

EXPERIMENTAL SPECIES REMOVAL:

- I. COMPARISON OF DISPERSAL STRATEGIES OF SIGMODON
HISPIDUS AND REITHRODONTOMYS FULVESCENS.
- II. ANALYSIS OF SIGMODON HISPIDUS AND REITHRODONTOMYS
FULVESCENS INTERACTIONS.

A Dissertation

Presented to

the Faculty of the Department of Biology

University of Houston

In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

by

James Joule

December 1973

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Sigmodon hispidus (the hispid cotton rat) and Reithrodontomys fulvescens (the fulvous harvest mouse) are the codominant rodent species on the Texas coastal prairie. Eight isolated 1.6 ha replicated plots were used to study dispersal strategies and the interspecific interactions of these rodents. Each replicate was live-trapped monthly for nineteen months. For two replicates all captured individuals were analyzed as to species, sex, body weight, and time and site of capture, and then marked and released. These replicates contained the control (resident) populations. In two replicates all Reithrodontomys were removed, in two replicates all Sigmodon were removed, and in two others both species were removed.

Monthly dispersal of individuals into plots where that species was previously removed was measured as to numbers per month, body weight, and sex. These data were tested against the population structure of control populations. The number of dispersers of both sexes of Sigmodon and Reithrodontomys were significantly correlated with monthly change in resident density. Sex ratio comparisons between dispersers and residents were found to be nonsignificant for both species. The rank order of size (age) classes of dispersers was significantly correlated to their presence in the control plots for male and female Sigmodon and for male Reithrodontomys. Significantly higher proportions of juvenile Reithrodontomys females were found to disperse. The rank-order template dispersal strategy found during this study has the advantage of introducing a stabilized age structure into newly acquired habitat space for these species.

Sigmodon reflected higher densities and population biomass in the plots where Reithrodontomys was also present. Sex ratios of Sigmodon reflected a higher percentage of males in the replicates containing sympatric populations of Reithrodontomys. Male and female Sigmodon experienced different selection pressure when the species composition was disturbed. These differences for Sigmodon were significant over the duration of the study. Sigmodon and Reithrodontomys reflected asynchronous breeding patterns in the control replicates. In the replicates where Reithrodontomys was removed, Sigmodon extended its breeding period. The higher densities and biomasses of Sigmodon and Reithrodontomys in the presence of each other imply the important relationships between the two species are facilitative, rather than competitive. Reithrodontomys reflected the same changes as Sigmodon during periods of increased density.

Possible mechanisms of facilitation between the rodents include:

- (a) buffering of severe predation pressure on either species by the presence of the other,
- (b) diminishment of intraspecific competition affected by a codominant, mixed-species mosaic, and
- (c) "active" facilitation of one species by another species.

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INTRODUCTION

Dispersal (immigration and emigration) is a characteristic property of the life histories of all species. Ecologically, dispersal can be viewed as having three important functions: (1) the maintenance of genetic variation within discrete, but compatible, populations through the exchange of individuals (Lidicker, 1962); (2) as a safety valve against resource limitation which can come about in local populations through a declining carrying capacity of the environment or an increasing population density (Lidicker, 1962); (3) and the acquisition of new or previously depopulated habitat space (Howard, 1960).

While these properties of dispersal are of obvious value, it is less apparent whether species engage in dispersal strategies that maximally ensure ecological goals such as the establishment of a new population in previously unoccupied habitat space. For instance, alternative dispersal strategies may be to disperse only young members of the resident population, or only females, or only pregnant females, or some combination of these strategies. Of course, only certain strategies may be available to a species because of natural limitations. Mayr (1963) discusses these natural limitations as the physical means and the "intrinsic factors" which influence a specific, active dispersal strategy. Mayr defined "intrinsic factors" as those physiological and psychological traits which cause species to react differently to the geographic barriers linked with dispersal. Within these limits, we can inquire into the types of strategies employed by closely related species when confronted with similar

environmental pressures.

Statement of the Problem

The purpose of this paper is to investigate the dispersal strategies of two sympatric rodents, the hispid cotton rat (Sigmodon hispidus, Say and Ord, 1825) and the fulvous harvest mouse Reithrodontomys fulvescens, Allen, 1895), into perturbed habitats. The monthly densities, sex ratios, and size (age) classes of dispersing Sigmodon and Reithrodontomys are investigated in three experimental field conditions: (1) cotton rat and harvest mouse dispersers found in area where both species were continually removed by live-trapping; (2) cotton rat dispersers found in areas where it was being removed, but the harvest mouse was allowed to remain; and (3) harvest mouse dispersers found in area where it was being removed, but the cotton rat was allowed to remain. These data are compared with monthly data taken from unperturbed, resident populations (controls) and the dispersal strategy of each is characterized.

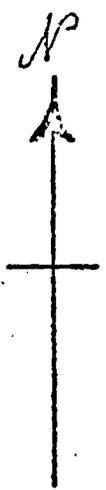
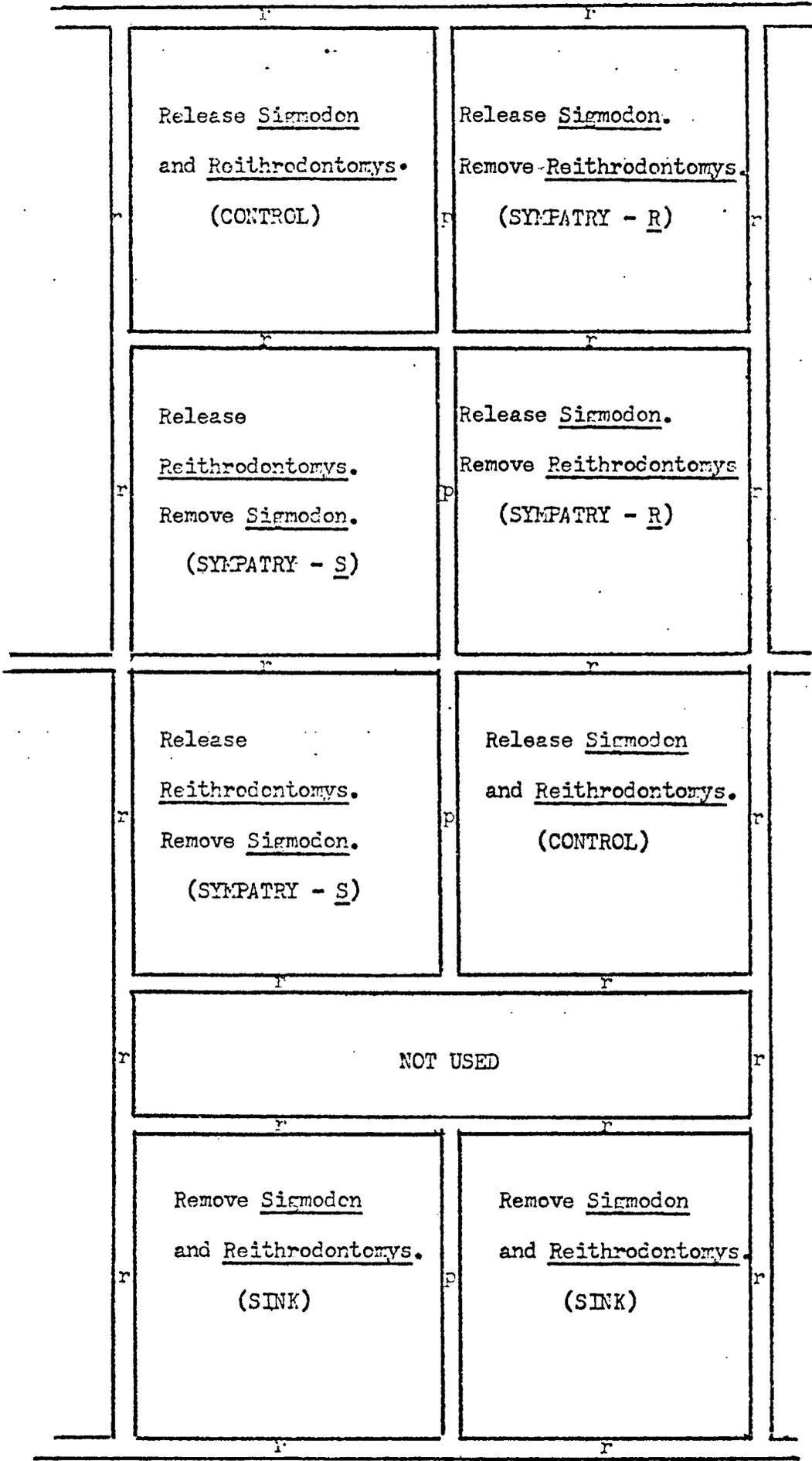
MATERIALS AND METHODS

This study was conducted at the University of Houston Coastal Center, a 360 ha field station situated 35 miles south of Houston, Texas. Vegetation on the Coastal Prairie consists of dense stands of Baccharis hamilifolia (sea-myrtle) inter-dispersed with Schizachyrium scoparius (little blue stem), Andropogon glomeratus (bushy beard-grass), Solidago spp. (goldenrod), Spartina patens (salt-meadow cord-grass), Gaura Lindheimeri (prairie gaura), Rubus trivialis (southern dewberry), Ampelopsis arborea (pepper-vine), Lonicera japonica (Japanese honeysuckle), Eupatorium serotinum (late boneset), and other less common herbaceous plants. Sparse stands of Sapium sebiferum (Chinese tallow trees) are present, mostly along road edges. The soil is hard clay loam (Bernard soil) which inhibits burrowing and limits most rodents to habitats above the ground.

Eight 1.6 ha plots, isolated from one another by 15 meter wide paved roads and mowed (and partially plowed) paths, were sampled monthly with Sherman live-traps (7.5 cm by 7.5 cm by 25 cm) from February 1972 through August 1973 (Figure 1). Two plots served as controls (no animals removed), all Reithrodontomys were removed from two plots (Sigmodon were marked and released), all Sigmodon were removed from two plots (Reithrodontomys were marked and released), and two plots served as "sinks" (both Sigmodon and Reithrodontomys were removed). The minor species inhabiting the areas were marked and released in all cases and did not appear to be actively affected by the experimental scheme. These removal-release manipulations were maintained during

FIGURE 1.

Diagram of the eight 1.6 ha plots, showing the positions of the Control, Sink, Sympatry-S, and Sympatry-R replicates. Vegetation and substrate are similar throughout the area. The r's indicate the separation of individual replicates by paved roads, and the p's indicate paths (see text).



each month of sampling; hence, these were continuous, rather than instantaneous, manipulations of the system.

Plots were sampled either in pairs or in groups of four, beginning on the first of each month. Between February 1972 and February 1973, each plot was sampled for four nights, and an entire sampling period ranged from eight to fourteen nights. During this time, over 90% of the Sigmodon and Reithrodontomys captures were recorded during the first three nights, using temporary removal techniques described below. Thereafter, monthly sampling of each plot was reduced to three nights. Individuals captured and released in a plot each month comprised the resident population of that plot. After the initial period (February 1972) when the manipulations were first applied individuals present in areas where that species was being removed were considered dispersers which moved into the plots between sampling periods.

The following procedure was used to sample each plot:

- (1) Traps were opened and baited with sliced apples prior to sundown of the first night.
- (2) Traps were checked an hour after sunrise of the following day. Captured animals were taken to the field station laboratory adjacent to the plots; and species, sex, site of capture, body weight, and reproductive condition were recorded. Clean, newly baited traps were placed at the sites of captures. Captures to be returned to the field were marked individually either with numbered Monel ear-tags (Sigmodon hispidus and Rattus spp.) or by toe-clipping

(all other species). These animals were maintained in separate opaque cages in the laboratory until their release, and given food and water ad libitum.

(3) Traps were left open on the ensuing day as there is little diurnal activity by rodents in this area. Data concerning the diel activity of the rodents inhabiting the plots will be discussed in another paper.

(4) On the second and third mornings (second morning after February 1973), captures were collected, analyzed, and housed in the same manner.

(5) After the fourth night's captures had been collected and recorded (third night after February 1973) all animals to be returned, according to the experimental design (Figure 1), were released at the exact sites of capture. The traps were closed and left on the grids until the following month.

We have determined in this and other studies at the Coastal Center, that the paved roads and mowed, partially plowed paths between plots effectively reduce small mammal movement to a small proportion of movement within plots. Although there was some seasonal movement across roads and paths, distinct populations were maintained. A similar technique was used by Morris (1969) to separate rodent populations in replicate plots. Discontinuities in the habitat eliminate two usual problems associated with trapping studies: (1) edge effect phenomena as described by Tanaka (1972); and (2) Holgate's (1966) contention that marked animals may be equally susceptible to

trapping, but may leave the sampling grid at a markedly constant rate. Roads and paths appear to be an adequate compromise between the use of fences (Caldwell and Gentry, 1965; Wiegart, 1972; Krebs et al., 1973), which are unnatural in that they allow no interplot movement and may inhibit predation; and a situation where there is no change in habitat quality between individual areas (Stickel, 1946; Smyth, 1968; Van Vleck, 1968). Additional information on the sampling area and methods are given by Joule and Jameson (1972) and Joule and Cameron (1973).

RESULTS

Resident Population Dynamics

The nineteen month study included data from 43,416 trap-nights. The number of individuals and total captures per species during that time are given in Table 1. The numerically codominant species, Sigmodon hispidus and Reithrodontomys fulvescens, comprised over 80% of the combined total for each of the categories in Table 1.

An examination of the resident populations is necessary to the characterization of the dispersal strategies. The dynamics of the Sigmodon and Reithrodontomys populations in the control plots are shown in Figure 2b. Monthly densities were estimated by the minimum number known to be alive method (Krebs, 1966). Monthly mean high and low temperatures, recorded with on site hygrothermographs, and three-point moving averages of these monthly means, showing seasonal climatological trends, are given in Figure 2a. Both species show two peaks in their annual population densities, with the early peaks being shorter in duration than the later ones. Sigmodon offspring from spring breeding were first captured when the temperature moving averages rose to 83.3°F (high) and 67.2°F (low) during 1972, and 85.7°F and 69.2°F in 1973. Offspring from the fall peak first appeared when these averages declined to 85.1°F and 69.2°F. The intermittent declines in the Sigmodon density pattern accompanied periods of extreme high and low monthly temperature. Inspection of Figure 2 shows mean monthly temperatures do not match the density behavior of Sigmodon as closely as the three-point averages. The Reithrodontomys peaks were off-set from Sigmodon by one to two months,

TABLE I

SPECIES LIST OF SMALL MAMMALS PRESENT AT THE UNIVERSITY OF HOUSTON COASTAL CENTER. TOTAL NUMBER OF INDIVIDUALS AND CAPTURES PER SPECIES ALONG WITH THE PERCENT ABUNDANCE OF EACH ARE GIVEN. NOTE THE NUMERICAL DOMINANCE OF SIGMODON HISPIDUS AND REITHRODONTOMYS FULVESCENS. THESE DATA REPRESENT 43,416 TRAPNIGHTS BETWEEN FEBRUARY 1972 AND AUGUST 1973.

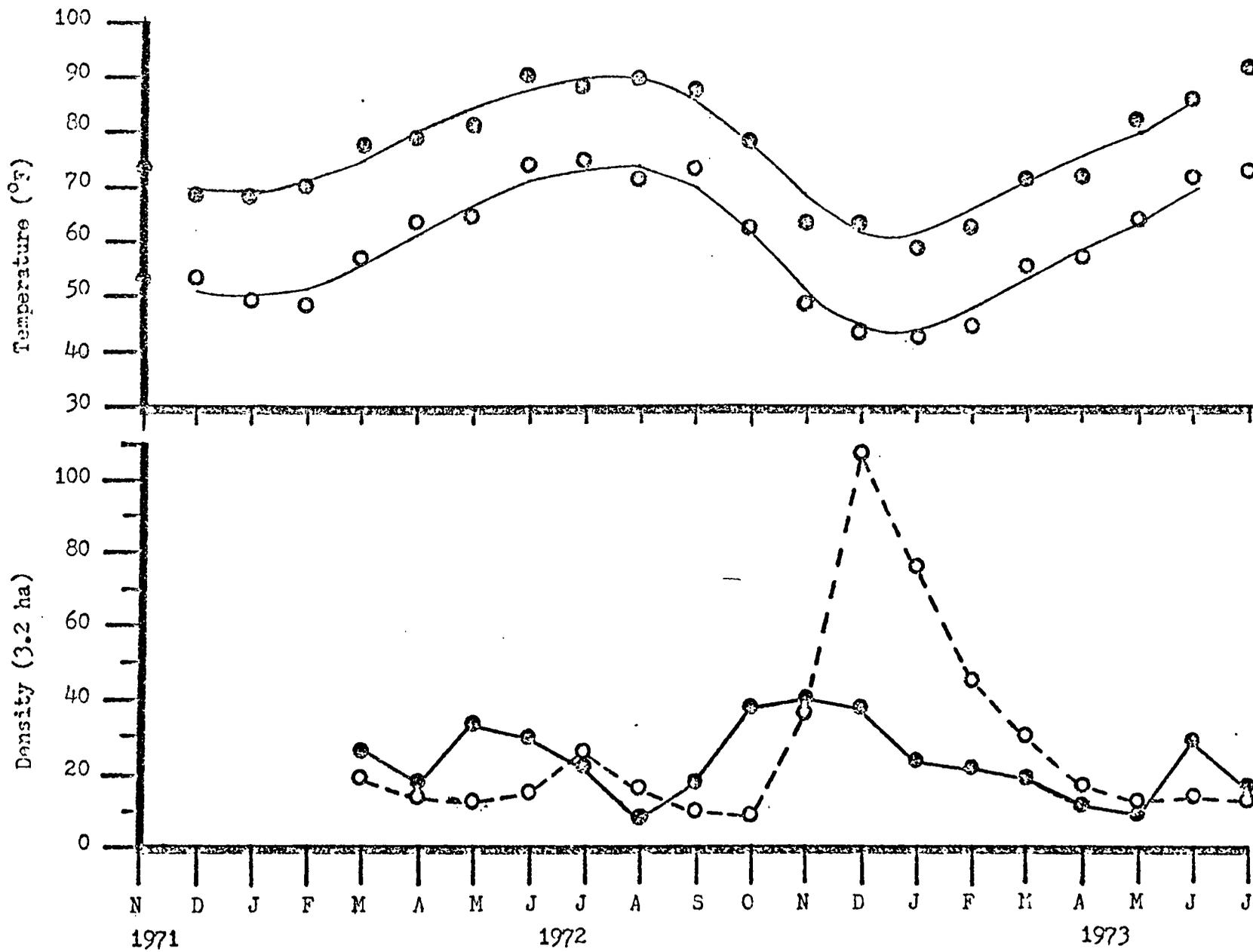
	<u>Individuals</u>	<u>%</u>	<u>Captures</u>	<u>%</u>
<u>Reithrodontomys fulvescens</u> (fulvous harvest mouse)	858	48.3	1269	48.6
<u>Sigmodon hispidus</u> (hispid cotton rat)	708	40.0	1082	41.4
<u>Oryzomys palustris</u> (eastern rice rat)	102	5.8	123	4.7
<u>Baiomys taylori</u> (pygmy mouse)	61	3.4	95	3.6
<u>Cryptotis parva</u> ¹ (least shrew)	17	1.0	17	0.7
<u>Rattus rattus</u> (black or roof rat)	13	0.7	13	0.5
<u>Rattus norvegicus</u> (brown or Norway rat)	12	0.7	12	0.5
<u>Neotoma floridana</u> (Florida wood rat)	1	0.1	1	0.0
<u>Mus musculus</u> ² (house mouse)	0	0.0	0	0.0
	<u>1772</u>		<u>2612</u>	

¹ Insectivore .

² Although none were taken during this study, Mus has been found in the area during previous studies.

FIGURES 2a AND 2b.

The combined monthly densities of the two 1.6 ha Control replicates for Sigmodon (solid line) and Reithrodontomys (broken line) are given in the lower graph (2b). The monthly values were estimated using the Minimum Number Known to be Alive Method (Krebs, 1966). The sexes within each species were pooled. The top graph (2a) shows the monthly mean high (squares) and low (circles) temperatures for the period of November 1971 to July 1973. The accompanying curves are three-point moving averages of the monthly means, showing the seasonal temperature trends.



occurring closer to the annual extreme high and low temperatures. The difference in amplitude between the early and late peaks of Reithrodontomys is more striking than for Sigmodon, with the fall peak yielding a density approximately four times greater than the early summer peak of the same year (1972).

The Sigmodon spring peak of 1972 occurred during May. A year later this peak was delayed one month, occurring in June 1973. The early summer peak of Reithrodontomys, which occurred in July, 1972, had not been recorded for 1973 as of the termination of this study (August, 1973). Lower mean temperatures were experienced during the winter-spring period of 1972-73 than were reflected by the same period in 1971-72. Snow, the first in twelve years for this area, was recorded in February 1973. The two separate snowfalls during this time each disappeared within two days, and, except for the low temperatures accompanying this phenomenon, had little effect upon rodent survival. However, this cold weather regime seems to have caused a definite reproductive delay. Further study is needed to determine the precision of this apparent cuing of rodent density dynamics to temperature, and its affect on subsequent temporal relationships between sympatric species.

Analysis of Sigmodon Dispersal

Demographic characteristics (numbers per month, sex ratio, and age classes) are considered for two separate perturbed conditions: (1) dispersing cotton rats which entered areas where cotton rats and harvest mice had previously been removed (these areas are referred to as Sink in Figure 1), and (2) dispersing cotton rats which entered

areas where cotton rats had been removed, but harvest mice were not removed (these areas are referred to as Sympatry-S). Each of these perturbed situations was compared with resident populations of cotton rats on areas where both cotton rats and harvest mice were sampled monthly and released (these areas are referred to as Control). Data from similarly perturbed plots were lumped. Data from the two plots labeled "release Sigmodon, remove Reithrodontomys (Sympatry-R)" are discussed under the analysis of Reithrodontomys dispersal.

