season for plants. There is the possibility that artificial reduction of kangaroo rats during late 1957 could have minimized the large population which had developed by the spring of 1958. It is difficult to try to estimate what would have been the delayed effects of artificial reduction on the observed populations. It is not known if rates of increase of the species might have been damped or stimulated by control measures.

It is possible that population reduction might have tended to remove the density-dependent limiting factors, such as those associated with social stress and endocrine function, which presumably affected kangaroo rats and cotton rats. For example, Howard (1958) reported an experiment in which, after six weeks, there were more individuals on a 20-acre test plot than there were before the rodent populations were reduced by poisoning.

It may be reasonable to attempt to predict times of expected high populations of rodent species. Control then, if desirable, need not be a continuing activity and expense. Instead, it could be timed to dampen or prevent great increases in populations. Blumenstock (1942) proposed that frequencies of droughts are statistically predictable. Some of the fluctuations of populations of rodents here investigated were associated with precipitation (Tables 1 and 4 to 8 inclusive and Figure 1). Therefore, to whatever extent they were affected by precipitation, the frequencies of the population fluctuations also may have been statistically predictable; for example, the decline of kangaroo rats during the 1956 drought and the population increases of kangaroo rats and cotton rats during the two years following the drought.

Foreknowledge of unusual densities of certain species may be derived by noting pronounced increases in breeding success. Useful for this purpose are samples of age composition of the population, frequency of pregnancy, and embryo counts such as those of cotton rats in the spring of 1958 (Tables 31 and 32).

Any attempt to determine the need for artificial control of rodents should recognize that distribution of each species is not random over a large area, such as a 160-acre pasture. Instead, each rodent species tends to occur markedly in association with particular environmental conditions, such as type of cover and degree of grazing.

Places of the presumed relative need for artificial control of kangaroo rats varied according to the conditions described above for time of need. During all periods of comparison, kangaroo rats were more abundant in heavily grazed pastures than in others (Tables 4 to 8 inclusive). Therefore, the presumed financial need for control of that species appeared greater on heavily than on lightly and moderately grazed pastures.

During 1956 and 1957, cotton rats were so scarce that attempts to reduce populations would have seemed pointless on any of the grazed pastures. During the 1958 irruption of cotton rats, there were no marked differences among pastures as to presumed financial need for control, except that the animals became numerous on the heavily grazed pastures a few weeks later than on the other pastures. If cotton rat control was needed during the latter half of 1958, it was probably needed in all pastures.

The possible need for artificial control of rodent species has been investigated experimentally in other grazing regions. For semidesert range in southern New Mexico, Norris (1950) concluded that control of rodents and rabbits was neither necessary nor worthwhile from the standpoint of forage production. His report concerned four 2½-acre plots studied during the period 1940-1948. In a dry year, 1940, the yield of usable grasses on the plot used only by rodents was 41 per cent less than on the plot which was closed to rodents, rabbits, and cattle. During a wet year, 1941, the yield was only 11 per cent less on the rodent-used plot than on the plot not used by rodents, rabbits, or cattle. After eight years, the yield of grasses was actually greater on the plot used by rodents and rabbits, but closed to cattle, than was the yield on the totally closed plot.

For areas in the Sierra Nevada foothills of California, Howard et al. (1959) concluded that the presence of ground squirrels (Citellus beecheyi) did affect heifer weights during the winter, when there was inadequate green feed. The experiments were made on two pastures, one containing approximately 36 and the other, 38 grazable acres. During the periods of comparison, ground squirrels were removed from the selected pasture by poisoning with Compound 1080.

On the basis of live-trapping estimates, the densities of the adult breeding populations of Citellus beecheyi reported by Howard et al. (o. c.) were at least five to fifteen times as great as the densities of Citellus spilosoma at the comparable stage of their breeding cycle during the present study (Tables 6, 7, and 8). Kangaroo rats (Dipodomys heermanni) and other rodent species were also present on the California study areas.

That study (Howard et al., o. c.) did not indicate the cost of the poisoning operations. Aside from the differences in weights gained by the heifers, the authors did not discuss benefits or losses which might be expected from the control of ground squirrels.

The present study emphasized the difficulties of trying to estimate indirectly the effects of rodent species on the range. Without controlled experiments, it was especially difficult to estimate rodent-cattle competition in quantitative terms. It is suggested, therefore, that comparative studies be attempted on large pastures from which rodent species and cattle are selectively excluded. The financial aspects of control of rodent species might in that way be investigated experimentally, as could long-term ecologic effects of that control.

It seemed unlikely that any short-term studies, such as those lasting only two or three years, could provide satisfactory bases for ascertaining the need for rodent control. If interest in the problem of rodent control is great enough, it should justify studies with an expenditure of effort comparable to that of the reseeding studies on the Southern Plains Experimental Range. The problem of range reseeding has been investigated there on several pastures of 25 to 50 acres each during a period of more than 12 years.

An actual need for artificial reduction of populations of range rodent species was not determined during this study. Observations on the uses of plants by rodents did not show that any of the rodent species competed with cattle for forage in readily measurable terms of quantity. There was some overlap in kinds of plants used by rodent species and cattle. There was, therefore, possibility of competition in qualitative terms. For the strictly limited purpose of reducing that unknown degree of possible competition, there was a possible need for rodent control. That possible need varied greatly from one pasture to another and even more so from one period to another. The possible need for control seemed not at all equally desirable for all species of rodents; neither was the possible need equally desirable for a given species at all times and places. Long-term experiments with rodent control are needed as bases for judging advisability of that control on sand sagebrush grassland, either from the standpoint of a private business investment or of public welfare.

SUMMARY

1. Objectives of this study were to determine comparative densities of rodent species populations, their relation to stages of plant succession, some effects on range lands, and times and places where rodent control may be needed.

2. Field observations were made from June, 1956, to November, 1958, on sand sagebrush grasslands of Harper and Woodward counties, Oklahoma. Comparisons were made on areas grazed at different rates by cattle and on areas ungrazed for 18 years.

3. Rodent species populations varied greatly from season to season on all areas observed.

4. Kangaroo rats were the most numerous species taken on grazed lands. The greatest estimated density of adult populations, 125 individuals per ten acres, was in heavily grazed pasture.

5. Grasshopper mice ranked second in numbers to kangaroo rats in the pastures in most periods. The greatest estimated densities of grasshopper mice were 26 and 28 individuals per ten acres, on lightly and heavily grazed pastures.

6. Cotton rats were rare on the pastures during most of the period of study but equalled or exceeded kangaroo rats in number during the latter part of 1958. The greatest estimated densities of cotton rats were from 60 to 121 individuals per ten acres on lightly and moderately grazed areas, several weeks before the presumed peak of the 1958 irruption.

7. Numbers of spotted ground squirrels appeared similar to those of grasshopper mice in late summers of 1956 and 1957. On the basis of total numbers active the year-round, however, spotted ground squirrels were only about half as numerous as grasshopper mice. The greatest estimated density of spotted ground squirrels was 12 per ten acres, including young of the year; this was on a heavily grazed area.

8. Seven other species constituted a minor portion of the total rodent numbers in all observed pastures at all times. They were the thirteen-lined ground squirrels, silky and hispid pocket mice, deer mice, wood rats, pocket gophers, and harvest mice. None of these species exceeded average densities of nine individuals per ten acres.

9. Kangaroo rats used areas where tall herbaceous cover was sparse and tended to avoid areas where it was dense. Generally, the dense herbaceous cover was on low flat areas between dunes.

10. Distribution of cotton rats was generally the converse of that of kangaroo rats, with regard to density of cover.

11. Generally, the dense herbaceous cover was on low flat areas between dunes. Its density was associated with precipitation and degree of grazing, and so were the average densities of populations of kangaroo rats and cotton rats over areas as large as ten acres or more.

12. During a wet year such as 1958, tall herbaceous cover was dense on the interdunal areas, and kangaroo rats then tended to be restricted to the dunes. In the drought period of 1956, the cover was sparse enough that all parts of grazed areas, dunal and interdunal, tended to be used by kangaroo rats.

13. A population decline of kangaroo rats was associated with drought. This was despite the fact that greater proportions of the pastures were usable to kangaroo rats during drought than during wet periods favorable for plant growth.

14. Cotton rats increased irruptively on all observed areas during 1958, the second year after the drought. The outbreak occurred first on croplands and ungrazed areas and last on heavily grazed pastures.

15. Rates of reproduction of kangaroo rats and cotton rats tended to vary inversely with population densities, as suggested by rates of pregnancy, embryo counts, and age composition of populations in different periods. Reproduction of cotton rats seemed to stop abruptly when numbers reached an apparent peak in late summer of 1958.