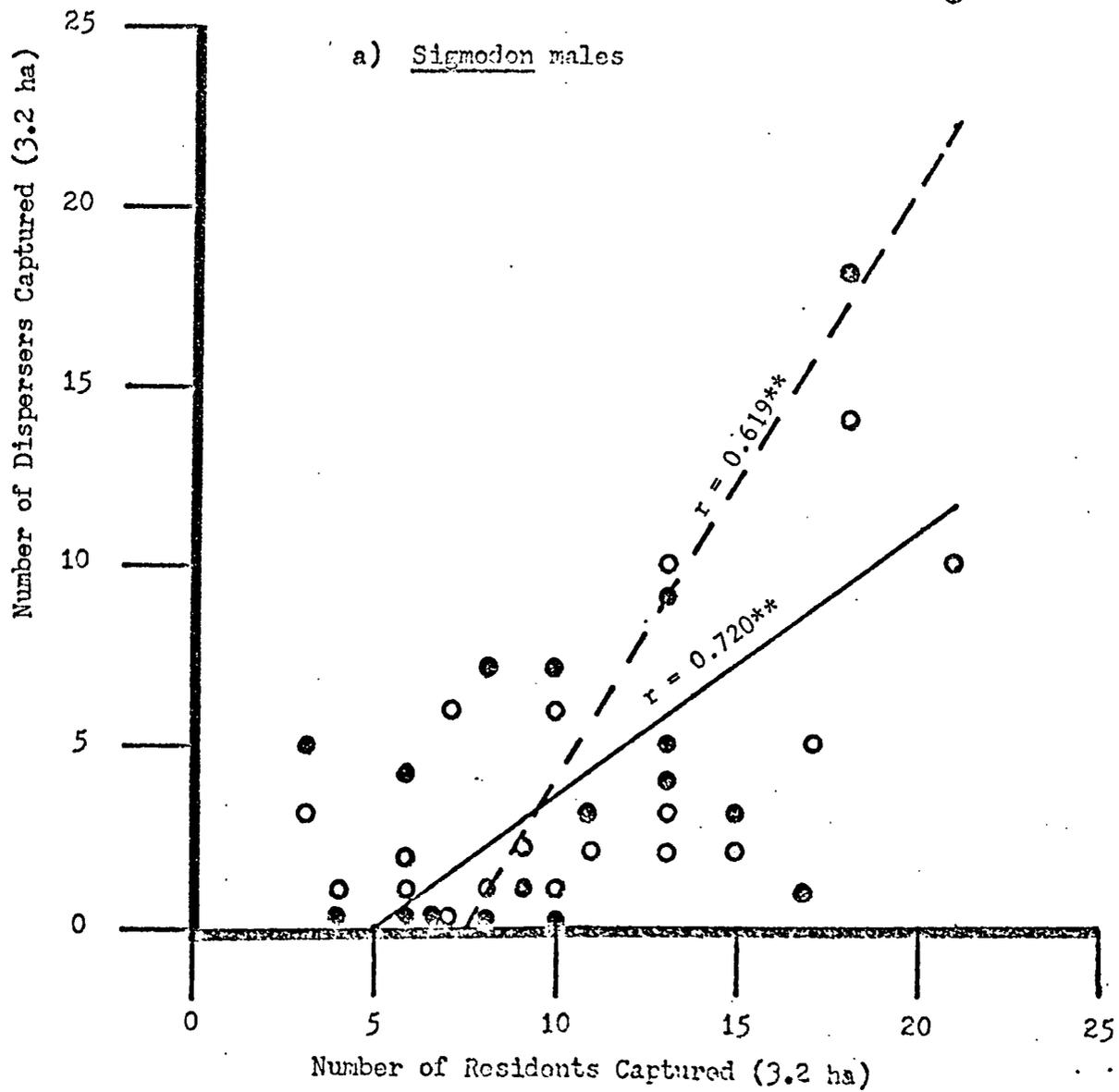
Pair-wise Pearson's product moment correlation coefficients (Sokal and Rohlf, 1969) were computed from the capture data (Appendix i), to test whether or not the numbers of Sigmodon dispersers converging into two types of perturbed areas are correlated with the size of the resident populations. The raw data, comparing each perturbed condition with the resident population densities, and the principle component axes are plotted in Figures 3a (males) and 3b (females). Although mark-recapture indices could be used for the resident populations, monthly removal of individuals in the perturbed areas prevented their usage under these situations. For consistency, raw capture data was used in all cases. The significant positive correlations (Figures 3a and 3b) obtained for Sigmodon indicate that the rate of dispersal by this species is directly related to the number of individuals found in the resident populations.

Comparisons of size class representatives contained in the samples of each perturbed condition (Sink and Sympatry-S) with those of the resident populations (Control) were made by arranging individuals into 30 gram weight classes (Table II). Data were pooled over

FIGURES 3a AND 3b.

Monthly relationships between the resident populations and dispersives are plotted for the Control-Sink (open circles, solid lines) and Control-Sympatry-S (closed circles, broken lines) comparisons of Sigmodon males (3a) and females (3b). The principle component axes are plotted for each comparison, and Pearson's product-moment correlation coefficients are given on the axes.

* = $P < 0.05$, ** = $P < 0.01$, and *** = $P < 0.001$.



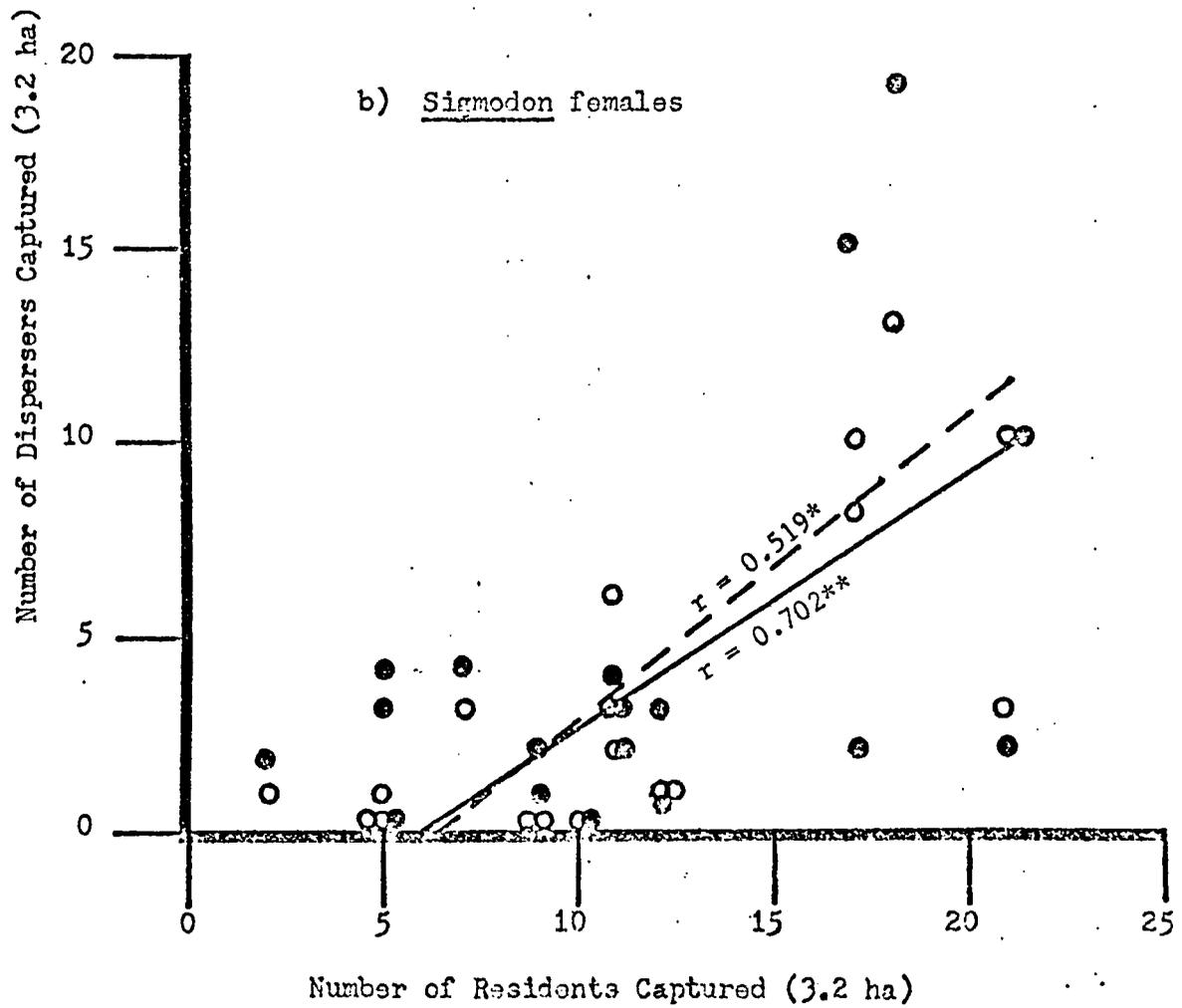


TABLE II

RAW CAPTURE COMPARISONS BETWEEN SIGMODON SIZE CLASSES FOUND IN THE RESIDENT POPULATIONS (CONTROL) AND THE DISPERSING SAMPLES (SINK AND SYMPATRY). DATA FOR EACH CLASS CATEGORY WERE SUMMED OVER THE FIVE MONTHS WHEN DISPERSAL WAS MOST PREVALENT (JUNE AND SEPTEMBER THROUGH DECEMBER, 1972). THESE FIVE MONTHS ACCOUNT FOR 76% OF THE MALES AND 73% OF THE FEMALES CAPTURED IN THE SINK AND SYMPATRY AREAS DURING THE FIRST TWELVE MONTHS OF THE STUDY. SPEARMAN'S RANK CORRELATION COEFFICIENT (r_s) IS GIVEN FOR EACH COMPARISON.

Males:

Size Classes (Grams)	Sink (si)	Control (c)	Sympatry (sym)	
0-30	3	6	12	
31-60	6	8	15	
61-90	11	21	16	
91-120	14	21	12	$r_s(\widehat{si-c}) = 0.873^*$
121-150	5	15	7	
151-180	5	3	2	$r_s(\widehat{sym-c}) = 0.736^*$
181+	1	0	1	
Totals	43	74	65	

Females:

Size Classes (Grams)	Sink (si)	Control (c)	Sympatry (sym)	
0-30	5	8	8	
31-60	8	26	9	
61-90	15	16	14	
91-120	6	16	14	$r_s(\widehat{si-c}) = 0.829^*$
121-150	2	12	5	
151-180	3	2	0	$r_s(\widehat{sym-c}) = 0.844^*$
181+	1	0	0	
Totals	40	80	50	

* = $P < 0.05$

the five months during 1972 when invasions into the perturbed areas were prevalent (June, September, October, November, and December). This method minimized the inclusion of data showing demographic changes in the resident populations during months not relevant to dispersal phenomena. Spearman's rank correlation (Seigel, 1954) was used to test for similarities in the distribution of size classes in the perturbed and control samples. As shown in Table II, the appearance of a size class on the perturbed replicates (Sink and Sympatry-S dispersers) correlated significantly with its rank order of presence within the Control populations (residents), for both males and females.

The sex ratio of the dispersers entering each of the perturbed areas was tested against the resident sex ratio (Control) using a Chi-square test of independence [2 x 2 tables: (number of each sex) males-females X (number of captures) Control-Sink and Control-Sympatry-S]. The five months of data used for size class analysis were used here, also. Differences within the comparisons of the Control and Sink ($\chi^2_{(1)} = 0.04$; $P > 0.50$) and the Control and Sympatry-S ($\chi^2_{(1)} = 1.72$; $P > 0.10$) sex ratios were found to be non-significant. The dispersal strategy of Sigmodon into artificially perturbed areas was shown to be independent of sex.

The above analyses imply that, rather than representing a single or subset of age classes, Sigmodon dispersers reflect a representative template, with respect to sex and age, of the resident population.

One fourth of the border of one Sympatry-S plot and one half of

the other had marked Sigmodon populations (resident) adjacent to them (see Figure 1). Assuming an equal influx of dispersers from the nearest points in all directions, it was expected that three-eighths (37.5 percent) of the Sigmodon dispersers taken in the lumped Sympatry-S plots should be previously marked individuals. Of the 162 cotton rats taken in these two replicates, 13.6 percent were marked individuals (12 males and 10 females). A t-test of percentages between the expected and observed values indicates the dispersal representation from the immediate surroundings was significantly lower than expected ($t_{(\infty)} = 5.06$; $P < 0.001$). Movement of marked cotton rats between the four replicates maintaining marked population was also low (8 males and 6 females during the eighteen months study). This included movement between the two Control replicates and the replicates labeled "release Sigmodon, remove Reithrodontomys (Sympatry-R)". Two marked Sigmodon were taken in the Sink replicates, separated from the other study plots by two roads and a sixty meter wide, unused field. These analyses imply that a significantly high proportion of cotton rats had origins outside the immediate perimeters of the perturbed areas, and rapidly converged into areas of low Sigmodon density.

Analysis of Reithrodontomys Dispersal

Similar to Sigmodon, the demography of dispersing harvest mice was considered for two separate perturbed conditions: (1) dispersing harvest mice which entered replicates where harvest mice and cotton rats had previously been removed (Sink) (Figure 1), and

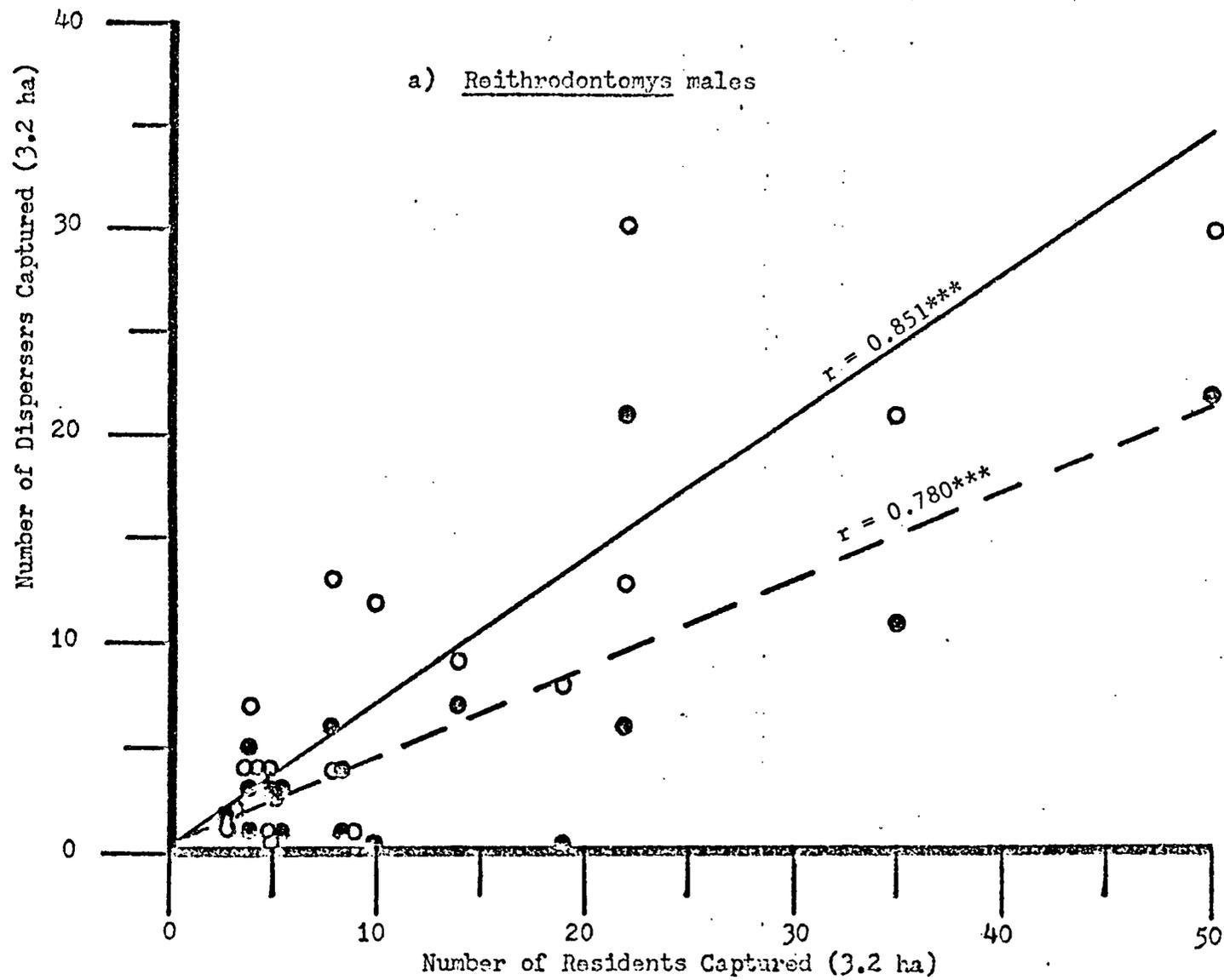
(2) dispersing harvest mice which entered replicates where harvest mice had been removed, but cotton rats were not removed (Sympatry-R, as in Figure 1). Data from these two perturbed situations were compared with the resident populations of harvest mice (Control). Information from the two replicates labeled "release Reithrodontomys, remove Sigmodon (Sympatry-S)" were not included here.

To test whether the numbers of Reithrodontomys dispersers entering the perturbed areas could be predicted from the number in the resident populations, pairwise correlation coefficients were computed from the raw capture data comparing the monthly number of dispersers (Sink and Sympatry-R) with the monthly numbers (Appendix ii) in the resident populations (Control). These data, comparing each perturbed condition with the resident populations, and the principle component axes are plotted in Figures 4a (males) and 4b (females). As was the case with Sigmodon, the rate of dispersal by Reithrodontomys was positively correlated with the density of the resident populations.

Size class comparisons of representatives contained in the samples of each perturbed condition (Sink and Sympatry-R) with those of the resident populations (Control) were made by arranging individuals into eight one-gram classes (Table III). The eight smallest classes were pooled because very few harvest mice were live-trapped weighing less than seven grams. Data used for this analysis were compiled from the four months when harvest mouse movement into the perturbed areas were most prevalent (November and December 1972, and January and February 1973). As with Sigmodon, both comparisons of Reithrodontomys males showed the appearance of size classes on the perturbed replicates

FIGURES 4a AND 4b.

Monthly relationships between the resident populations and dispersives are plotted for the Control-Sink (open circles, solid lines) and Control-Sympatry-R (closed circles, broken lines) comparisons for Reithrodontomys males (4a) and females (4b). The principle component axes are plotted for each comparison, and Pearson's product-moment correlation coefficients are given on the axes. *** = $P < 0.001$.



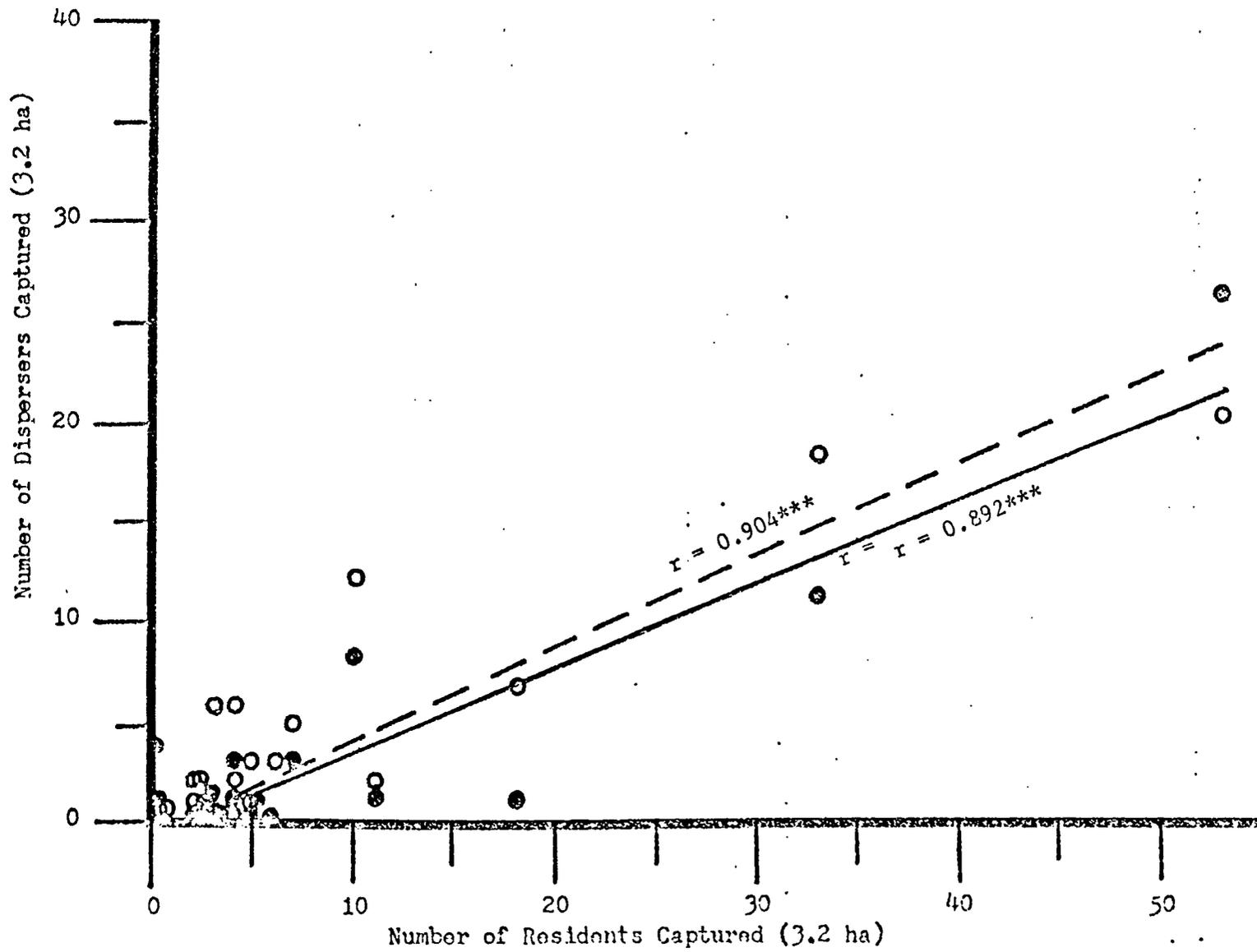


TABLE III

RAW CAPTURE COMPARISONS BETWEEN REITHRODONTOMYS SIZE CLASSES FOUND IN THE RESIDENT POPULATIONS (CONTROL) AND THE DISPERSING SAMPLES (SINK AND SYMPATRY). DATA FOR EACH CLASS CATEGORY WERE SUMMED OVER THE FOUR MONTHS WHEN DISPERSAL WAS MOST PREVALENT (NOVEMBER AND DECEMBER 1972, JANUARY AND FEBRUARY 1973). THESE FOUR MONTHS ACCOUNT FOR 70% OF THE MALES AND 71% OF THE FEMALES CAPTURED IN THE SINK AND SYMPATRY AREAS DURING THE FIRST TWELVE MONTHS OF THE STUDY. SPEARMAN'S RANK CORRELATION COEFFICIENT (r_s) IS GIVEN FOR EACH EACH COMPARISON.