16. A large proportion of the individuals of all rodent species studied seemed to restrict their movements to certain areas termed homesteads. This process of spacing of individuals within their species' habitat was presumably one of the factors which tended to limit the number of individuals which could survive on a given area.

17. The diet of the total rodent population on the observed areas was complex. Kangaroo rats ate mostly seeds, and grasshopper mice, mostly arthropods. Green plant matter was a large part of cotton rats' diet. Some species, such as ground squirrels, ate relatively large proportions of all three types of food.

18. Knowledge of food species used by and populations of rodent species is not an adequate basis for estimating amounts of range vegetation used by rodents. Too little is known about actual rates of food consumption by each species.

19. In addition to the unknown quantity which they ate, rodents carried off or cut and left undetermined amounts of vegetation on the ground.

20. Estimates of total forage disappearance also seem an inadequate basis for attempting to estimate the amount of forage removed by rodents. Many factors other than rodents may have been involved in forage disappearance.

21. One of the plant species cut most often by kangaroo rats was sand dropseed. It was one of the most abundant forage species for cattle in heavily grazed pastures.

22. Kangaroo rats were presumed to be the chief possible competitors of cattle for forage. Kangaroo rats seemed to be the most numerous rodent species on all of the grazed areas observed in six of seven years in which rodent populations have been studied since 1940.

23. The possibility of competition between cattle and kangaroo rats seemed greater in heavily grazed than in other pastures.

24. In all pastures, the possibility of competition between cattle and kangaroo rats seemed greater during drought than at other times.

25. Cotton rats also were presumed to be important possible competitors of cattle during a year of population irruption such as 1958.

26. The actual degree of presumed competition between cattle and any rodent species was not determined.

27. Data on rodent populations, foods used by rodents, and total forage disappearance are not adequate bases for estimating the possible competition of rodents with cattle, in terms of economic effects on a ranching enterprise.

28. This study did not indicate a clear-cut need for rodent control in the sense of artificial reduction of rodent species populations.

29. The possible need for rodent control should be investigated by more direct means than those used to date on sand sagebrush grassland. The problem suggests need for long-term studies in which rodent species and cattle may be selectively excluded from experimental areas.

LITERATURE CITED

Allan, Philip F. 1944. Mating behavior of Dipodomys ordii Richardsoni. Jour. Mamm., 25: 403-404.

Blair, W. Frank. 1954. Mammals of the Mesquite Plains biotic district in Texas and Oklahoma, and speciation in the Central Grasslands. Texas Jour. Sci., 6: 235-264.

Blumenstock, George, Jr. 1942. Drought in the United States analyzed by means of the theory of probability. U. S. Dept. Agric. Tech. Bull. No. 819: 1-63.

Bole, B. P., Jr. 1939. The quadrat method of studying small mammal populations. Cleveland Mus. Nat. Hist. Sci. Pub., 5: 15-77.

Calhoun, John B. and James U. Casby. 1958. Calculation of home range and density of small mammals. Public Health Monogr. No. 55: 1-24.

Christian, John J. 1959. Control of populations in rodents by interplay between population density and endocrine physiology. Wildl. Dis., 2: 1-38.

Davis, W. B. 1958. Invasion. Texas Game and Fish, 16: 8-9.

Dice, L. R. 1941. Methods for estimating populations of mammals. Jour. Wildl. Mgt., 5: 398-407.

__________. 1952. Measure of the spacing between individuals within a population. Ann Arbor: Univ. Mich., Contr. Lab. Vert. Biol., 55: 1-23.

Elton, Charles. 1942. Voles, mice and lemmings. Oxford: Clarendon Press, 496 pp.

__________. 1958. The ecology of invasion by animals and plants. London: Methuen and Co. Ltd., 181 pp.

Evans, F. C. 1942. Studies of a small mammal population in Bagley Wood, Berkshire. Jour. Anim. Ecol., 11: 182-197.

Fitch, H. S. 1948. Habits and economic relationships of the Tulare Kangaroo rat. Jour. Mamm., 29: 5-35.

__________ and J. R. Bentley. 1949. Use of California annual-plant forage by range rodents. Ecol., 30: 306-321.

Frank, F. 1957. The causality of microtine cycles in Germany. Jour. Wildl. Mgt., 21: 113-121.