Males:

Size Classes (Grams)	Sink (si)	Control (c)	Sympatry (sym)	
0-7.99	5	6	0	
8-8.99	11	14	9	
9-9.99	17	25	8	
10-10.99	30	27	17	$r_s(\text{si} \sim \text{c}) = 0.911^{**}$
11-11.99	21	30	12	
12-12.99	4	18	7	$r_s(\text{sym} \sim \text{c}) = 0.863^{**}$
13-13.99	3	6	4	
14+	2	4	2	
Totals	93	130	59	

Females:

Size Classes (Grams)	Sink (si)	Control (c)	Sympatry (sym)	
0-7.99	8	9	3	
8-8.99	7	8	7	
9-9.99	12	25	12	
10-10.99	5	15	13	$r_s(\text{si} \sim \text{c}) = 0.274\text{ns}$
11-11.99	6	23	3	
12-12.99	7	16	2	$r_s(\text{sym} \sim \text{c}) = 0.357\text{ns}$
13-13.99	6	9	3	
14+	6	5	2	
	57	110	45	

** = $P < 0.01$; ns = nonsignificant ($P > 0.05$).

to be significantly correlated with the rank order of their presence in the resident populations. However, the size-order of harvest mice females in both perturbed areas deviated from the resident populations yielding nonsignificant correlations. Inspection of these data shows there was a higher representation of smaller size classes in the perturbed areas. Female Reithrodontomys juveniles appear to be immediately inclined toward dispersal activity.

Sex ratios of the two perturbed conditions were tested against the sex ratio of the resident harvest mouse populations, using the same four months as were used during the size class analysis. Comparisons between the sex ratios of the Control and Sink ($\chi^2_{(1)} = 2.00, P > 0.10$), and Control and Sympatry-R ($\chi^2_{(1)} = 0.10, P > 0.50$) data were found to be nonsignificant. As with Sigmodon, no evidence was found here for differential dispersal between sexes. Three-eighths of the borders of the Sympatry-R replicates had adjacent marked Reithrodontomys populations (see Figure 1). Over the eighteen months of the study 150 harvest mice were taken from the Sympatry-R plots, of which 14.0% were marked individuals (16 males and 5 females). A t-test of percentages, testing the null hypothesis that dispersives into a depopulated area originates with equal intensities from all direction along the perimeter of the perturbed area(s) (Stickel, 1946), shows the representation by marked individuals was significantly lower than expected ($t_{(\infty)} = 4.77, P < 0.001$). Only two marked harvest mice were taken in the Sink plots, which were separated from the rest by a small, unused plot (Figure 1). Movement of marked harvest mice between the four replicates maintaining

resident populations was also small (6 males and 4 females). This includes movement between the Control replicates and the two replicates labeled "release Reithrodontomys, remove Sigmodon (Sympatry-S)".

As found for cotton rats, harvest mice dispersers appear to have a wide range of origins, and are able to rapidly concentrate in areas of low harvest mouse densities.

DISCUSSION

The dispersal strategies of Sigmodon and Reithrodontomys are density dependent and appear to be in synchrony with seasonally changing environmental conditions. Myers and Krebs (1971) obtained low correlations between the numbers of dispersers per unit time and the density phases of Microtus pennsylvanicus and M. ochrogaster cycles. Dispersal activity was positively correlated with density during the initial increase phases of both species, but not during the peak and declining phases. Thus, a linear relationship between density and dispersal was not found. These low comparisons led Myers and Krebs to reject the hypothesis that dispersal is a principle regulatory mechanism for Microtus. During the present study, significant positive correlations between the resident densities and numbers of dispersers throughout time were obtained for both Sigmodon and Reithrodontomys. The dispersal patterns of these species into depopulated areas were not significantly altered by the presence of the other species. Hence for these species, dispersal appears to be a regulatory mechanism.

The significantly lower than expected percentage of marked individuals of both species entering the perturbed areas implies that an unexpectedly low proportion of dispersers originated from the immediate surroundings. However, an assumption of this measure is that all animals from the immediate perimeter were marked prior to capture in the perturbed areas. Careful scrutiny of the mechanics underlying the present experiment indicate this assumption may not be valid, because (1) sampling, and consequently the

opportunity for marking, was done only once per month, and (2) many of the dispersing individuals of both species were juveniles which may have been born and migrated between sampling periods. Possibly, a study involving more intensive sampling and marking over shorter intervals during times of heavy dispersal (peak densities of resident populations) would reveal that a high number of dispersers had their origins close by. If so, the results would follow those of Stickel (1946) where the "key source" of Peromyscus leucopus invaders into into a previously trapped-out area were those individuals along the immediate perimeter.

Periodic sampling of other areas of the Coastal Centers showed that the control populations in this study continued to reflect unperturbed conditions throughout the experiment (density, population biomass, and sex ratio).

Other investigators have suggested that subadult males are inordinately represented in dispersing cohorts of some rodent species (Van Vleck, 1968). Stickel (1946), Terman (1965) and Smith (1966) found juvenile and young adult (approaching sexual maturity) Peromyscus of both sexes account for a high percentage of the dispersing individuals. In this study, the size class and sex ratio comparisons between individuals in resident and perturbed replicates indicate dispersing cotton rats reflect a rank-order template of the established population structure. The same was true for harvest mouse males, but not for females, wherein a disproportionately higher number of juveniles dispersed.

Fisler (1971), working with Reithrodontomys megalotis longicaudus, R. raviventris raviventris, and R. r. halicoetes, found the males of all three species had significantly wider ranges of movement than females. The females exhibited secretive habits over small areas, causing Fisler to postulate that a high proportion of males were needed to successfully inseminate potentially breeding females. R. fulvescens, in the present study, reflects similar behavior, wherein most females appear to disperse early in life (subadult), thereafter remaining faithful to a particular area throughout the rest of their life history. Reithrodontomys males, like Sigmodon, maintain the potential for a wide amount of movement through all stages of life.

Cotton rat and harvest mouse density patterns show within year seasonal changes, probably cued by temperature trends (Odum, 1955; Haines, 1961, 1963, 1971; Goertz, 1964; Packard, 1968; Wiegand, 1972; Fleharty, etal, 1972; Joule and Jameson, 1972). Odum (1955) and Haines (1971) report the Sigmodon hispidus density pattern is cyclic. They allow that major oscillations take place within each year, but believe that interyear differences in amplitude follow a cyclical pattern. Haines (1963, 1971) related these differences to between year changes in local climate. Odum's (1955) conclusion may have been biased by his experimental design. For eleven consecutive years (1944-1954) he censused cotton rat densities for three days during the first two weeks of May and again between October 20 and November 20. Corresponding environmental information were not reported. The

measured densities during the fall ranges from 2 to 59 animals, with three distinct peaks noted during the eleven years. As shown by the present study, censusing cotton rat populations during a particular month between years does not insure sampling of the same phenologic phase. For example, we recorded a spring peak density in May 1972, but in May 1973 the population was at a low, not peaking until the following month (Figure 2). Such temporal variability, linked to between-year climatic differences and leading to different reproductive patterns, may have led other investigators to conclude Sigmodon densities are cyclical. Some of these investigators have also suggested that periodic increases in disease and parasitism are related to Sigmodon density declines (Goertz, 1964; Haines, 1971; Fleharty, et al., 1972). In the present study, as well as previous studies, by Dunaway and Kaye (1961), Goertz (1964), and Haines (1961, 1963, 1971), temperature was highly correlated with the density of Sigmodon, leading us to tentatively conclude the cotton rat is an environmental tracker rather than a cycler. We are continuing to monitor Sigmodon densities to clarify this point.

Previous dispersal studies, for the most part, provided no discontinuities between the areas of the source populations and artificially created sinks. Also, the artificially depopulated areas often were small in comparison to the home range(s) of the rodents being studied. A general tendency of rodent males to wander more than females (Howard, 1960), specifically reported for Sigmodon by Stickel and Stickel (1949) and Goertz (1964), implies a higher

probability of their presence in small adjacent areas. Packard (1968) reported the movements of male and female R. fulvescens were approximately equal. Discontinuities in the habitat between areas (roads and paths during the present study) appear to compensate for behavioral differences between the cotton rat sexes and allow the study of dispersing individuals without interference from edge effect phenomena.

Two kinds of dispersal behavior are apparent within this Sigmodon - Reithrodontomys system. An age-class templated, density-dependent strategy, directly related to properties of the established populations of their origins, best describes the characteristics of male and female Sigmodon and male Reithrodontomys dispersers. The dispersal strategy of Reithrodontomys females is also density dependent, but here, a disproportionate number of younger age classes are represented in the dispersers. The strategy of template age-class dispersal is of particular importance for a colonizing species as it insures a stabilized population immediately and, within limits of environmental variability, eliminates population oscillates and contributes to rapid establishment. Such a dispersal strategy, while of obvious local importance in colonization of depopulate areas and in establishment of a dominance relation with sympatric species, may also play an important role in the northward expansion of Sigmodon hispidus (Cockrum, 1948). The Sympatry (-S and -R) plots were attempts to record the effects of preemption by one species on the dispersal success of the other. Neither species appeared to be effected by the other's preliminary advantage in a given plot. Further studies on the interactions between these two species are discussed elsewhere (Joule, 1973).

SUMMARY

Dispersal, a characteristic property of the life histories of all species, can be viewed as having three important ecological functions: (1) maintenance of genetic variation between discrete populations, (2) a density safety valve against resource limitation, and (3) acquisition of new or previously depopulated habitat space. The type of dispersal strategy reflected depends upon natural limitations of the species. This study characterizes the dispersal strategies of two sympatric rodents, the hispid cotton rat (Sigmodon hispidus) and the fulvous harvest mouse (Reithrodontomys fulvescens).

Eight 1.6 ha plots were sampled monthly, of which two plots served as controls (no animals removed), two plots had all Reithrodontomys removed, two plots had all Sigmodon removed, and two plots served as "sinks" (both Sigmodon and Reithrodontomys were removed). These manipulations were maintained throughout the eighteen months of the study. Each plot was sampled monthly for four days from February 1972 to February 1973, and for three days thereafter until the end of the study (August 1973), using temporary removal technique. Roads and mowed, partially plowed paths separated individual plots.

During the eighteen month study, which included 43,416 trap-nights, the cotton rat and harvest mouse comprised over 80 per cent of the combined total number of individuals and captures recorded. Annual changes in the densities of the two species appear to be correlated with temperature changes. Interyear differences in the density patterns of the species appear to be due to cold weather extremes encountered during the second year (1973).

Demographic characteristics (numbers per month, sex ratio, and

age classes) of dispersing cotton rats were considered for two separate perturbed conditions: (1) dispersing Sigmodon which entered areas where both cotton rats and harvest mice had previously been removed, and (2) dispersing cotton rats which entered areas where the rats have been removed but not the mouse. These data were compared to control Sigmodon populations inhabiting unperturbed plots. Pair-wise Pearson's product moment correlation coefficients showed significant relationship between the number of monthly dispersers entering both types of perturbed situations and the control densities, for both male and female cotton rats. The appearance of size classes on the perturbed plots correlated significantly with their rank order of their presence in the control populations. Sex ratios of dispersing cotton rats were not significantly different than the controls. Rather than representing a single or subset of age classes, Sigmodon dispersers reflect a representative template, with respect to sex and age, of the resident population.

Similar to Sigmodon, the demography of dispersing harvest mice was considered for two separate perturbed conditions: (1) dispersing harvest mice which entered replicates where harvest mice and cotton rats had previously been removed, and dispersing harvest mice which entered replicates where mice had been removed but cotton rats were allowed to remain. Similar to Sigmodon, pair-wise correlation coefficients reflected a significant relationship between the number of dispersing harvest mice and the density of the resident populations for both male and female harvest mice. Size class comparisons between the dispersing and resident harvest mice samples showed, dispersing harvest

mouse males reflect a rank order representation of resident population structure, but that female dispersers reflect a high percentage of younger classes. The sex ratios of the dispersing and resident harvest mouse sample did not differ significantly.

The dispersal strategies of Sigmodon and Reithrodontomys are density dependent. A significant number of the dispersers of both species originated from areas other than the immediate surroundings of the experimental plots. Periodic sampling of other areas confirmed that the control populations continued to reflect unperturbed conditions throughout the experiment. Although some investigators suggest that subadult males, or juvenile and subadults of both sexes account for a high percentage of rodent dispersal, the present study indicated that dispersal representatives of Sigmodon males and females and Reithrodontomys males are a rank-order template of established population structure. The deviation from this trend was found for Reithrodontomys females, and may be linked to their secretive movements over permanent small areas during the adult stages of their life history. The correlation of Sigmodon density patterns to seasonal temperature changes characterizes the species as an environmental tracker rather than a true cycler. The roads and paths of the present study compensated for the usual difficulties of edge effects and differential movements of sexes. A templated age-class dispersal strategy is of particular importance for colonizing species as it insures a stabilized population immediately, and within the limits of environmental variability, eliminates population oscillations and contributes to rapid establishment.

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APPENDIX i

NUMBER OF MONTHLY CAPTURES OF SIGMODON RESIDENTS (CONTROL) AND DISPERSERS (SINK AND SYMPATRY-S) FROM MARCH 1972 THOUGH AUGUST 1973. NUMBERS IN PARENTHESSES INDICATE THE NUMBER OF INDIVIDUALS WITHIN THE MONTHLY SAMPLES WHICH HAD BEEN PREVIOUSLY MARKED.

<u>Month</u>	<u>Males</u>			<u>Females</u>		
	<u>Sink</u>	<u>Control</u>	<u>Sympatry-S</u>	<u>Sink</u>	<u>Control</u>	<u>Sympatry-S</u>
Mar 1972	2(0)	15(13)	3(0)	2(0)	11(9)	4(1)
Apr	0	7(7)	0	0	10(9)	0
May	2(0)	13(5)	4(1)	3(0)	21(7)	2(1)
Jun	10(0)	13(7)	5(3)	10(0)	17(13)	2(2)
Jul	2(0)	11(6)	3(0)	6(0)	11(9)	3(2)
Aug	3(0)	3(3)	5(1)	0	5(5)	3(2)
Sep	6(0)	10(0)	7(1)	3(0)	7(3)	4(0)
Oct	14(0)	18(3)	18(0)	13(0)	18(6)	19(0)
Nov	10(0)	21(10)	26(3)	8(0)	17(11)	15(0)
Dec	3(0)	13(8)	9(1)	10(0)	21(12)	10(0)
Jan 1973	2(0)	9(9)	1(0)	1(0)	12(12)	3(1)

APPENDIX i (CONTINUED)

<u>Month</u>	<u>Males</u>			<u>Females</u>		
	<u>Sink</u>	<u>Control</u>	<u>Sympatry-S</u>	<u>Sink</u>	<u>Control</u>	<u>Sympatry-S</u>
Feb 1973	1(0)	8(7)	0	1(0)	12(11)	1(0)
Mar	1(0)	10(7)	0	0	9(9)	1(0)
Apr	1(0)	4(4)	0	0	5(5)	0
May	1(0)	6(2)	0	1(0)	2(2)	2(0)
Jun	5(1)	17(3)	1(0)	3(0)	11(3)	2(0)
Jul	6(1)	7(3)	7(2)	0	9(7)	2(1)
<u>Aug</u>	<u>2(0)</u>	<u>6(3)</u>	<u>4(0)</u>	<u>1(0)</u>	<u>5(4)</u>	<u>4(1)</u>
Totals	71(2)	191(100)	93(12)	62(0)	203(137)	77(11)

APPENDIX ii

NUMBER OF MONTHLY CAPTURES OF REITHRODONTOMYS RESIDENTS (CONTROL) AND DISPERSERS (SINK AND SYMPATRY-R) FROM MARCH 1972 THROUGH AUGUST 1973. NUMBERS IN PARENTHESES INDICATE THE NUMBER OF INDIVIDUALS WITHIN THE MONTHLY SAMPLES WHICH HAD BEEN MARKED PREVIOUSLY.

<u>Month</u>	<u>Males</u>			<u>Females</u>		
	<u>Sink</u>	<u>Control</u>	<u>Sympatry-R</u>	<u>Sink</u>	<u>Control</u>	<u>Sympatry-R</u>
Mar 1972	12(0)	10(4)	0	5(0)	7(3)	3(0)
Apr	4(0)	8(5)	6(1)	6(1)	3(3)	0
May	4(0)	5(3)	1(0)	2(0)	2(1)	0
Jun	13(0)	8(6)	4(0)	6(0)	4(1)	3(0)
Jul	8(0)	19(9)	0	3(0)	6(1)	0
Aug	1(0)	9(5)	1(0)	0	4(4)	1(1)
Sep	6(0)	4(3)	3(0)	0	0	1(0)
Oct	1(0)	3(2)	2(1)	0	0	4(1)
Nov	30(0)	22(2)	21(0)	12(0)	10(1)	8(0)
Dec	30(0)	50(16)	22(4)	20(0)	53(7)	26(1)
Jan 1973	21(1)	35(24)	11(4)	18(0)	33(25)	11(1)

APPENDIX ii (CONTINUED)

<u>Month</u>	<u>Males</u>			<u>Females</u>		
	<u>Sink</u>	<u>Control</u>	<u>Sympatry-R</u>	<u>Sink</u>	<u>Control</u>	<u>Sympatry-R</u>
Feb 1973	13(0)	22(20)	6(1)	7(0)	18(17)	1(0)
Mar	9(0)	14(13)	7(3)	2(0)	11(11)	1(0)
Apr	1(0)	5(5)	3(0)	3(1)	5(4)	1(0)
May	2(0)	4(1)	1(0)	1(0)	2(1)	1(0)
Jun	4(0)	5(2)	3(2)	1(0)	5(4)	0
Jul	4(1)	4(2)	5(0)	2(0)	4(2)	2(1)
<u>Aug</u>	<u>0</u>	<u>5(4)</u>	<u>3(1)</u>	<u>0</u>	<u>2(1)</u>	<u>1(1)</u>
Totals	163(2)	232(126)	99(17)	88(2)	170(86)	65(6)

EXPERIMENTAL SPECIES REMOVAL:

II. ANALYSIS OF SIGMODON HISPIDUS AND
REITHRODONTOMYS FULVESCENS INTERACTIONS.

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INTRODUCTION

Species packing and sorting are of primary importance during times of colonization and community construction (Hutchinson, 1959; MacArthur and Levins, 1967; MacArthur and Wilson, 1967; MacArthur, 1970). Shugart and Hett (1973) demonstrated this phenomenon in a number of successional communities by measuring significant declines in species turnover rates (immigration and extinction) in successional seres. Overt competitive interactions appear to diminish as coexisting species evolve differences in resource utilization (MacArthur and Levins, 1964; Rosenzweig and Winakur, 1969; Rosenzweig and Sterner, 1970; Cameron, 1971) and community regulation moves from physical control and toward biological accommodation (Sanders, 1970; Futuyma, 1973). However, the potential for competitive exclusion is maintained, lending autonomy to the established community. For mammals, this potential is manifest by aggressive behavior (agonism), chemical communication, and/or vocalization (Eisenberg, 1966; Ralls, 1971; Eisenberg and Kleinman, 1972).

Although species appear to have evolved mechanisms for both competitive exclusion and coexistence, observation and experimental documentation of exclusion has prevailed among ecological investigations. This has been particularly true for mammal studies. Field studies of interspecific interactions between small mammals fall into four categories:

(1) Observations of same species in different locations.

Cameron (1964) in North America, and Corbet (1961) on the British

Isles observed that mainland populations of two microtine genera inhabited different plant communities (Cleithronomys inhabits forests and Microtus inhabits grassland). Spatial separation between these genera corresponded directly to the ecotone between the different habitat types. On adjacent islands with noticeably similar vegetation one or the other rodent genus was recorded, not both. The authors concluded that habitat separation of these species on the mainland was due to competitive exclusion, and not to different obligatory habitat preferences. They postulated that the first arriving migrants from the mainland established barriers of pre-emption against the later-arriving individuals of the other genus. For rodents, establishment of single species populations through pre-emption is referred to as the "beachhead effect" (Cameron, 1964; Morris, 1969).

(2) Experimental species removal from contiguously allopatric small mammal populations. Koplín and Hoffman (1968) monitored the contiguously allopatric system of Microtus pennsylvanicus (grassland hydrosere) - M. montanus (xeric) microallopatric system. Removal of M. pennsylvanicus from the mesic areas prompted the movement of M. montanus into these areas. Parallel trapping of control areas showed no movement of M. montanus into the mesic areas containing undisturbed populations of M. pennsylvanicus. Stoeker (1972), manipulating the same system in reverse, removed M. montanus from the "dry areas" and successfully monitored movement of M. pennsylvanicus into this habitat. Sheppe (1961) showed that the removal of Peromyscus oreas from the basin of a ravine allowed

P. maniculatus, which had been previously recorded only on the sides of the ravine, to move to the bottom. Sheppe (1967) also performed this experiment on contiguous populations of Mus musculus and P. maniculatus inhabiting a ranch building. Removal of M. musculus was followed by an increase in abundance of P. maniculatus. Unfortunately, neither of Sheppe's experiments were compared to control situations; hence, inference affirming the reason(s) P. maniculatus entered the two different areas following removal of the resident species is speculative. These experiments suggest the absence of one species at a given site is caused by the presence of another (exclusion).

(3) Species additions and rearrangements in areas of contiguous allopatry. Vaughan and Hansen (1964) worked with the habitat relationships of two gophers, Thomomys bottae and T. talpoides, at the interface of their geographic ranges. Selected areas were cleared by live-trapping, followed by the introduction of mixed densities of the two fossorial rodents. By the end of the experiments T. talpoides was dominant both in areas formerly occupied by only T. talpoides and also in areas formerly occupied by only T. bottae. T. bottae appeared to accrue territory within its range through pre-emption rather than by differential habitat selectivity or superior exclusion mechanisms. Sheppard (1971) investigated contiguously allopatric chipmunk species (Eutamias amoenus and E. minimus) by removing portions of the resident populations of each species and introducing members of the excluded species. By the end of the first year the introduced cohorts of each species had diminished, and the

original species had recolonized (presumably through immigration from adjacent areas). At the end of two years all trace of the introduced E. amoenus cohort had disappeared, while some E. minimus persisted in the area of their introduction along with evidence of breeding. The results of these studies support the hypothesis that habitat per se was not the limiting factor between the species involved, but rather the relative abilities of the interacting organisms to fit into available habitat space.

(4) Field enclosures containing selected species compositions.

Caldwell (1964) and Caldwell and Gentry (1965) studied the Mus musculus - Peromyscus polionotus system, and Grant (1969, 1971) studied the Clethrionomys gapperi - Microtus pennsylvanicus and Peromyscus maniculatus - M. pennsylvanicus systems in fenced enclosures. The enclosures used by these workers contained parts of the natural habitat of the species under study; each species selected different micro-habitats. The M. musculus - P. polionotus study was not accompanied by single-species controls. The two studies involving M. pennsylvanicus were compared to single species controls, and indicated allopatry was maintained by interspecific interactions, not by habitat selectivity alone. Again, these studies implicate active exclusion mechanisms.

Interspecific interactions, commonly referred to as competitive interactions, are of two types: interference and exploitation (Miller, 1967; Ayala, 1969, 1972). Interference may be viewed as the price competing species must pay in order to share or win a particular resource, while exploitation refers to how effective a

particular resource is utilized by a species with respect to resource availability. Presumably, competing species have a negative effect upon one another. Laboratory studies of aggressive behavior (agonism) between species stress interference potentials, while ignoring the possible effects of exploitation between the same species. The separate conclusions obtained through studies of each of these two types of competition do not necessarily compliment one another (Pitelka, 1951; Ripley, 1959, 1961; MacArthur and Hutchinson, 1959; Orians and Collier, 1963; Heller, 1971; Brown, 1971). Hence, laboratory studies may or may not corroborate situations found under natural conditions (Murie, 1971).

The above discussion considered methodologists for measuring competitive exclusion (barriers between species populations). Properties of coexistence (not exclusion) should be of greater interest, from the viewpoint of community dynamics and organization, because mechanisms of coexistence lend insight into higher order interactions and emphasize the roles of species populations within a community context. Community interactions between sympatric species may be described as one species having a positive (+), negative (-), or null (0) effect upon another (Odum, 1971; May, 1972): neutralism (0,0) exploitive and/or interference competition (-,-), amensalism (0,-), parasitism or predation (+,-), commensalism (0,+), and proto-cooperation (non-obligatory) or mutualism (obligatory) (+,+).

Statement of the Problem

Preliminary investigation has revealed the codominant rodent populations (Sigmodon hispidus and Reithrodontomys fulvescens)

inhabiting the fields of the University of Houston Coastal Center show measurable changes in density, mean body weight (biomass), and sex ratio in response to experimental field manipulations (Joule and Jameson, 1972). This study attempts to quantify and characterize the interspecific relationship between the two species by measuring the changes which take place in cotton rat populations when the harvest mouse is experimentally removed from the cotton rat's field environment, and the changes which take place in the harvest mouse populations when the cotton rat is removed. These data are compared with control data, wherein both species were measured in the same physical environment. Differences are detected by comparing densities, population, biomass, sex ratio, survivorship, and size (age) class distribution under experimental and control conditions.

Theoretically, under laboratory conditions (population cages), the important parameters of the environment surrounding the experimental populations can be regulated artificially and kept constant over time. After a period of time, the population densities of the experimental models usually approximate an asymptote, but only by the constant replenishment of food, and other resources - and then very poorly so. As there is no recruitment through immigration (i) and no loss through emigration (e), equilibrium levels in these studies are the measured results of equal birth (b) and death (d) rates.

The Volterra logistic equations, describing the instantaneous growth rates of two species competing for similar limiting resources, have been used to quantify interspecific interactions in the laboratory (Gause, 1934; Ayala, 1969). Here, these equations are presented

in a form useful in describing the field relationship between Sigmodon and Reithrodontomys:

$$\begin{aligned}\Delta N_S/dt &= (b+i-d-e)_S N_S (1 - N_S/K_S - \alpha N_R/K_S) \\ \Delta N_R/dt &= (b+i-d-e)_R N_R (1 - N_R/K_R - \beta N_S/K_R)\end{aligned}\quad (1)$$

where:

s = subscripted logistic parameter characteristic for Sigmodon.

r = subscripted logistic parameter characteristic for Reithrodontomys.

b, i = rates of population recruitment (birth and immigration).

d, e = rates of population loss (death and emigration). In a closed system (e. g. laboratory cultures) movement in and out of the system is not considered. Under those conditions the growth term (b-d) is referred to as the intrinsic rate of increase (r_m).

N_x = density (or population biomass) of species x at a given time in the presence of the other species.

K_x = density (or population biomass) of species x at a given time "in the absence of the other species". Under closed conditions this parameter is also referred to as the carrying capacity per unit habitat volume for a particular species population.

α, β = coefficients of the struggle for existence (Gause, 1934), competition coefficients (Slobodkin, 1961), measure of the inhibitory effect of one individual of one species on the growth of the other species (Ayala, 1969). Here, α is the effect of one Reithrodontomys upon Sigmodon,

and β is the effect of one Sigmodon upon Reithrodontomys.

$\Delta N_x/dt$ = change in density (or population biomass) of species
x in a mixed-species population.

Under field conditions certain parameters included in the Volterra equations are difficult or impossible to measure accurately. Field sampling of Sigmodon and Reithrodontomys allows the measurement of only the free-living portions of the populations. In particular, birth rates (b) cannot be measured directly, thus complete values for the term $b+i-d-e$ are not possible. However, if equilibrium is assumed ($\Delta N_x/dt = 0$), the equations can be written:

$$\begin{aligned} 0 &= (b+i-d-e)_S N_S (1 - N_S/K_S - \alpha N_R/K_S) \\ 0 &= (b+i-d-e)_R N_R (1 - N_R/K_R - \beta N_S/K_R) \end{aligned} \quad (2)$$

From here, the troublesome $(b+i-d-e)$ can be eliminated from both equations, such that:

$$\begin{aligned} 0 &= K_S - N_S - \alpha N_R \\ 0 &= K_R - N_R - \beta N_S \end{aligned} \quad (3)$$

N_S , K_S , N_R , and K_R can be estimated by empirical measurement and from these the interaction coefficients for the two-species system can be estimated:

$$\alpha = \frac{K_S - N_S}{N_R} \quad \beta = \frac{K_R - N_R}{N_S} \quad (4)$$

Four different results are possible for two species interacting in a restricted space (resource volume) (Slobodkin, 1961):

Case I: Either N_S or N_R may be the sole survivor depending upon the initial densities:

$$\alpha > K_S/K_R \text{ and } \beta > K_R/K_S$$

Case II: Coexistence between the two species:

$$\alpha < K_S/K_R \text{ and } \beta < K_R/K_S$$

Case III: N_S will always be the sole survivor.

$$\alpha < K_S/K_R \text{ and } \beta > K_R/K_S$$

Case IV: N_R will always be the sole survivor.

$$\alpha > K_S/K_R \text{ and } \beta < K_R/K_S$$

The measured values of α and β can be viewed as indices of interaction between two species. The modes of these interactions can be qualitatively described by the density or population biomass relationship of N/K for each species: $N/K < 1$ (competition), $N/K > 1$ (facilitation), and $N/K = 1$ (no measureable interaction).

Monthly values of density and biomass for Sigmodon and Reithrodontomys recorded under the two previously described field situations were used to characterize the relationships governing this sympatric system.

MATERIALS AND METHODS

This study was conducted at the University of Houston Coastal Center, a 900 acre field station situated 35 miles south of Houston, Texas.

Vegetation on the coastal plain consists of dense stands of Baccharis hamillifolia (sea-myrtle) interdispersed with an abundance of Schizachyrium scoparius (little blue stem), Andropogon glomeratus (bushy beardgrass), Solidago spp. (goldenrod), and Rubus trivialis (southern dewberry). A number of minor species also occur: Spatina patens (salt-meadow cordgrass), Spartina spartinae (gulf cordgrass), Gaura Lindheimeri (prairie gaura), Ampelopsis arborea (pepper vine), Lonicera japonica (Japanese honeysuckle), and Eupatorium serotinum (late boneset). Sparse stands of Sapium sebiferum (Chinese tallow tree) are present, mostly along the road edges. The soil is hard clay loam (Bernard soil) which inhibits burrowing and limits most rodents to habitats above the ground.

Nine small mammal species inhabit the fields at the Coastal Center (Table I). Sigmodon hispidus (hispid cotton rat) and Reithrodontomys fulvescens (fulvons harvest mouse) are abundant, and were selected for two-species perturbation analysis during this study.

Potential small mammal predators inhabiting the grass-shrub fields of the Coastal Center include: (I) Avian - Circus cyaneus (marsh hawk), Buteo jamaicensis (red-tailed hawk), Elanus leucurus (white-tailed kite), Tyto alba (barn owl), Strix varia (barred owl), and Lanius ludovicianus (loggerhead shrike); (II) Reptilian -

TABLE I

SPECIES LIST OF SMALL MAMMALS PRESENT AT THE UNIVERSITY OF HOUSTON COASTAL CENTER. TOTAL NUMBER OF INDIVIDUALS AND CAPTURES PER SPECIES ALONG WITH THE PERCENT ABUNDANCE OF EACH ARE GIVEN. NOTE THE NUMERICAL DOMINANCE OF SIGMODON HISPIDUS AND REITHRODONTOMYS FULVESCENS. THESE DATA REPRESENT 43,416 TRAP-NIGHTS BETWEEN FEBRUARY 1972 AND AUGUST 1973.

	<u>Individuals</u>	<u>%</u>	<u>Captures</u>	<u>%</u>
<u>Reithrodontomys fulvescens</u> (fulvous harvest mouse)	858	48.3	1269	48.6
<u>Sigmodon hispidus</u> (hispid cotton rat)	708	40.0	1082	41.4
<u>Oryzomys palustris</u> (eastern rice rat)	102	5.8	123	4.7
<u>Baiomys taylori</u> (pygmy mouse)	61	3.4	95	3.6
<u>Cryptotis parva</u> ¹ (least shrew)	17	1.0	17	0.7
<u>Rattus rattus</u> (black or roof rat)	13	0.7	13	0.5
<u>Rattus norvegicus</u> (Norway or brown rat)	12	0.7	12	0.5
<u>Neotoma floridana</u> (Florida wood rat)	1	0.1	1	0.0
<u>Mus musculus</u> ² (house mouse)	0	0.0	0	0.0
	<u>1772</u>		<u>2612</u>	

¹Insectivore.

²Although none were taken during this study, Mus has been found in the area during previous studies.

Elaphe obsoleta lindheimeri (Texas rat snake), Pituophis melanoleucus sayi (bullsnake), Lampropeltis getulus goini (blotched kingsnake), L. g. holbrooki (speckled kingsnake), Natrix rhombifera rhombifera (diamond-backed water snake), and Agkistrodon piscivorus leucostoma (western cottonmouth); and (III) Mammalian - Canis latrans (coyote), Urocyon cinereoargenteus (grey fox), Lynx rufus (bobcat), Procyon lotor (raccoon), Felis domesticus (feral house cat), and Canis familiaris (feral dog).

Removal (perturbation) experiments utilizing the two most common rodent species, Sigmodon and Reithrodontomys, were conducted from February 1972 to August 1973. Six 1.6 ha plots, isolated from one another by 15 meter wide paved roads or mowed (partially plowed) paths were live-trapped monthly (Figure 1). Reithrodontomys was removed from two plots. Sigmodon populations inhabiting these plots are designated as the K_S populations. In two other plots Sigmodon was removed. The Reithrodontomys populations in these plots were designated as the K_r populations. A third set of two replicat plots served as controls. The Sigmodon and Reithrodontomys populations were monitored monthly and released. The populations were designated N_S (for Sigmodon) and N_r (for Reithrodontomys).

Manipulations (release and removal) were maintained monthly in conjunction with live-trap assessments. Artificial introductions of rats and mice to build up species populations in the areas of release were not conducted. Vegetation was fairly homogeneous among plots, each of which contained a grid of 81 trap sites in 9 rows of 9 sites each at 15 meter intervals, with one 7.5 cm x 7.5 cm x 25 cm

FIGURE 1

Field design of the study plots. Each plot is 1.6 ha in area. Fifteen meter wide paved roads (r) and paths (p) surround each plot. The manipulations of the rodent densities, as indicated for each plot, were carried out monthly (see text).

	r	r		
r	<p>Release <u>Sigmodon</u> and <u>Reithrodontomys</u>. (CONTROL) $\underline{N}_s, \underline{N}_r$</p>	p	<p>Release <u>Sigmodon</u>. Remove <u>Reithrodontomys</u>. (PERTURBED) \underline{K}_s</p>	r
r	<p>Release <u>Reithrodontomys</u>. Remove <u>Sigmodon</u>. (PERTURBED) \underline{K}_r</p>	p	<p>Release <u>Sigmodon</u>. Remove <u>Reithrodontomys</u>. (PERTURBED) \underline{K}_s</p>	r
r	<p>Release <u>Reithrodontomys</u>. Remove <u>Sigmodon</u>. (PERTURBED) \underline{K}_r</p>	p	<p>Release <u>Sigmodon</u> and <u>Reithrodontomys</u>. (CONTROL) $\underline{N}_s, \underline{N}_r$</p>	r
	r	r		



Sherman livetraps per site. The six plots were sampled either pairwise or in groups of four during each month. Originally, each plot was sampled for four days per month. During the first year of the study it was noticed, using the temporary removal technique described below, over 90% of Sigmodon and Reithrodontomys were taken in the first three days. Thus, after February 1973, the sampling for each plot was reduced to three days per month for the remainder of the study.

The following procedure was used to sample each plot:

- (1) Traps were opened and baited with sliced apples prior to sundown of the first night.
- (2) Traps were checked the following day an hour following sunrise. Traps with captured animals were taken to the field station laboratory adjacent to the plots and washed, newly baited traps were placed at the sites of captures. Species, sex, site of capture, and body weight were taken for each captured animal. Captures to be returned to the field were marked individually either with numbered Monel eartags (Sigmodon hispidus and Rattus spp.) or by toe-clipping (other species). Each animal was maintained in a separate opaque cage and given food and water ad libitum until its release.
- (3) Traps were left open during the day as there was little diurnal activity of rodents in this area. Data concerning diel activity of these rodents, will be discussed in another paper.

(4) On the second and third mornings (second only after February 1973), captures were collected, analyzed, and housed in the same manner.

(5) After the fourth night captures (third night after February 1973) had been collected and recorded, all animals (first through fourth night captures) to be returned, according to the experimental requirements of the plot being sampled (see Figure 1), were released at the exact sites of capture. The traps were closed and left on the grids until the following month, hence forming a permanent component of the habitat.

During seven trapping periods in 1971 (the year prior to perturbation) data were taken on the rodent populations inhabiting each of the areas. The mowed paths had not yet been installed; there were three 3.6 ha plots instead of the present six 1.6 ha plots. The data taken during these periods have been reported in part by Joule and Cameron (1973). The three large plots did not differ significantly in their densities of Sigmodon and Reithrodontomys. Within each species there was no significant difference in sex ratio and mean weight per sex between the plots. After hypothetically dividing the data in each 3.6 ha plot into two 1.8 ha subplots and testing over six areas, nonsignificant differences were obtained for all cases. Based on the homogeneity of rat populations and plots, the decision was made to subdivide the three 3.6 ha plots into six equal replicates and initiate the study. The paths were cut on January 6, 1972, and have been maintained by frequent

plowing and mowing. The first samples were taken in February 1972. At this time the perturbations (removal and release) of the co-dominant rodent populations were initiated (Figure 1). Samples from all six replicates were taken monthly thereafter, with March 1972 being the first month to yield data concerning the manipulations.

We have determined, during this and previous studies at the Coastal Center, that the paved roads and mowed paths between plots effectively reduce small mammal movement to a small percent of movement within plots, subject to seasonal variation (Joule, 1973). Although there is some movement across roads and paths, discrete populations of each species were maintained. The discontinuities (roads and paths) in the general habitat reduced two usual problems associated with trapping studies: (1) edge effect phenomena as described by Tanaka (1972), and (2) Holgate's (1966) contention that marked animals may be equally susceptible to live-trapping but may leave the sample area at a constant rate. Roads and paths appear to be an adequate compromise between the use of fences (Caldwell and Gentry, 1965; Grant, 1969, 1971; Krebs et. al., 1973), which are unnatural in that they allow no interplot movement and may interfere with predation; and a situation where there is no change in habitat quality between individual study areas (Stickel, 1946; Smyth, 1968; Van Vleck, 1968). Additional information on the sampling areas and methods used here are given by Joule and Jameson (1972) and Joule and Cameron (1973).

RESULTS

Habitat Overlap Between Sigmodon and Reithrodontomys

The pooled control replicate plots contained 162 trapsites (81 per replicate). The degree of common space utilization by Sigmodon and Reithrodontomys, within the vegetational mosaic of Bacharris, Solidago, Andropogon, Schizachrium, and Rubus, was determined with an Index of Overlap (I.O.). This index, used by Koplín and Hoffman (1968) to quantify the degree of habitat separation between Microtus montanus and M. pennsylvanicus, is the complement of the Index of Distinctiveness used by Brewer (1963). The pooled data from the nineteen months of the present study were used to determine: (1) number of sites where both major species were captured, (2) number of sites where only Sigmodon was captured, (3) number of sites where only Reithrodontomys was captured, and (4) number of sites where neither major species was captured. The Index of Overlap, expressed as a percentage is:

$$I. O. = (B/(B + R)) + (B/(B + S)) / 2 \times 100$$

where:

B = number of sites where both Sigmodon and Reithrodontomys were captured,

R = number of sites where Reithrodontomys was captured, but not Sigmodon,

S = number of sites where Sigmodon was captured, but not Reithrodontomys.

Of the 162 potential sites of capture, both species were captured at 124, only Sigmodon at 9, only Reithrodontomys at 24, and neither species at 5. Of the 133 sites where Sigmodon was captured,

93.2% also had Reithrodontomys. Of the 148 sites where Reithrodontomys was captured, 83.3% also had Sigmodon. The resultant high Index of Overlap (88.5%) demonstrates these species are not separated spatially. Although this method does not give information about the seasonal overlap between the species, the potential for a high degree of co-utilization was found. However, this is simply a measurement of overlap, not interaction. Once overlap has been established interaction must then be demonstrated by other measures.

Numerical Responses

Monthly densities of Sigmodon and Reithrodontomys were estimated for the N (mixed-species control) and K (single species) plots by calculating the minimum number known to be alive during each period (Krebs, 1966). This estimate is obtained by summing two counts: (1) the actual number caught at time t and (2) the number of previously marked individuals caught after time t, but not at that time. Raw data for the first and last months of the study are reported (February 1972 and August 1973); but, because densities by this method cannot be estimated for these, they were not included in the analysis. Density estimates were calculated separately for each sex of each species. The values for each sex were then pooled to obtain the monthly estimates of N and K per species. The monthly numerical responses for Sigmodon are given in Figure 2 (pooled sexes), and Appendices i (males) and ii (females); and for Reithrodontomys in Figure 3, and Appendices iii (males) and iv (females). Monthly values of α and β , along with

FIGURE 2.

Estimated monthly densities of Sigmodon (pooled sexes) for the control plots containing both Sigmodon and Reithrodontomys (broken line), and the experimental plots containing Sigmodon with Reithrodontomys removed (solid line). With one exception (July 1972), Sigmodon reflected higher monthly densities in the presence of Reithrodontomys. Densities are expressed for the pooled replicates of similarly manipulated plots (3.2 ha).