Frank, William J. 1950. Rodent populations and their reactions to grazing intensities on sand sagebrush grasslands in the Southern Great Plains region. Stillwater, Okla.: Okla. A. & M. Coll. Unpubl. Ph.D. Thesis. 204 pp.

Great Plains Committee. 1936. The future of the Great Plains. Washington: U. S. Govt. Printing Office. 194 pp.

Grinnell, Joseph. 1932. Habitat relations of the giant kangaroo rat. Jour. Mamm., 13: 305-320.

Hawbecker, A. C. 1940. The burrowing and feeding habits of Dipodomys venustus. Jour. Mamm., 21: 388-396.

Hayne, D. W. 1949. Calculation of size of home range. Jour. Mamm., 30: 1-18.

Hibbard, C. W. 1941. Paleoecology and correlation of the Rexroad fauna from the Upper Pliocene of southwestern Kansas, as indicated by the mammals. Univ. of Kans. Sci. Bull. 27: 79-104.

__________. 1954a. Second contribution to the Rexroad fauna. Trans. Kans. Acad. Sci., 57: 221-237.

__________. 1954b. A new Pliocene vertebrate fauna from Oklahoma. Papers Mich. Acad. Sci., Arts and Letters, 39: 339-359.

Howard, W. E. 1958. Field-rodent control research needs. Davis: Univ. of Calif. Field Sta. Administration. 11 pp. mimeographed.

__________, K. A. Wagnon, and J. R. Bentley. 1959. Competition between ground squirrels and cattle for range forage. Jour. Range Mgt., 12: 110-115.

Jacot, A. P. 1940. The fauna of the soil. Quart. Rev. Biol., 15: 28-58.

Jellison, W. L. et al. 1958. Observations on diseases in outbreak of Microtus. Trans. N. Amer. Wildl. Conf., 23: 137-145.

Kalela, O. 1957. Regulation of reproductive rate in subarctic populations of the vole Clethrionomys rufocanus (Sund). Ann. Acad. Sci. Fennicae Series A, Sect. IV (Biol.) No. 34: 1-60.

Kuhnelt, Wilhelm. 1955. A brief introduction to the major groups of soil animals and their biology. Proc. Univ. Nottingham Second Easter School in Agric. Sci. London: Butterworths Sci. Pub., 29-41.

Lack, D. R. 1954. The natural regulation of animal numbers. Oxford: Clarendon Press. 343 pp.

Leopold, Aldo. 1953. Game management. New York: Charles Scribner's Sons. 481 pp.

McCulloch, Clay Y., Jr. 1959. Effects of rodents and rabbits on estimates of forage disappearance. Proc. Okla. Acad. Sci., 39: (in press).

__________ and Jack M. Inglis. Breeding cycle of the kangaroo rat. Ms.

McIlvain, E. H. et al. 1955. Nineteen-year summary of range improvement studies at the U. S. Southern Great Plains Field Station, Woodward, Oklahoma. Woodward Progress Rept. 5506. U. S. D. A., Agric. Res. Serv. October, 37 pp.

McMurry, F. B. 1942. A report on the early summer population of rodents and rabbits on the Southern Plains Experimental Range near Woodward, Oklahoma. U. S. Dept. Int., Fish and Wildl. Serv. Ms. 25 pp.

__________. 1943. A second report on the early summer population of rodents and rabbits on the Southern Plains Experimental Range near Woodward, Oklahoma. U. S. Dept. Int., Fish and Wildl. Serv. Ms. 21 pp.

__________. 1947. A third report on the early winter population of rodents and rabbits on the Southern Plains Experimental Range near Woodward, Oklahoma. U. S. Dept. Int., Fish and Wildl. Serv. Ms. 44 pp.

Miller, G. S., and R. J. Kellogg. 1955. List of North American recent mammals. U. S. National Museum Bull. 205. 954 pp.

Murphy, Paul W. 1955. Ecology of the fauna of forest soils. Proc. Univ. Nottingham Second Easter School in Agric. Sci. London: Butterworths Scientific Pub., 99-123.

Monson, Gale. 1943. Food habits of the banner-tailed kangaroo rat in Arizona. Jour. Wildl. Mgt., 7: 98-102.

__________ and W. Kessler. 1940. Life history notes on the banner-tailed kangaroo rats, Merriam's kangaroo rat, and the white-throated woodrat in Arizona and New Mexico. Jour. Wildl. Mgt., 4: 37-43.