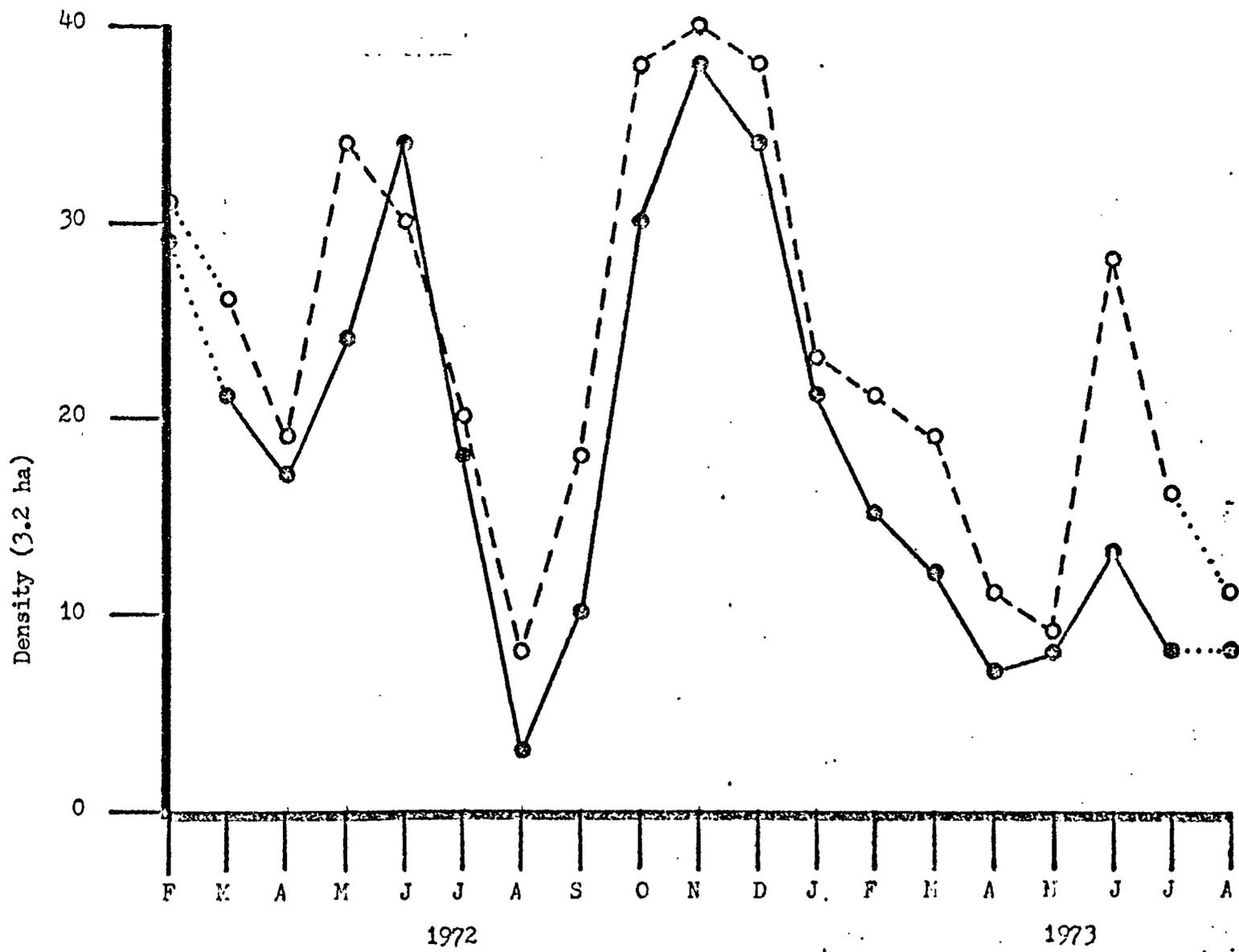
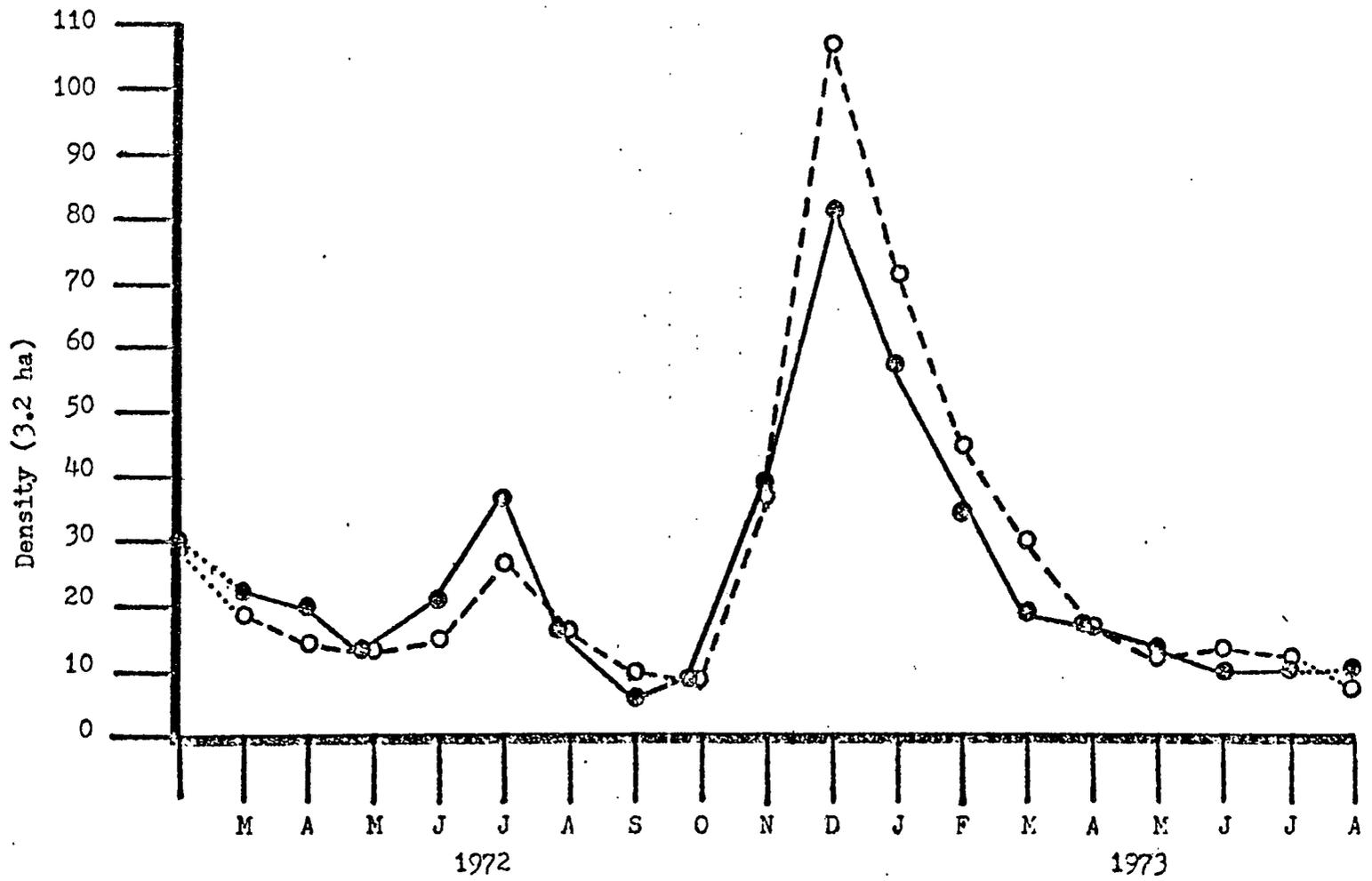


FIGURE 3.

Estimated monthly densities of Reithrodontomys (pooled sexes) for the control plots containing both Reithrodontomys and Sigmodon (broken line), and the experimental plots containing Reithrodontomys with Sigmodon removed (solid line). Densities are expressed for the pooled replicates of similarly manipulated plots (3.2 ha).



corresponding values of K_S/K_T and K_T/K_S , were calculated using the pooled density values pooled over sexes (Table II).

Disregarding the numerical values, the interaction coefficients (α and β) reflected both positive and negative signs during the months of the study. However, the majority of the monthly coefficients were negative, especially for the effects of Reithrodontomys on Sigmodon. The data not only fits the coexistence model of the Volterra equations (Case II, $\alpha < K_1/K_2$, $\beta < K_2/K_1$) during every month of the study, but seem to indicate facilitation between these species! Additional tests will help to make these interactions clearer.

A Wilcoxon matched-pairs signed-rank test (Siegel, 1956) was used to test the null hypothesis that Sigmodon densities in the N_S and K_S plots were not consistently different in relation to each other $[H_0: p(N_S > K_S) = p(N_S < K_S)]$. Since a directional difference between N_S and K_S could not be predicted, a priori, a two-tailed region of rejection was used. A significant departure from equality was found ($T_{(16)} = 6.5$; $P < 0.001$). The alternative hypothesis, that the density patterns of the N_S and K_S populations showed a consistent difference in ordinal relationship through time, was accepted $[H_1: p(N_S > K_S) \neq p(N_S < K_S)]$. Inspection of the data in Figure 2 shows the N_S densities (Sigmodon with Reithrodontomys present) were consistently higher than the K_S densities (Sigmodon, with Reithrodontomys absent). The reverse was true only during June 1972. These results indicate the presence of Reithrodontomys has a facilitative effect upon Sigmodon density, ($N_S/K_S > 1$), and

TABLE II

DENSITY ESTIMATES OF ALPHA (EFFECT OF AN INDIVIDUAL REITHRODONTOMYS UPON SIGMODON) AND BETA (EFFECT OF AN INDIVIDUAL SIGMODON UPON REITHRODONTOMYS) AND A COMPARISON OF THESE VALUES TO THE RELATED RATIOS OF THE MONTHLY CARRYING CAPACITIES OF THE TWO SPECIES. K_s AND K_r ARE EXPRESSED AS ESTIMATED DENSITIES (SEE TEXT).

<u>MONTH</u>	<u>ALPHA</u>	<u>K_s/K_r</u>	<u>BETA</u>	<u>K_r/K_s</u>
February 1972	-0.07 ¹	0.97 ¹	+0.03 ¹	1.04 ¹
March	-0.26	0.96	+0.12	1.05
April	-0.14	0.85	+0.32	1.18
May	-0.77	1.85	0.00	0.54
June	+0.27	1.62	+0.20	0.62
July	-0.15	0.50	+0.46	2.00
August	-0.31	0.19	0.00	5.33
September	-1.14	1.67	-0.06	0.60
October	-0.89	3.33	0.00	0.30
November	-0.06	1.00	+0.05	1.00
December	-0.04	0.42	-0.66	2.38
January 1973	-0.03	0.37	-0.61	2.71
February	-0.13	0.44	-0.52	2.27
March	-0.23	0.63	-0.58	1.58
April	-0.27	0.47	0.00	2.14
May	-0.09	0.67	+0.11	1.50
June	-1.25	1.63	-0.14	0.62
July	-0.80	1.00	-0.13	1.00
August	-0.43 ¹	0.73 ¹	+0.36 ¹	1.38 ¹

¹ Density estimates (MNKA) cannot be used for these months, and these data are not included in the analysis.

appears to be responsible for negative α 's (effect of Reithrodontomys on Sigmodon) recorded throughout the study (Table 2).

A Wilcoxon's matched-pairs signed-rank test also was used to test for significant differences between the Reithrodontomys densities in the N_r (Sigmodon present) and K_r (Sigmodon absent) plots ($T_{(13)} = 37.5$; $P > 0.50$). No consistent trend in ordinal differences between these densities was found. Hence, the null hypothesis was accepted in this case $[H_0: p(N_r > K_r) = p(N_r < K_r)]$. From these data, it was impossible to determine an overall effect of Sigmodon upon Reithrodontomys, but, again some evidence of facilitation was present (approximately half of the measured β 's were negative). This interaction form appears to be especially true during the months of highest Reithrodontomys densities (Figure 3, Table 2).

The monthly densities of each species (N_s , K_s , N_r , and K_r), the interaction coefficients (α and β), and the effect of time (T) were compared in pair-wise fashion, using Pearson's product-moment correlation analysis (Sokal and Rohlf, 1969) (Table 3). Time was treated as a vector of integers beginning with the first monthly measure of the perturbed effects (March 1972 = 1) and terminating with the last month of density estimation (July 1973 = 17). Four significant comparisons were found and suggest the following relationships for the densities of Sigmodon and Reithrodontomys under control and single-species conditions:

- (1) β was negatively (inversely) correlated with N_r . The effect of Sigmodon on Reithrodontomys became negative and more intense in this direction as the density of Reithrodontomys in the control plots increased. This is readily seen in Figure 3,

TABLE III

CORRELATION MATRIX OF THE MONTHLY DENSITIES OF SIGMODON AND REITHRODONTOMYS. ESTIMATED PARAMETERS COMPARED ARE TIME (T), THE EFFECT OF AN INDIVIDUAL REITHRODONTOMYS UPON SIGMODON (α), THE EFFECT OF AN INDIVIDUAL SIGMODON UPON REITHRODONTOMYS (β), MONTHLY DENSITIES OF SIGMODON IN THE CONTROL PLOTS (Ns), MONTHLY DENSITIES OF REITHRODONTOMYS IN THE CONTROL PLOTS (Nr), MONTHLY DENSITIES OF SIGMODON IN THE PLOTS WHERE REITHRODONTOMYS WAS REMOVED (Ks), MONTHLY DENSITIES OF REITHRODONTOMYS IN THE PLOTS WHERE SIGMODON WAS REMOVED (Kr).

	<u>T</u>	α	β	<u>Ns</u>	<u>Nr</u>	<u>Ks</u>	<u>Kr</u>
<u>T</u>	1	-.210	-.453	-.277	.109	-.381	.045
α	ns	1	.038	-.042	.450	.310	.568
β	ns	ns	1	.026	-.605	.128	-.400
<u>Ns</u>	ns	ns	ns	1	.355	.918	.388
<u>Nr</u>	ns	ns	**	ns	1	.422	.967
<u>Ks</u>	ns	ns	ns	***	ns	1	.511
<u>Kr</u>	ns	*	ns	ns	***	ns	1

ns = nonsignificant (P 0.05); * = P 0.05; ** = P 0.01; *** = P 0.001.

where Reithrodontomys reflected two density peaks during the study. The minor spring peak shows a higher density in the K_r populations. The major fall peak (approximately four times the magnitude of the spring peak) shows a higher density in the control populations (N_r). Comparison of harvest mouse densities suggests the presence of Sigmodon has a positive effect during times of high density, similar to the significant facilitative effect that Reithrodontomys has upon Sigmodon ($N_r/K_r > 1$).

(2) α was positively correlated with K_r . The effect of Reithrodontomys upon Sigmodon decreased as the density of Reithrodontomys increased under single species conditions. K_r densities were higher than N_r densities in the spring. The reverse was true during the fall peak (Figure 3). These harvest mouse peaks occurred immediately following the peaks and initial declines of the cotton rat peaks. Most of the monthly α values were negative. However, they approached closer to zero as the K_r densities increased. Hence, less facilitation of Sigmodon by Reithrodontomys occurred as the Reithrodontomys densities rose. But, as previously shown, more facilitation of Reithrodontomys by Sigmodon occurred as Reithrodontomys rose.

(3) N_s was positively correlated with K_s . Assuming the densities of Sigmodon in the control plots were at equilibrium with the environment during all months of the study, the high correlation found between these control populations

and the Sigmodon populations under single-species conditions implies the Ks populations were also at equilibrium. Although the matched-pairs signed-rank test between the two conditions indicates the two densities are at significantly different levels, evidence here indicates that the perturbed Sigmodon populations maintained an equilibrium state after the removal of Reithrodontomys was initiated.

(4) Nr was positively correlated with Kr. As with Sigmodon, it is assumed the monthly Reithrodontomys densities under the control conditions are in equilibrium with the environment. The significant correlation between the Nr and Kr densities implies that the single species populations were also in equilibrium.

Population Biomass Responses

Population biomass estimates for Sigmodon and Reithrodontomys, under Ns and Ks conditions, were obtained by first multiplying the monthly density estimate per sex of each species by the corresponding mean weights of the raw monthly samples. Then male and female data under each experimental condition were pooled. The monthly biomass responses of Sigmodon: Figure 4 (pooled sexes), and Appendices i (males) and ii (females); and Reithrodontomys: Figure 5 (pooled sexes), and Appendices iii (males) and iv (females) . Monthly values of α and β , along with corresponding values of Ks/Kr and Kr/Ks, were calculated using the pooled biomass values (Table 4).

FIGURE 4.

Monthly population biomass of Sigmodon (sexes pooled) for the control plots containing both Sigmodon and Reithrodontomys (broken line), and the experimental plots containing Sigmodon with Reithrodontomys removed (solid line). With one exception (July 1972), Sigmodon reflected a higher monthly population biomass in the presence of Reithrodontomys. Population biomass is expressed for the pooled replicates of similarly manipulated plots (3.2 ha).

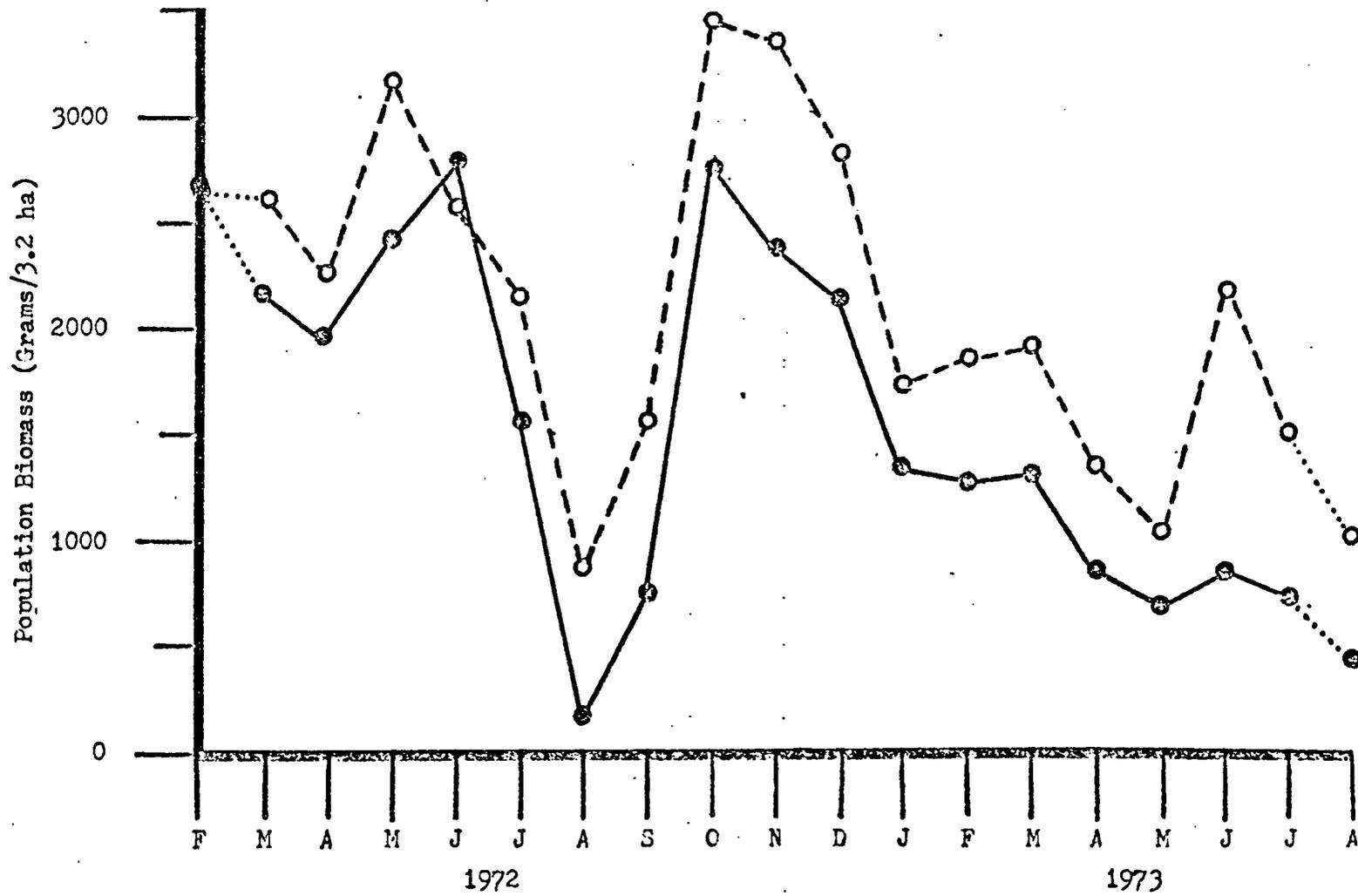


FIGURE 5.

Monthly population biomass of Reithrodontomys (sexes pooled) for the control plots containing both Reithrodontomys and Sigmodon (broken line), and the experimental plots containing Reithrodontomys with Sigmodon removed (solid line). Population biomass is expressed for the pooled replicates of similarly manipulated plots (3.2 ha).

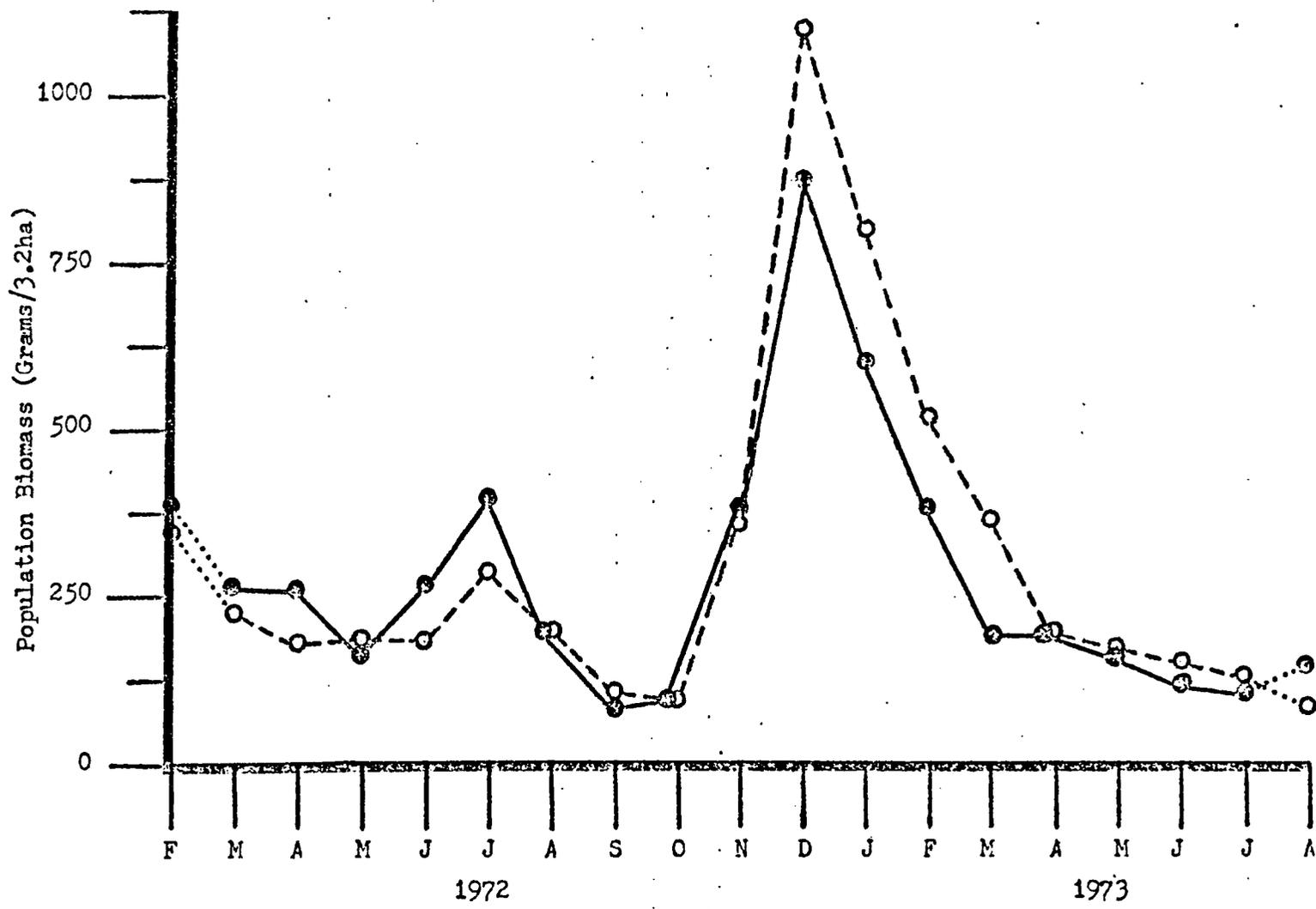


TABLE IV

BIOMASS ESTIMATES OF ALPHA (EFFECT OF AN INDIVIDUAL REITHRODONTOMYS UPON SIGMODON) AND BETA (EFFECT OF AN INDIVIDUAL SIGMODON UPON REITHRODONTOMYS) AND A COMPARISON OF THESE VALUES TO THE RELATED RATIOS OF THE MONTHLY CARRYING CAPACITIES OF THE TWO SPECIES. K_s AND K_r ARE EXPRESSED AS ESTIMATED BIOMASSES IN GRAMS (SEE TEXT).

<u>MONTH</u>	<u>ALPHA</u>	<u>K_s/K_r</u>	<u>BETA</u>	<u>K_r/K_s</u>
February 1972	+0.13 ¹	7.01 ¹	+0.02 ¹	0.14 ¹
March	-2.05	8.02	+0.02	0.13
April	-1.64	7.47	+0.04	0.13
May	-4.15	14.27	-0.01	0.07
June	+1.18	10.33	+0.04	0.10
July	-2.02	3.94	+0.05	0.25
August	-3.54	0.88	+0.01	1.13
September	-6.62	9.45	-0.02	0.11
October	-6.94	28.62	0.00	0.04
November	-2.75	6.25	+0.01	0.16
December	-0.61	2.49	-0.08	0.40
January 1973	-0.50	2.26	-0.12	0.44
February	-1.12	3.40	-0.07	0.29
March	-1.67	6.18	-0.08	0.16
April	-2.66	4.54	-0.01	0.22
May	-2.26	4.36	+0.01	0.23
June	-9.54	8.95	-0.02	0.11
July	-7.65	7.93	-0.01	0.13
August	-7.26 ¹	3.08 ¹	+0.06 ¹	0.33 ¹

¹Biomass estimates cannot be made for these months, and these data are not included in the analysis.

TABLE V

CORRELATION MATRIX OF THE MONTHLY BIOMASSES OF SIGMODON AND REITHRODONTOMYS. ESTIMATED PARAMETERS COMPARED ARE TIME (T), THE EFFECTS OF AN INDIVIDUAL REITHRODONTOMYS UPON SIGMODON (α), THE EFFECT OF AN INDIVIDUAL SIGMODON UPON REITHRODONTOMYS (β), MONTHLY DENSITIES OF SIGMODON IN THE CONTROL PLOTS (N_s), MONTHLY DENSITIES OF REITHRODONTOMYS IN THE CONTROL PLOTS (N_r), MONTHLY DENSITIES OF SIGMODON IN THE PLOTS WHERE REITHRODONTOMYS WAS REMOVED (K_s), MONTHLY DENSITIES OF REITHRODONTOMYS IN THE PLOTS WHERE SIGMODON WAS REMOVED (K_r).

	<u>T</u>	α	β	<u>N_s</u>	<u>N_r</u>	<u>K_s</u>	<u>K_r</u>
<u>T</u>	1	-.346	-.447	-.407	.106	-.551	.085
α	ns	1	-.098	.012	.512	.319	.628
β	ns	ns	1	.086	-.715	.162	-.470
<u>N_s</u>	ns	ns	ns	1	.131	.916	.210
<u>N_r</u>	ns	*	**	ns	1	.147	.950
<u>K_s</u>	*	ns	ns	***	ns	1	.273
<u>K_r</u>	ns	**	*	ns	***	ns	1

ns = nonsignificant (P 0.05); * = P 0.05; ** = P 0.01; *** = P 0.001.

Generally, differences between populations existing under single-species and mixed-species (control) conditions may be reflected by either numerical changes, biomass changes, or both. In the present study numerical differences between K and N plots were closely paralleled by biomass differences, i.e., the interaction coefficients (α and β) reflected both positive and negative values and supported the necessary requirements for coexistence between Sigmodon and Reithrodontomys (Case II; Slobodkin, 1961). Also, as with density, a Wilcoxon's matched-pairs signed-rank test of population biomass responses for Sigmodon showed a significant trend toward higher monthly biomasses when Reithrodontomys was present ($T_{(13)} = 1.0$; $P < 0.001$). The comparison between the N and K Reithrodontomys populations reflected a nonsignificant difference over time ($T_{(15)} = 51.0$; $P > 0.50$) similar to that obtained for density, but the negative β reveal that there is some facilitation during certain times of year.

Pearson's product-moment correlation analysis was used to test for relationships between the month population biomass responses of Sigmodon and Reithrodontomys under single and mixed-species conditions, the interaction coefficients, and time. The six significant comparisons (Table 5) suggest the following relationships for the monthly population biomasses of Sigmodon and Reithrodontomys under single-species and control conditions:

- (1) K_s negatively (inversely) correlated with time (T).

The study extended over a period of 18 months. Therefore, any short period (e.g. seasonally directed) relationships may be phased out of the final analysis, since Sigmodon went through three complete oscillations of density and

biomass, and Reithrodontomys two. The inverse relationship between the duration of the study and the Sigmodon populations in the plots where Reithrodontomys was absent resulted from an increased dampening in the biomass of these populations through time (Figure 4). This was especially evident during the spring 1973 peak, which showed an increase in the biomass of the control populations but no increase in the single species populations. Density responses for this group did show enough of an increase during this period to maintain a nonsignificant relationship with time.

(2) β negatively correlated with K_r . The effect of Sigmodon upon Reithrodontomys varied between positive and negative effects throughout the study. During the relatively brief spring peak, when the single species harvest mouse populations were greater than the control populations, the values of β were positive. However, during the larger fall peak Reithrodontomys monthly biomass was greater in the control plots. As with the numerical responses, it appears that during times of large biomass increases, Sigmodon has a facilitative effect on Reithrodontomys ($N_r/K_r > 1$).

(3, 4, 5, and 6) The following significant relationships for biomass were also found during the density analysis, and the implications of these were discussed in the previous section (Numerical Responses).

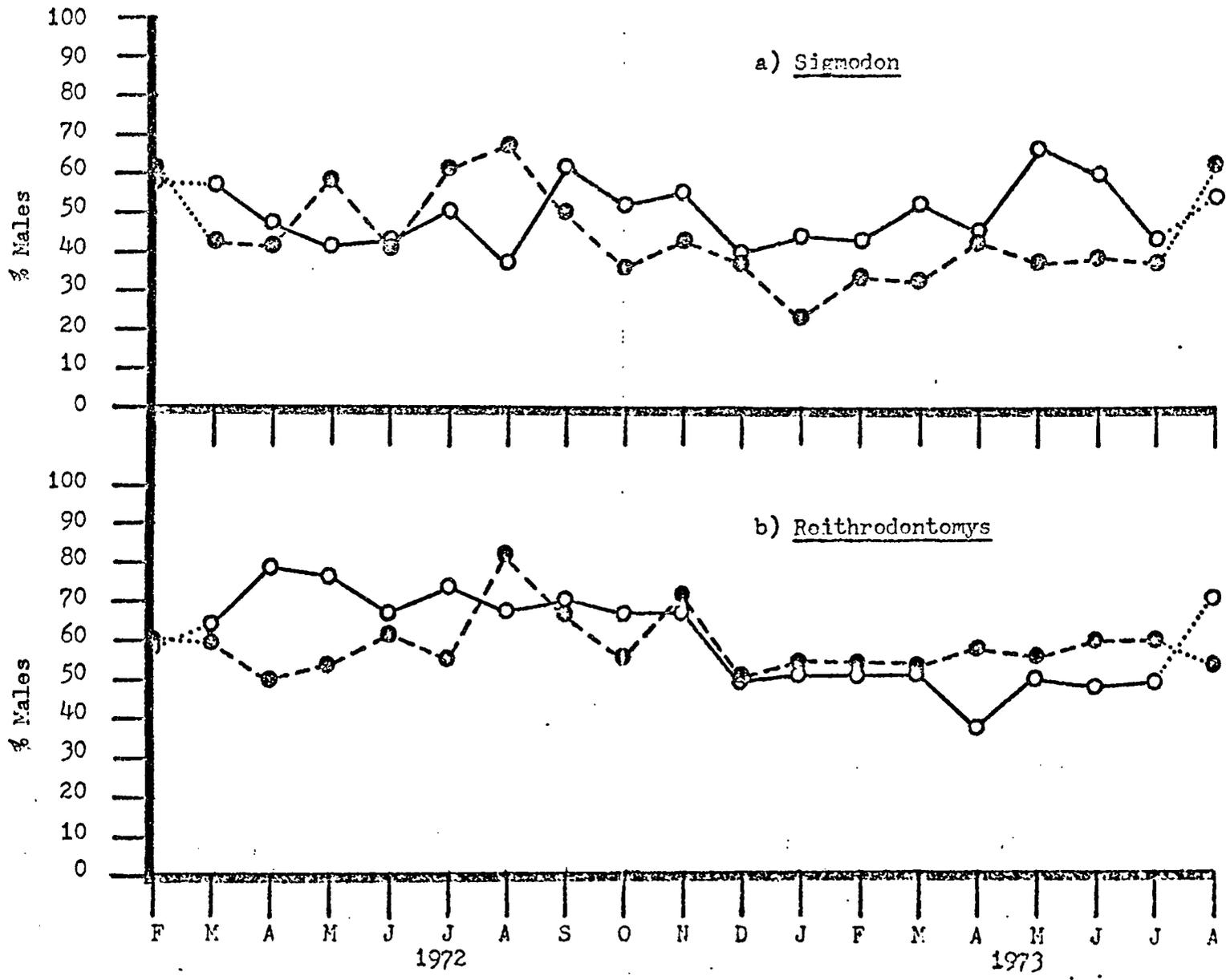
- (a) β negatively correlated with N_r .
- (b) α positively correlated with K_r .
- (c) N_s positively correlated with K_s .
- (d) N_r positively correlated with K_r .

Sex Ratio Responses

Consideration of population sex ratio is important in determining if the experimental manipulations differentially selected toward males or females. Changes in sex ratio for small mammals are often difficult to explain due to small sample sizes typically encountered while using these systems as experimental models (Myers and Krebs, 1971). Although partially offset by the precise trapping routine, the same problem arose during the present study. Nevertheless, exploration of sex ratio is valuable to determine if experimental manipulations were sex selective for either species. Monthly comparisons of sex ratios were made of each species between the N and K situations (Sigmodon: Figure 6a and Appendices v and vi; Reithrodontomys: Figure 6b and Appendices vii and viii). These comparisons, using the chi-square tests of independence, tested the null hypothesis that there was no change in sex ratio between plot conditions [2 x 2 Tables: sexes (males-females) X experimental condition (N - K)]. Even if it is assumed that the sex ratio at birth is 50:50, a universal strategy argued by Fisher (1958), there is no reason to expect that a given species will maintain this ratio within the free-living adult population (Joule and Jameson, 1972).

FIGURE 6a AND 6b.

Monthly sex ratios of Sigmodon (a) and Reithrodontomys (b) for the pooled control (broken lines) and pooled experimental (solid lines) plots.



Hence, a test of independence, rather than goodness of fit test, allows the detection of changes without relying on implied expectations. No significant differences in sex ratio were found for the monthly comparisons of either species, so the null hypothesis was accepted $[H_0: \text{sex ratio (N)} = \text{sex ratio (K)}]$. If these proportions of males and females were to remain constant with an increase in sample size, significant differences could be detected, consistent with the simulations by Myers and Krebs (1971).

A sign test (binomial) of the relative percentage of males per species for the two experimental conditions was used to test the null hypothesis that there was no significant difference between the N and K populations throughout time $[H_0: p(\text{per cent males}(N > K)) = p(\text{per cent males}(N < K))]$. Since the direction of difference could not be predicted, a priori, a two-tailed test was used. A significant difference was found over the seventeen months of data for Sigmodon per cent males $(N_S > K_S) = 13$, per cent males $(N_S < K_S) = 3$; $P < 0.05$, and the alternative hypothesis that the control (N_S) plots maintained a consistently higher proportion of males, especially evident toward the end of the experiment, was accepted. For Reithrodontomys, a consistent difference between the N and K plots over the months of the study was found per cent males $[(N_R > K_R) = 8, \text{ per cent males } (N_R < K_R) = 8; p = 0.40]$. The null hypothesis of equality through time could not be rejected.

The significant differences in per cent males for the N and K Sigmodon populations is easily seen by inspecting the relative behavior of the two curves from September 1972 through the termination of the study

(Figure 6a). After August 1972, the percentage of males in the Ns plots rose above that of the Ks plots (Figure 6a). During this period, the pooled monthly minimum number known alive in the control plots were 125 males and 127 females. Over the same period, the sum of these monthly densities for Sigmodon in the plots where Reithrodontomys was removed (Ks plots) were 73 males and 118 females. This represents a difference of 52 males but only 9 females between the two experimental groups, leading to a significant difference in the pooled percentages of males between the groups ($\chi^2(1) = 5.24; P < 0.05$). Over the same period, the pooled samples for Reithrodontomys yielded 181 males and 160 females in the control plots, compared with 157 males and 120 females in the plots where Sigmodon had been removed. A nonsignificant difference was reflected between the pooled samples of the two experimental conditions ($\chi^2(1) = 0.66; P > 0.50$).

Estimated Survivorship

Individual survival for each species under the two types of experimental conditions was calculated by summing over the total number of months a particular individual was known to be alive. The period, in months, between individual recruitment (first capture = birth or immigration) and loss (last capture = death and emigration) was considered to be that individual's survival on a given plot. Each time an individual was captured and released, survival was assumed to extend into the next month. Hence, survival time is reported as the period between two sampling periods. Individuals known to be alive during the first sampling period (February 1972) and

FIGURE 7a AND 7b.

Survivorship curves for Sigmodon males (a) and females (b) for the pooled control (broken lines) and pooled experimental (solid lines) plots. The mean survivorship (months) for each curve is also given.

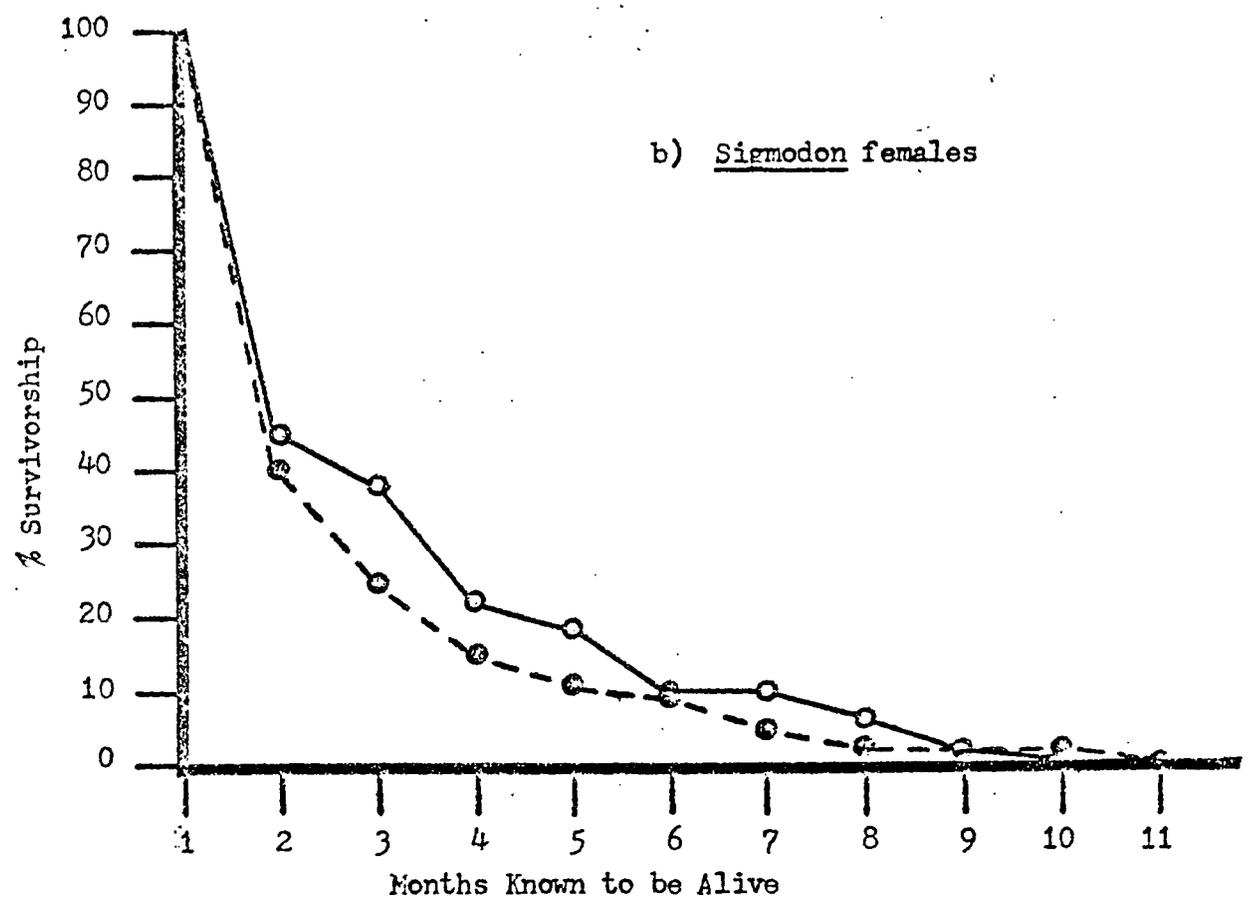
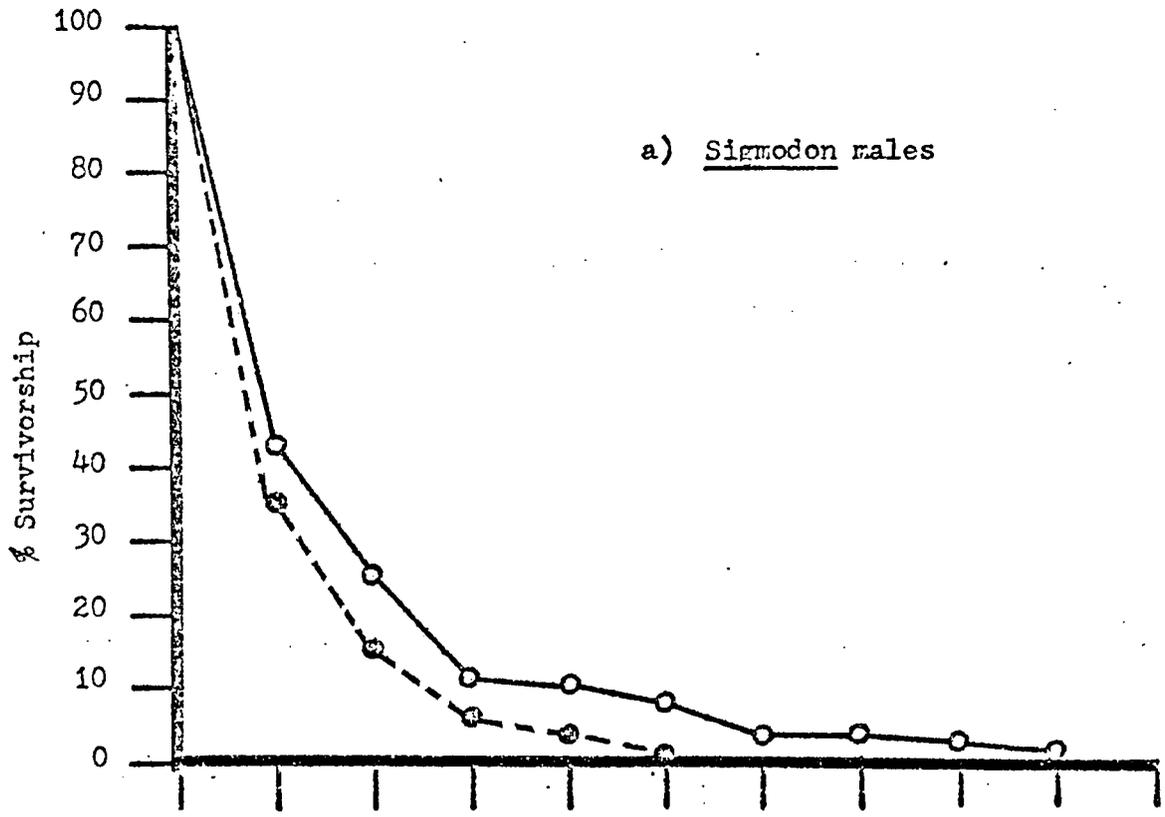
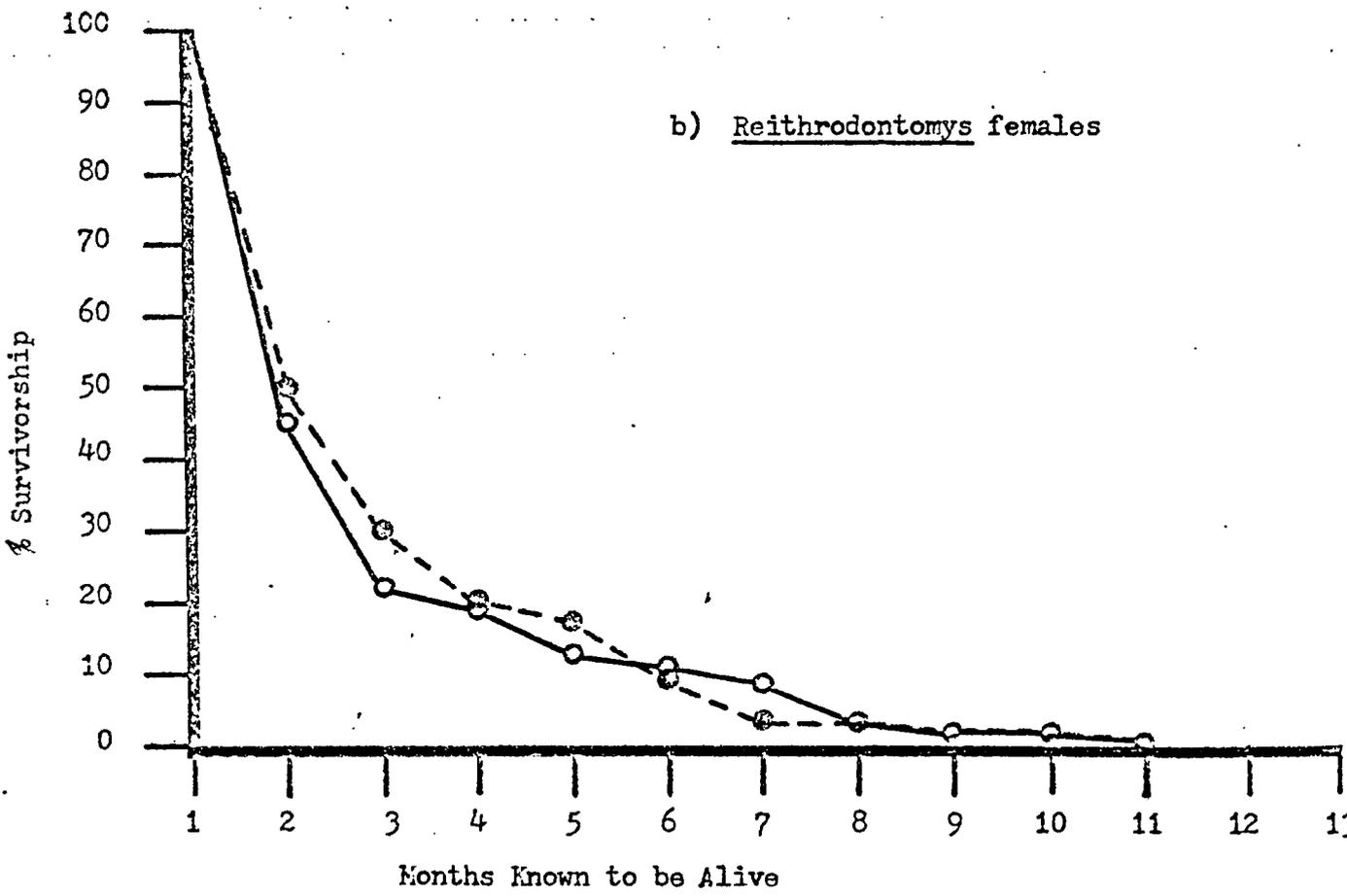
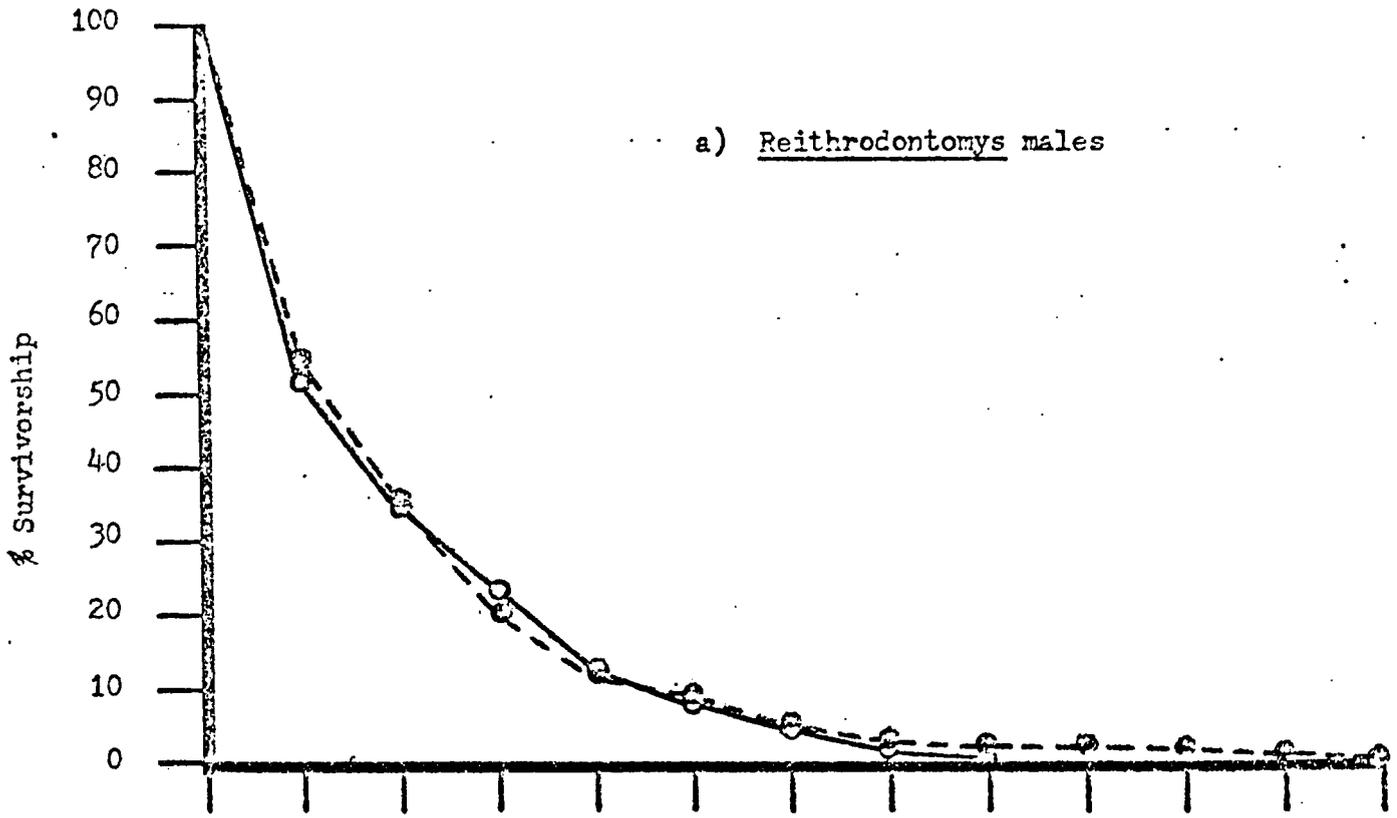