Naumov, N. P. 1936. On some peculiarities of ecological distribution of mouse-like rodents in Southern Ukraine. Problems of Ecol. and Biocenology, 2: 170-195. (In Russian; summary in English.)

Norris, J. J. 1950. Effect of rodents, rabbits, and cattle on two vegetation types in semidesert range land. N. M. Exper. Sta. Bull. 353: 1-23.

Parker, K. W. and D. A. Savage. 1944. Reliability of the line interception method in measuring vegetation on the Southern Great Plains. Jour. Amer. Soc. Agron., 36: 97-110.

Phillips, Paul. 1936. The distribution of rodents in overgrazed and normal grasslands of central Oklahoma. Ecol., 17: 673-679.

Reynolds, H. G. 1950. Relation of Merriam kangaroo rats to range vegetation in southern Arizona. Ecol., 31: 456-463.

__________. 1958. The ecology of the Merriam kangaroo rat (Dipodomys ordii Mearns) on the grazing lands of southern Arizona. Ecol. Monogr., 28: 111-127.

Rosasco, M. E. 1955. Studies of population dynamics of certain rodents of the Great Salt Lake Desert. Univ. of Utah and Army Chem. Corps, Dugway, Utah: Symposium on Ecology of Disease Transmission in Native Animals, 23-28.

Savage, D. A. and V. G. Heller. 1947. Nutritional qualities of range forage plants in relation to grazing with beef cattle on the Southern Plains Experimental Range. U. S. Dept. Agric. Tech. Bull. No. 943: 1-61.

Shaw, W. T. 1934. The ability of the giant kangaroo rat as a harvester and storer of seeds. Jour. Mamm., 15: 275-286.

Spencer, Donald A. 1958. Biological aspects of the 1957-1958 meadow mouse irruption in the Pacific northwest. U. S. Dept. Int., Fish and Wildl. Serv., Wildl. Res. Lab., Denver. 9 pp.

Stickel, Lucille F. 1946. The source of animals moving into a depopulated area. Jour. Mamm., 27: 301-307.

__________. 1950. Populations and home range relationships of the box turtle Terrapene C. Carolina (Linnaeus). Ecol. Monogr., 20: 351-378.

__________. 1954. A comparison of certain methods of measuring ranges of small mammals. Jour. Mamm., 35: 1-15.

Stebler, A. M. 1958. Research and management in wildlife conservation. Proc. Okla. Acad. Sci., 38: 186-193.

Tappe, D. T. 1941. Natural history of the Tulare kangaroo rat. Jour. Mamm., 22: 117-148.

Trowbridge, A. H. 1941. Rodents and rabbits in relation to grazing on the Southern Plains Experiment Range near Woodward, Oklahoma. U. S. Dept. Int., Fish and Wildl. Serv. Ms. 55 pp.

__________. 1942. Rodents and rabbits in relation to grazing on the Southern Plains Experiment Range near Woodward, Oklahoma. U. S. Dept. Int., Fish and Wildl. Serv. Ms. 34 pp.

Underhill, A. H. 1941. Estimation of a breeding population of chub suckers. Trans. N. Amer. Wildl. Conf., 251-256.

United States Department of Commerce. 1956. Climatological data Oklahoma. Annual summary, 1955, 64: 194-204.

__________. 1957. Climatological data Oklahoma. Annual summary 1956, 65: 182-194.

__________. 1959. Climatological data Oklahoma. Annual summary 1958, 67: 188-199.

Vorhies, C. T. and W. P. Taylor. 1922. Life history of the kangaroo rat Dipodomys spectabilis spectabilis Merriam. U. S. Dept. Agric. Bull. 1091. 40 pp.

Waterfall, U. T. 1952. A catalogue of the flora of Oklahoma. Stillwater: Okla. State Univ. Research Foundation. 91 pp.

Wood, A. E. 1935. Evolution and relationship of the heteromyid rodents with new forms from the Tertiary of western North America. Annals Carnegie Mus., 24: 73-262.