FIGURE 8a AND 8b.

Survivorship curves for Reithrodontomys males (a) and females (b) for the pooled control (broken lines) and pooled experimental (solid lines) plots. The mean survivorship for each curve is also given.



those known to be alive at the termination of the study (August 1973) were not included in the analysis. Only those individuals that appeared and disappeared during the months of the study were considered. No individual of either species survived throughout the entire study.

Survivorship in Sigmodon hispidus populations under the experimental and control conditions is given in Figure 7a and Appendix vii (males), and Figure 7b and Appendix viii (females). Comparisons between survival in the N and K plots were not significantly different for males or females (Kolmogorov-Smirnov tests, Sokal and Rohlf, 1969). However, it should be noted that the cumulative death frequencies of males inhabiting the plots where Reithrodontomys was removed were greater during each month than those of the control populations (Reithrodontomys present). Also, the longest period of survival for an individual in the K_S plots was 5-6 months, while two individuals in the control plots survived past eight months. Individual survival times for Sigmodon females was about the same between the two types of plot conditions.

Survival of Reithrodontomys is given in Figure 8a and Appendix ix (males), and Figure 8b and Appendix x (females). Comparisons between the curves of the two conditions were not significantly different for either sex (Kolmogorov-Smirnov tests, Sokal and Rohlf, 1969). However, none of the males on the control plots survived past the eighth month, while on the K_R plot (Sigmodon absent) two males survived past the eleventh month. Individual survival times for the females were about the same under both conditions. Hence, individual animals appeared to have equal survivorship.

Using monthly intervals as age units, both species reflected Type III survivorship curves (Slobodkin, 1961), wherein there is a high probability of death throughout ages for a given individual.

Size (Age) Class Distributions

Cotton rat age class during a given month of the study were estimated from size (body weight). This was done using the criteria of Odum (1955): 0-59.99 grams = juveniles and subadults (nonbreeders), 60-109.99 grams = young adults (active during one breeding period), 110+ grams = old adults. For each month, each experimental condition yielded a raw sample cohort of individuals which could be placed into one of these three categories. The frequencies of each age group throughout the study is given in Figure 9a (control populations), Figure 9b (perturbed populations, Reithrodontomys removed), and Appendix viii (both kinds of populations). Sexes were pooled during each month. The appearance of juveniles and subadults (on-set of spring breeding) was the same for both conditions in the spring of 1972 (May). Although both populations went through the predictable summer decline in density, the occurrence of juveniles persisted on the plots where Reithrodontomys was removed, while in the control plots breeding appears to have subsided.

Harvest mouse age classes during a given month were also estimated by size criteria: 0-8.99 grams = juveniles and subadults (nonbreeders), 9.00-11.99 = young adults (first time breeders), and 12.00+ = old adults. The frequency of each age group throughout the study is given in Figure 10a (control populations), Figure 10b (perturbed

FIGURE 9a AND 9b.

Monthly size class distributions for Sigmodon (sexes pooled) for the pooled control plots with Reithrodontomys present (a), and the pooled experimental plots with Reithrodontomys absent (b). For both graphs: the lower white area represents the monthly frequency of juveniles and subadults (0.00 - 59.99 grams), the dark area represents the monthly frequency of young adults (60.00 - 109.99 grams), and the upper white area represents the frequency of old adults (110.00+ grams).

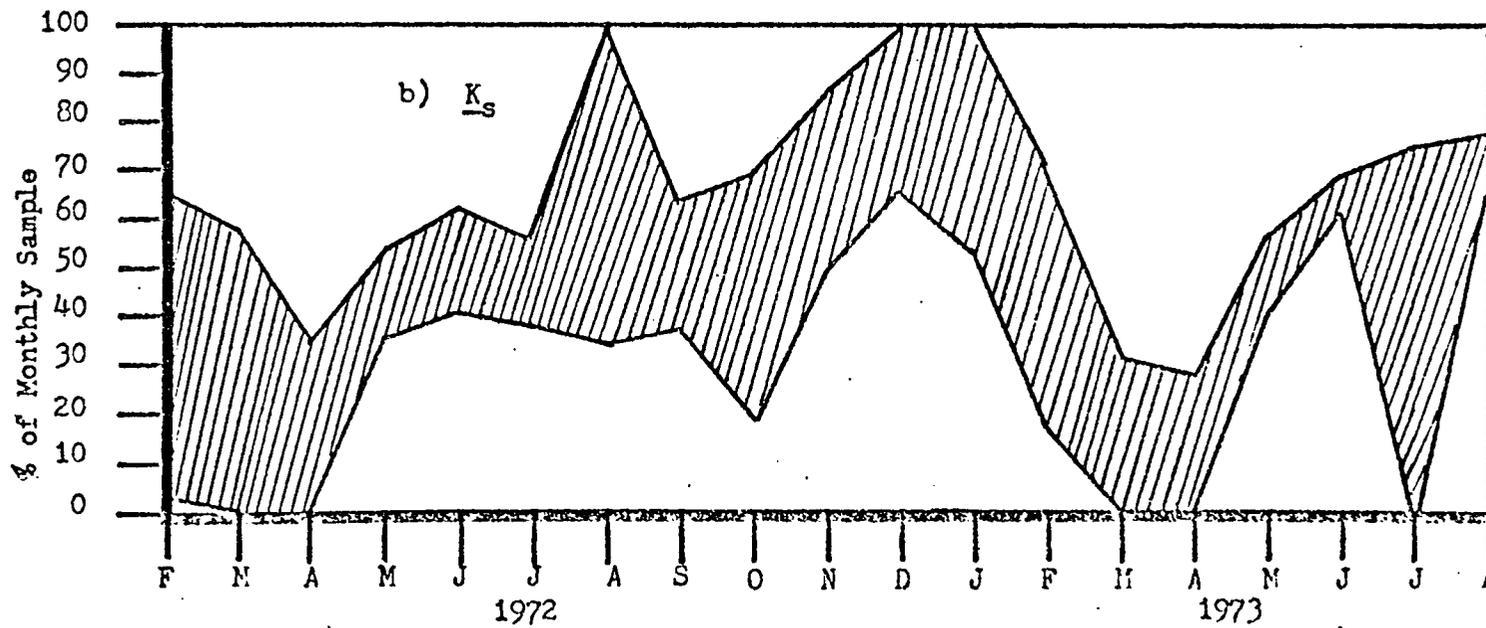
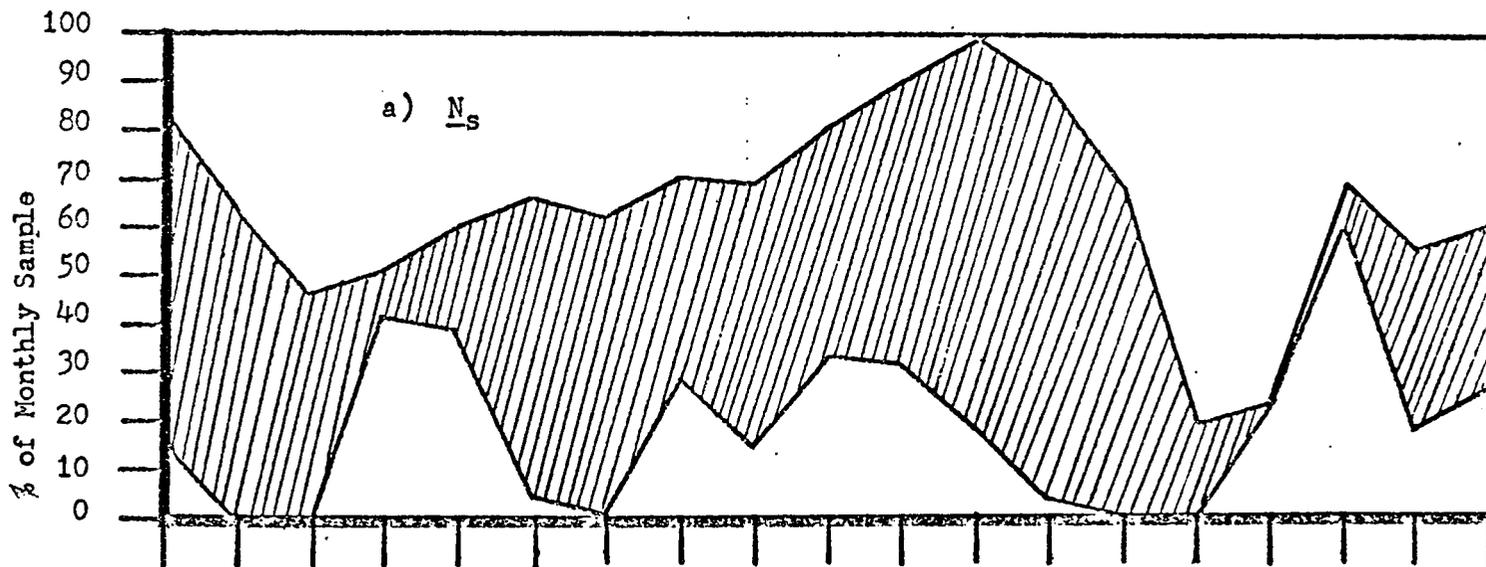


FIGURE 10a AND 10b.

Monthly size class distributions for Reithrodontomys (sexes pooled) for the pooled control plots with Sigmodon present (a), and the pooled experimental plots with Sigmodon removed (b). For both graphs: the lower white area represents the monthly frequency of juveniles and subadults (0.00 - 8.99 grams), the dark area represents the monthly frequency of young adults (9.00 - 11.99 grams), and the upper white area represents the frequency of old adults (12.00+ grams).

populations), and Appendix viii (both populations). Sexes were pooled for each experimental condition during each month. Both populations initiated breeding during the same months throughout the entire study. Differences between the two situations appeared at the onset of fall reproduction in September 1972. This is the period when the control density and biomass became larger than that in the perturbed plots. During September 1972, the control plots contained all old adults and the perturbed plots all young adults. The breeding potential by these separate age classes may have resulted in a greater production of individuals for the next generation in the control plots. Survival in the perturbed plots was slightly higher for both males and females than in the control populations. Whether this small difference led to the wide difference in age class structure of September 1972, will have to be pursued further.

DISCUSSION

Demographic Responses

The annual density pattern of Sigmodon hispidus has been well documented (Odum, 1955; Haines, 1961, 1972; Goertz, 1964, 1965a, b; Chipman, 1966; Wiegart, 1972; Fleharty, et al., 1972; and Joule, 1973). Although these studies were conducted north of the present study (Georgia, central Texas, Oklahoma, and Kansas), all but one reported an annual bimodal density pattern corresponding to that observed during this study. In Kansas, along the northern border of its geographic range, Sigmodon reflects single annual density peak which occurs in late summer and autumn (Fleharty, et al., 1972). The breeding peaks of the present study, one in late spring followed by another in early fall, appear to correspond to the annual temperature pattern (Joule, 1973). The mid-summer and winter depressions occur during the annual high and low temperature extremes. In the northerly portions of its range (see Hall and Kelson, 1954), Sigmodon hispidus spring breeding densities are noticeably smaller than in the fall. In the mid-portion of the range (present study), the spring and fall density peaks were approximately equal (11 per cent of annual density in May 1972 and 13 per cent in November 1972). As Cockrum (1948) and Dunaway and Kaye (1961) have shown, severe winter conditions stress this species along the northern perimeter of its range. Fleharty and Choate (1973) have found evidence of fat cycling during winter conditions in Kansas, and suggest that energy partitioned to combat winter extremes by the northern populations may be utilized for reproductive purposes by the southern populations. This supports evidence that northern populations

exhibit attenuated spring density increases, followed by noticeably larger fall peaks, in response to the harvesting of that summer's primary production.

Reithrodontomys fulvescens also exhibits an annual bimodal density pattern (Packard, 1968; Joule, 1973), with highest densities during December and January. The present study showed a marked difference between the early summer peak (July 1972, 7 per cent of the annual density) and the late-fall peak (December 1972, 28 per cent of the annual density). Other studies have followed the local density patterns of this species with similar results (Joule and Jameson, 1972; Joule and Cameron, 1973). The asynchronous relationship between Sigmodon and Reithrodontomys densities, population biomass, and breeding patterns over months, as are evidenced by nonsignificant correlations in density (Table II), population biomass (Table IV), and differences in monthly age class frequencies (Figures 9a, 9b, 10a, and 10b), indicates that these species may cue on limiting resources which at the same time diminish the probability of interspecific interference.

Significant positive correlations between the monthly densities and population biomass of Sigmodon in the N_S (Reithrodontomys present) and K_S (Reithrodontomys absent) plots were found. Assuming the cotton rat populations in the control plots (N_S) were responding to changes in the environment, the significant correlations between these populations and the perturbed populations (K_S) imply that both were in equilibrium with the environment. This property was maintained, though a significant ordinal difference was found for the month by month relationship between the N_S and K_S curves.

Similarly, positive correlations of Reithrodontomys density and biomass were found when comparing the N_r (Sigmodon present) and K_r (Sigmodon removed) populations. Unlike Sigmodon, the Reithrodontomys N_r and K_r populations did not reflect a significant ordinal difference in amplitude throughout the study. However, during the major breeding peak of late fall 1972, the control populations (N_r) exceeded the densities and population biomass found in the perturbed plots (K_r).

Monthly density and population patterns of Reithrodontomys in the N_r and K_r plots were positively correlated, supporting the assumption that both populations maintained an equilibrium pattern with changes in the environment. A comparison of amplitude between the two types of harvest mouse situations reflect equal periods of density and population biomass superiority. Differences in annual density pattern between the two species may, in part, have been responsible for the detection of a difference in the Sigmodon populations, but not for Reithrodontomys. The cotton rat showed three major oscillations in density during the study while Reithrodontomys showed one major peak (late fall 1972) and one minor peak (late spring 1972). Life history differences may have biased the detection of differences for harvest mice over the same period. If adaptive differences between the control and perturbed situation are manifest at the time of density increase, then Sigmodon had the greater opportunity for reflecting changes during the time of the study.

In the spring of 1973, cotton rat populations inhabiting the perturbed areas (Reithrodontomys removed) showed a very minor increase in density, and no measureable increase in biomass. Also, the cotton rat

populations in these perturbed areas showed a significant inverse relationship of population biomass with time, a property not detected during density analysis. This may be due to the reflection of a greater percentage of juveniles and subadults, as well as the lower survival of males, in these plots. These details imply that the K_s populations may not have reached an adjusted equilibrium level by the termination of the experiment.

Sigmodon sex ratios showed a higher proportion of males in the control populations, when compared with the perturbed populations. This trend became clear during September 1972, and continued to the end of the study (ten months later). Assuming the cotton rat population inhabiting the perturbed areas (Reithrodontomys removed) underwent different selection pressures than the controls, the effect was manifest, in part, in the sex ratio patterns. The intraspecific male agonism of Sigmodon hispidus (Summerlin and Wolfe, 1968; Wolfe and Summerlin, 1970, 1973; Roberts, 1971) leads, in the laboratory, to a dominance hierarchy. The effects of such a hierarchy upon field estimates of population parameters have been discussed by Joule and Cameron (1973) and Wolfe and Summerlin (1973). Also, cotton rat males maintain larger territories and wander more than females in the field (Stickel and Stickel, 1954; Goertz, 1964). One of the potential consequences of the high mobility and hierarchial relationship between males is a polygynous form of mate selection. Giesel (1971) postulated that optimal strategy for a polygynous system introduced to new environmental conditions is for the males to undergo more stringent selection. Holding other life history parameters constant, the disproportionate culling of the

males does not hinder the potential reproductive effort of the next generation. If this culling is too extensive, however, mate selection is hindered due to isolation by distance with the result that reproductive success diminishes.

Reithrodontomys responded differently to removal of the codominant member than did Sigmodon. Both sexes showed similar responses to the density manipulations and the sex ratios of the control and experimental populations did not differ significantly during this study (Figure 6b). During a thirty month study, Packard (1968) did not find a significant departure from a 1:1 ratio for pooled data. Fisler (1971), working with three subspecies (Reithrodontomys megalotus longicaudus, R. raviventris raviventris, and R. r. halicoetes), found a consistent skewness within all populations toward a higher proportion of males. Fisler found the females to be secretive, covering relatively small areas, and suggested an abundance of males are required to inseminate an adequate number of reproductively active females. A similar skewness toward more harvest mouse males was found, at times, in the present study. A study of the movement patterns of R. fulvescens shows the males are mobile throughout all stages of their life span, while most female movement is restricted to the younger age classes (prior to sexual maturity) (Joule, 1973). This dichotomy of behavior is similar to that reported by Fisler (1971) for other species of the genus. There is no reason at present, to believe that the sex ratio of harvest mice is skewed toward more males at birth.

Monthly size (age) class measurements and survivorship patterns of cotton rats corroborated differences in density and biomass patterns

found between the \underline{N}_S and \underline{K}_S plots. Male mean survivorship in the perturbed plots (\underline{K}_S) was lower (not statistically significant) than in the control areas (\underline{N}_S), explaining the lower sex ratio (percent males) found in these plots. The monthly size class structures show the juveniles and subadults (0.0 - 59.99 grams) in the control plots closely follow monthly changes in density and population biomass. This group is well represented during population peaks, but becomes less important during interim declines. However, in the perturbed plots (harvest mice removed) a large proportion of smaller (younger) individuals was present during the mid-summer decline, suggesting that successful breeding continued during this time. Between the spring and fall cotton rat peaks, harvest mice reflect a minor late-spring peak. By continually removing harvest mice from the perturbed Sigmodon populations (\underline{K}_S), the impact of Reithrodontomys upon Sigmodon was altered. Evidence of subadults and juveniles in the perturbed plots during harvest mouse increases in the control plots suggest that the activity of harvest mice normally interferes with and temporarily terminates, in some way, the annual breeding behavior of cotton rats in this particular community.

To summarize, the Sigmodon populations inhabiting the perturbed areas (Reithrodontomys removed) reflected lower densities, population biomass, sex ratios, and survivorship of males than those populations inhabiting the control plots (Reithrodontomys present). These comparisons are evidence of facilitation between Sigmodon and Reithrodontomys. Reithrodontomys populations inhabiting the perturbed areas reflected lower densities and population biomass than the control populations during periods of increased density, further supporting the hypothesis

that the relationship between the two rodents is facilitative.