APPENDIX

APPENDIX

A List of Plant Names[1] Used in This Report

Scientific Name	Common Name
Amaranthus spp.	Pigweed
Ambrosia psilostachya, var. *lindheimeriana*	Western Ragweed
Andropogon hallii	Sand Bluestem
Andropogon scoparius	Little Bluestem
Argemone intermedia	Pricklepoppy
Artemisia filifolia	Sand Sagebrush
Bouteloua curtipendula	Side-Oats Grama
Bouteloua gracilis	Blue Grama
Bouteloua hirsuta	Hairy Grama
Buchloe dactyloides	Buffalo Grass
Calamovilfa gigantea	Big Sandreed
Cenchrus pauciflorus	Field Sandbur
Cassia fasciculata	Showy Partridgepea
Chenopodium spp.	Lambsquarter
Chloris verticillata	Windmill Grass
Commelina erecta	Curlyleaf Dayflower
Cristatella jamesii	Cristatella

[1] Scientific names were taken from the catalogue by Waterfall (1952).

Scientific Name	Common Name
Croton glandulosus, var. _septentrionalis_	Croton
Croton texensis	Croton
Cycloloma atriplicifolium	Tumble Ringwing
Cyperus schweinitzii	Flatsedge
Dalea villosa	Hairy Prairie Clover
Descurainia pinnata	Tansymustard
Eragrostis trichodes	Sand Lovegrass
Eriogonum annuum	Annual Eriogonum
Euphorbia spp.	Euphorbia
Festuca octoflora	Six-Weeks Fescue
Froelichia floridana, var. _campestris_	Snake Cotton
Helianthus annuus	Common Sunflower
Hoffmanseggia densiflora	Indian Rushpea
Lepidium densiflorum	Prairie Pepperweed
Lespedeza spp.	Lespedeza
Linaria canadensis, var. _texana_	Oldfield Toadflax
Lithospermum incisum	Narrowleaf Gromwell
Machaeranthera pinnata	Ironplant Goldenweed
Mentzelia stricta	Sand Mentzelia
Oenothera spp.	Evening Primrose
Panicum virgatum	Switch-Grass
Paspalum ciliatifolium, var. _stramineum_	Sand Paspalum
Physalis subglabrata	Taperleaf Groundcherry

Scientific Name	Common Name
Plantago purshii	Pursh Plantain
Poa arachnifera	Texas Bluegrass
Polygonum convolvulus	Wild Buckwheat
Portulaca oleracea	Common Purslane
Prunus angustifolia	Sand Plum
Rhus aromatica	Skunkbrush Sumac
Salsola kali, var. tenuifolia	Common Russianthistle
Salvia azurea, var. grandiflora	Pitcher Sage
Setaria glauca	Yellow Bristlegrass
Silene antirrhina	Sleepy Catchfly
Specularia biflora	Small Venuslookingglass
Sporobolus cryptandrus	Sand Dropseed
Strophostyles leiosperma	Small Wildbean
Tephrosia virginiana	Tephrosia
Tradescantia occidentalis	Prairie Spiderwort
Triplasis purpurea	Purple Sandgrass
Vicia villosa	Hairy Vetch
Viola kitaibeliana, var. rafinesquii	Johnnyjumpup

VITA

Clay Young McCulloch, Jr.

Candidate for the Degree of

Doctor of Philosophy

Thesis: POPULATIONS AND RANGE EFFECTS OF RODENTS ON THE SAND SAGEBRUSH GRASSLANDS OF WESTERN OKLAHOMA

Major field: Zoology

Biographical:

Personal Data: Born at Durango, Colorado, March 14, 1924, the son of Clay Y. and Alice Gramly McCulloch.

Education: Was graduated from Durango High School in 1941. Undergraduate studies at Fort Lewis Branch of Colorado A. and M. College at Hesperus, University of Colorado at Boulder, and Colorado A. and M. College at Fort Collins. Received the Bachelor of Science degree from Colorado A. and M. College in 1948, with a major in General Science and Arts. Completed the undergraduate requirements for a major in Game Management at Colorado A. and M. College in 1950. Graduate study at the University of Idaho, Moscow, 1950-1952. Received the Master of Science degree from the University of Idaho in June, 1953, with a major in Wildlife Management. Began studies at Oklahoma State University in 1955. Completed requirements for the Doctor of Philosophy degree in July, 1959. Elected to the societies of Xi Sigma Pi, Phi Sigma, and Sigma Xi (Associate).

Professional Experience: Range surveys, Bridger National Forest, Wyoming, 1949. Biologist, Arizona Game and Fish Department, 1952-1955. Member of the Wildlife Society, American Society of Mammalogists, American Society of Range Management, Ecological Society of America, and the Oklahoma Academy of Science.