Interspecific Interactions

Several lines of evidence from the present study suggest the effect of Reithrodontomys on Sigmodon is positive. There is reduced Sigmodon density and biomass when Reithrodontomys is removed. Also, although Reithrodontomys seems to hinder Sigmodon reproduction, the survivorship of Sigmodon males is lower reflecting lower monthly sex ratios when Reithrodontomys is removed. Precise evaluation of the effect of Sigmodon upon Reithrodontomys, however, is still under investigation, although some data from this study (specifically the relationship between N_r and K_r during the fall-winter 1972 density peak) suggests that Reithrodontomys can support higher densities and biomass in the presence of Sigmodon than when Sigmodon is removed. At this point, one of two qualitative descriptions fit the interactions occurring in this codominant rodent system: commensalism (one-way facilitation) or proto cooperation (two-way facilitation). One-way facilitation has been found in an intertidal community of starfish and sea anemones, using similar food resources (Dayton, 1973).

If facilitative relations are important in the Sigmodon-Reithrodontomys sympatric system, then one species is a component of the environmental carrying capacity of the other species and the parameter K (theoretical carrying capacity density or population biomass in the Volterra equations) is not suitably defined for this study. In this study, interspecific interactions were measured by selective removal techniques. Empirical data on species interactions are usually taken by carefully constructed single- and mixed-species

populations in the laboratory where measured supply of limiting resource is provided artificially. These simple systems provide assessments of K unaccompanied by the "noise" of a natural community. If a consumer of a given portion of limited available resource is removed, this should provide an additional portion of this resource for the remaining species and its density and/or population biomass should increase until the new environmental K is reached. This trend did not occur in the present study (see Figures 3, 4, 5, and 6) suggesting that a straight mapping of population (density or biomass) onto available limiting resources (quantity) lacks biological reality due to facilitative relations between Reithrodontomys and Sigmodon. What appears to have been measured is a non-linear relationship of population to carrying capacity, an interaction developed within a complex, biologically-accomodated, stable sere. The parameters measured during this study were the "observed carrying capacities" for Sigmodon and Reithrodontomys with and without their codominant sympatric member being present. These observed K 's were less than the theoretical K due to facilitative relations, hence K in the Volterra equations approaches a theoretical maximum only when both species are present (as they are part of each other's carrying capacity).

Unlike laboratory controlled situations, experimentation with natural populations involves the use of systems which rarely achieve constant, measureable asymptotes of density and/or biomass. The magnitude and direction of the parameters of the environmental hyper-volume (community) are constantly changing, and these changes are met by similar alterations in the properties of the inhabiting populations

(Vandemeer, 1972). Seasonal temperatures, precipitation, annual occurrences of short- and long-day plants, etc. are non-random events onto which resident populations map predictable portions of their adaptive strategies. Among these strategies is the reflection of an equilibrium ensemble of densities (and/or biomass) for each species, moving from predictable state to predictable state. Systems having these dynamic, but predictable, properties are considered stable (Lewontin, 1969). For these cases, the necessary assumptions for equilibrium ($dN_1/dt = dN_2/dt = 0$) must be asserted in a relative sense. Intrinsic changes of this kind are reoccurring systematic changes within a structurally stable community and represent shifts within the conformation limits of a given equilibrium set. Assumptions pertaining to changes in density or biomass are nullified when there is an unpredictable deviation in population behavior, not simply because of an adjustment in the absolute values of the parameters over time.

There are indications that the Sigmodon-Reithrodontomys sympatric system of the present study is in equilibrium even though the long-term trend is oscillatory. Both interaction coefficients were correlated with monthly Reithrodontomys densities and population biomass.

α , the effect of a single Reithrodontomys individual upon Sigmodon, was positively correlated with the monthly Reithrodontomys densities in the perturbed plots. At first, this connection may not be clear, since it involves an interaction between two species coupled with the density pattern of one species in the absence of the other. However, in the mixed-species situation, where the interaction was recorded, the measureable potential for the interaction appears to have been

dissipated. So, this potential must be detected from a parallel single-species situation in which the involved interaction properties have not been diminished. The other statistically significant correlation involving the interaction coefficients showed β (the effect of Sigmodon upon Reithrodontomys) to be inversely (negatively) correlated with N_r . These two correlations of interaction coefficients are inter-related, one showing the potential effects upon Sigmodon and the other showing that the potential effects are masked when the two species are found together. Additionally, relationships involving an inverse (negative) correlation of the harvest mouse biomass in the perturbed plots with β was found. This links the behavior of the two types of harvest mouse populations, further supporting the assumption that an equilibrium state was achieved in the perturbed plots. Here again, the behavior of an interaction measure is coupled with the dynamics of a single species situation.

Recently, Ayala (1969) studied two species of Drosophila in the laboratory, which, apparently overlapping completely in their space and food requirements, coexisted in greater densities and biomass when isolated from one another. Ayala stated that his finding contradicted the "competitive exclusion principle". Several arguments question the validity of this study and its conclusion. Ito (1970) criticized Ayala's rationale of calculating grand means for density and biomass over time and then using these values as instantaneous estimates of N and K . Ayala thereby ignored the implications of variation in density and biomass through time even though such variation was explicit in his reported data. Similarly, Gause (1971) claimed that Ayala had

reported only a portion of the interaction potential between these species since larval interactions had been ignored. In the present study, α and β were calculated from the monthly responses of density and biomass and overall conclusions were drawn from the accumulated evidence of periodic measures of the system rather than from annual average. Hence, the continued contrasts over time between N and K populations of each species led to the conclusions of this study rather than the pooled effects without regard for time. As with Drosophila, Sigmodon and Reithrodontomys have two important life history stages, (a) a pre-weaning (nestling) stage where the individual is subjected to isolation and parental care and (b) a post-weaning (juveniles, sub-adults, adults, and old adults) stage where the individuals have direct access to community resources and the potential for interspecific interaction is present. The post-weaning individual (that portion subject to live-trapping) is the important stage of direct contact between different species, and hence is the appropriate stage to consider in the investigation of interspecific interactions.

Two hypotheses which might explain the mechanism of facilitation between Sigmodon and Reithrodontomys are: (a) Predation - Schnell (1968) has shown predation is a major mortality factor in S. hispidus populations. Choice and relative quantity of rodent prey items of the barred owl (Strix varia) has been preliminarily studied at the Coastal Center. Fresh owl pellets containing the skulls of Sigmodon and Reithrodontomys were examined. Comparison with concurrent trapping records of the rodent populations indicates that the barred owl selects its prey in approximately the same ratio as its occurrence in

the field (reflected by the trapping records). If the total predator impact upon local populations of Sigmodon and Reithrodontomys is as non-selective as that of the barred owl and if predation intensity remains constant over all plots regardless of the experimental conditions, then single-species (perturbed) populations would be subject to twice the intensity of predation controls. This effectively reduces population size in a K situation to a greater degree than in a N situation and would account for the decreased densities found in K plots.

(b) Interference through intraspecific interaction - Interspecific interactions may enhance a populations performance (facilitation) by serving as a deterrent or buffer to intraspecific strife. Milne (1962) claimed intraspecific competition was the primary density dependent regulating mechanism inherent in populations. Preston (1973) studied interactions between five cohabiting species of coral-dwelling xanthid crabs (Trapezia spp.), inferring the addition of species lessened the intensity of competition (interference) throughout the species composition. In a sympatric two-species mixture the probability of the nearest neighbor being of the same species is lower than in a single species situation. Lessening of conspecific nearest-neighbor meetings dampens the potential for intraspecific interactions. And, even if different species do not actively assert themselves upon one another, their presence offers a break in the conspecific continuum and lessens the intensity of these interactions. Svedsen and Armitage (1973) have likewise cited studies showing many species react more directly to their mirror image (conspecific image) than to other

species. Removal of Reithrodontomys may increase intensity of intra-specific interactions in Sigmodon and may explain the dampening of its density and population biomass.

(c) "Active" facilitation of one species by another species -

Enhancement of food or space resource availability for one species by the presence of another species, to date, has not been measured for small mammals. However, the possibility that such relationships do exist cannot be overlooked.

Elucidation of mechanisms of coexistence and facilitation between these species is currently being investigated. Space utilization can be linked to density and food (energy) to biomass. Since both of these population parameters changed in concert during the present study, questions concerning the precise mechanisms of interaction between Sigmodon and Reithrodontomys are still unanswered. Preliminary studies of food resources (gut analyses) and spatial heterogeneity (Index of Overlap) have failed to provide mechanisms of resource partitioning between these species. One aspect of habitat utilization that has shown promise is temporal partitioning (diel and seasonal). The annual density patterns and daily activity patterns of these species are asynchronous (Joule, 1973; Cameron, unpublished data). In addition, there is rudimentary evidence that Reithrodontomys utilize the vertical component of the habitat by climbing in Baccharis bushes. These modes of habitat utilization and their utility in promoting coexistence are under intensive investigation.

SUMMARY

Species packing and sorting are of primary importance during times of colonization and community construction, but become less important as community regulation moves from physical control and toward biological accommodation. Field studies of small mammals have for the most part studied exclusion mechanisms which fall into the following four categories: (1) observations of same species in different locations, (2) experimental species removal from contiguous allopatric small mammal populations, (3) species additions and rearrangement in areas of contiguous allopatry, and (4) field enclosures containing selected species compositions. Interspecific interactions, commonly referred to as competitive interactions, presume that competing species have a negative effect upon one another. Properties of coexistence (not exclusion) should be of greater interest, from the viewpoint of community dynamics and organization, because mechanisms of coexistence lend insight into higher order interactions and emphasize the roles of species populations within a community.

Using measurements of change in density, population biomass, sex ratio, age class structure, and survivorship, this study characterizes the interspecific relationship between Sigmodon hispidus (the hispid cotton rat) and Reithrodontomys fulvescens (the fulvous harvest mouse) by measuring the changes that take place when the harvest mouse is experimentally removed from the cotton rat's environment, and the changes which take place in the harvest mouse populations when the cotton rat is removed. Since the experiment was conducted under field conditions, population recruitment included birth and emigration, and population loss included death and emigration. The Volterra logistic

equations were modified to include these necessary parameters of natural population. The measured values of α and β , derived from the Volterra equations can be used to qualitatively describe modes of interactions between sympatric species by measuring the N/K relationship for each species: $N/K < 1$ (competition), $N/K > 1$ (facilitation), and $N/K = 1$ (no measurable interaction). Monthly values of density and biomass for Sigmodon and Reithrodontomys recorded under the single- and mixed-species field situations were used to characterize the relationships governing this sympatric system.

Nine small mammals species inhabit the fields at the University of Houston Coastal Center, of which the hispid cotton rat (Sigmodon hispidus) and the fulvous harvest mouse (Reithrodontomys fulvescens) are the most abundant. Six 1.6 ha plots, isolated from one another by 15 meter wide paved roads and paths were live-trapped monthly and the results of density manipulations were measured. Vegetation was homogeneous among plots, each of which contained 81 trap sites in 9 rows of 9 sites each at 15 meter intervals. Each plot was sampled for four days from February 1972 to February 1973, and then for three days throughout the rest of the study, using temporary removal techniques. The plots were sampled for one year prior to the commencement of manipulations, to ensure homogeneity of rodent populations between plots. The roads and paths provided barriers against random movement and allowed discrete populations to be maintained per experimental condition.

Sigmodon showed a significant increase in density and population biomass over time in the presence of Reithrodontomys supporting the hypothesis that interactions between these species are facilitative.

Sigmodon sex ratios reflected a higher proportion of males when Reithrodontomys was present, and this was supported by the increased survivorship of the males under these conditions. Breeding, normally curtailed in mid-summer, remained active for Sigmodon where Reithrodontomys was absent. Sigmodon is presumed to have a polygynous form of breeding behavior. Greater selection against males in the perturbed plots supports this hypothesis.

In contrast to Sigmodon, significant differences between the control and perturbed populations of Reithrodontomys were not reflected throughout the experiment. However, during its annual breeding peak (late fall - winter) Reithrodontomys did reflect facilitated population characteristics in the presence of Sigmodon.

Three hypotheses may explain the facilitative relationships between the cotton rat and the harvest mouse: (1) predation, (2) interference through intraspecific interactions, and (3) "active" facilitation of one species by another species. Mechanisms of coexistence and facilitation between these species are currently being investigated.

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APPENDIX 1

SIGMODON MALES: MONTHLY ESTIMATES OF MINIMUM NUMBER KNOWN TO BE ALIVE (N), MONTHLY MEAN WEIGHTS OF CAPTURED SAMPLES ($\bar{X} \pm$ S.E.), AND ESTIMATED MONTHLY BIOMASSES IN GRAMS ($B = N \times \bar{X}$); AS MEASURED FOR THE POOLED REPLICATES OF THE CONTROL POPULATIONS (REITHRODONTOMYS PRESENT) AND THE PERTURBED POPULATIONS (REITHRODONTOMYS REMOVED).

MONTH	<u>REITHRODONTOMYS</u> PRESENT			<u>REITHRODONTOMYS</u> ABSENT		
	<u>N</u>	$\bar{X} \pm$ S.E.	<u>B</u>	<u>N</u>	$\bar{X} \pm$ S.E.	<u>B</u>
Feb 1972	18 ¹	90.27 \pm 6.85	1625 ¹	18 ¹	103.01 \pm 6.03	1824 ¹
Mar	15	109.10 \pm 6.91	1637	9	121.04 \pm 5.52	1089
Apr	9	118.45 \pm 8.98	1066	7	126.82 \pm 9.59	887
May	14	114.33 \pm 15.03	1601	14	105.10 \pm 16.99	1471
Jun	13	102.55 \pm 15.53	1333	14	94.71 \pm 13.30	1326
Jul	11	108.38 \pm 13.45	1192	11	95.73 \pm 17.08	1053
Aug	3	97.40 \pm 6.18	292	1	62.87 ²	63
Sep	11	87.70 \pm 12.11	965	5	77.93 \pm 22.39	390
Oct	20	90.98 \pm 8.12	1820	11	83.60 \pm 12.09	920
Nov	22	85.69 \pm 6.36	1885	16	63.56 \pm 9.67	1016
Dec	15	85.02 \pm 6.20	1275	13	66.69 \pm 7.29	867

APPENDIX 1 (CONTINUED)

<u>MONTH</u>	<u>REITHRODONTOMYS PRESENT</u>			<u>REITHRODONTOMYS ABSENT</u>		
	<u>N</u>	<u>X ± S.E.</u>	<u>B</u>	<u>N</u>	<u>X ± S.E.</u>	<u>B</u>
Jan 1973	10	88.33 ± 4.55	883	5	68.72 ± 16.69	344
Feb	9	103.93 ± 7.35	935	5	103.32 ± 14.96	517
Mar	10	120.55 ± 8.09	1206	4	122.15 ± 8.43	489
Apr	5	128.25 ± 8.74	641	3	121.24 ± 17.73	364
May	6	111.40 ± 19.89	668	3	66.56 ± 47.43	200
Jun	17	77.59 ± 14.47	1319	5	78.86 ± 24.36	394
Jul	7	104.45 ± 14.34	731	3	107.39 ± 10.78	322
Aug	6 ¹	66.48 ± 37.42	399 ¹	5 ¹	42.74 ± 28.27	214 ¹

¹Raw samples of first and last months of the study. These samples do not fit the density estimator (Minimum Number Known to be Alive), and were not used in the analysis.

²Monthly estimate of mean body weight taken from a single individual.

APPENDIX ii

SIGMODON FEMALES: MONTHLY ESTIMATES OF MINIMUM NUMBER KNOWN TO BE ALIVE (N), MONTHLY MEAN WEIGHTS OF CAPTURED SAMPLES ($\bar{X} \pm$ S.E.), AND ESTIMATED MONTHLY BIOMASSES IN GRAMS ($B = N \times \bar{X}$); AS MEASURED FOR THE POOLED REPLICATES OF THE CONTROL POPULATIONS (REITHRODONTOMYS PRESENT) AND THE PERTURBED POPULATIONS (REITHRODONTOMYS REMOVED).

MONTH	<u>REITHRODONTOMYS</u> PRESENT			<u>REITHRODONTOMYS</u> ABSENT		
	<u>N</u>	$\bar{X} \pm$ S.E.	<u>B</u>	<u>N</u>	$\bar{X} \pm$ S.E.	<u>B</u>
Feb 1972	13 ¹	77.47 \pm 6.19	1007 ¹	11 ¹	77.51 \pm 4.40	853 ¹
Mar	11	89.05 \pm 4.77	979	12	89.02 \pm 5.97	1068
Apr	10	118.89 \pm 7.99	1189	10	107.76 \pm 6.06	1078
May	20	79.07 \pm 12.21	1581	10	93.95 \pm 15.92	940
Jun	17	73.60 \pm 9.98	1251	20	73.60 \pm 9.84	1472
Jul	11	87.47 \pm 8.91	962	7	74.89 \pm 15.89	524
Aug	5	120.31 \pm 11.78	602	2	59.85 ²	120
Sep	7	76.00 \pm 18.57	532	5	73.11 \pm 14.69	366
Oct	18	90.50 \pm 9.24	1629	19	97.66 \pm 8.90	1856
Nov	18	82.90 \pm 9.28	1492	22	62.67 \pm 7.40	1379
Dec	23	67.27 \pm 6.57	1547	21	61.46 \pm 4.56	1291

APPENDIX ii (CONTINUED)

MONTH	REITHRODONTOMYS PRESENT			REITHRODONTOMYS ABSENT		
	N	$\bar{X} \pm S.E.$	B	N	$\bar{X} \pm S.E.$	B
Jan 1973	13	67.01 \pm 3.92	871	16	63.06 \pm 4.44	1009
Feb	12	77.88 \pm 4.51	935	10	77.55 \pm 8.43	776
Mar	9	81.13 \pm 4.01	730	8	104.08 \pm 10.04	833
Apr	6	121.51 \pm 10.75	729	4	128.90 \pm 13.48	516
May	3	129.88 \pm 12.12	390	5	100.62 \pm 31.04	503
Jun	11	79.42 \pm 16.62	874	8	60.32 \pm 19.82	483
Jul	9	97.71 \pm 17.44	879	5	86.13 \pm 22.20	431
Aug	5 ¹	122.89 \pm 16.55	615 ¹	3 ¹	72.30 \pm 29.65	217 ¹

¹Raw samples of first and last months of the study. These samples do not fit the density estimator (Minimum Number Known to be Alive), and were not used in the analysis.

²Monthly estimate of mean body weight taken from a single individual.

APPENDIX III

REITHRODONTOMYS MALES: MONTHLY ESTIMATES OF MINIMUM NUMBER KNOWN TO BE ALIVE (N), MONTHLY MEAN WEIGHTS OF CAPTURED SAMPLES ($\bar{X} \pm \text{S.E.}$), AND ESTIMATED MONTHLY BIOMASSES IN GRAMS (B = $N \times \bar{X}$); AS MEASURED FOR THE POOLED REPLICATES OF THE CONTROL PLOTS (SIGMODON PRESENT) AND THE PERTURBED POPULATIONS (SIGMODON REMOVED).

MONTH	<u>SIGMODON</u> PRESENT			<u>SIGMODON</u> ABSENT		
	<u>N</u>	<u>X ± S.E.</u>	<u>B</u>	<u>N</u>	<u>X ± S.E.</u>	<u>B</u>
Feb 1972	17 ¹	12.35 ± 0.30	210 ¹	18 ¹	12.60 ± 0.43	227 ¹
Mar	12	12.36 ± 0.54	148	13	13.01 ± 0.52	169
Apr	11	12.61 ± 0.25	139	10	13.07 ± 0.41	131
May	10	14.66 ± 0.62	147	7	14.13 ± 0.35	99
Jun	10	12.06 ± 0.79	121	13	11.80 ± 0.52	153
Jul	19	11.09 ± 0.45	211	20	11.75 ± 0.54	235
Aug	11	12.06 ± 0.57	133	13	12.75 ± 0.70	166
Sep	7	10.92 ± 0.39	77	4	13.64 ± 0.60	56
Oct	6	10.32 ± 3.01	62	5	12.19 ± 1.07	61
Nov	24	9.72 ± 0.42	233	27	10.49 ± 0.28	283
Dec	52	10.46 ± 0.24	544	42	10.66 ± 0.25	448

APPENDIX iii (CONTINUED)

MONTH	SIGMODON PRESENT			SIGMODON ABSENT		
	N	$\bar{X} \pm S.E.$	B	N	$\bar{X} \pm S.E.$	B
Jan 1973	36	11.10 \pm 0.19	400	31	10.69 \pm 0.28	331
Feb	23	11.71 \pm 0.22	269	18	11.51 \pm 0.34	207
Mar	15	12.21 \pm 0.31	183	11	11.89 \pm 0.34	131
Apr	6	12.20 \pm 0.49	73	9	13.16 \pm 0.27	118
May	6	13.15 \pm 0.74	79	7	14.07 \pm 0.83	98
Jun	6	11.69 \pm 1.48	70	6	10.91 \pm 1.13	65
Jul	6	11.40 \pm 1.08	68	6	10.93 \pm 0.83	61
Aug	5 ¹	12.46 \pm 1.04	62 ¹	6 ¹	12.25 \pm 0.55	74 ¹

¹Raw samples of first and last months of the study. These samples do not fit the density estimator (Minimum Number Known to be Alive), and were not used in the analysis.

APPENDIX iv

REITHRODONTOMYS FEMALES: MONTHLY ESTIMATES OF MINIMUM NUMBER KNOWN TO BE ALIVE (N), MONTHLY MEAN WEIGHTS OF CAPTURED SAMPLES ($\bar{X} \pm$ S.E.), AND ESTIMATED MONTHLY BIOMASSES IN GRAMS ($B = N \times \bar{X}$); AS MEASURED FOR THE POOLED REPLICATES OF THE CONTROL POPULATIONS (SIGMODON PRESENT) AND THE PERTURBED POPULATIONS (SIGMODON REMOVED).

MONTH	<u>SIGMODON</u> PRESENT			<u>SIGMODON</u> ABSENT		
	<u>N</u>	<u>$\bar{X} \pm$ S.E.</u>	<u>B</u>	<u>N</u>	<u>$\bar{X} \pm$ S.E.</u>	<u>B</u>
Feb 1972	12 ¹	11.12 \pm 0.51	133 ¹	12 ¹	12.92 \pm 0.64	155 ¹
Mar	7	10.80 \pm 0.41	76	9	11.11 \pm 0.54	100
Apr	3	12.69 \pm 0.41	38	10	13.16 \pm 1.06	132
May	3	13.06 \pm 0.69	39	6	11.68 \pm 0.39	70
Jun	5	12.03 \pm 1.14	60	8	14.77 \pm 1.11	118
Jul	7	10.67 \pm 0.66	75	16	10.29 \pm 0.43	165
Aug	5	13.52 \pm 0.72	68	3	13.67 ²	41
Sep	3	11.66 ³	35	2	11.95 ³	24
Oct	3	11.66 ³	35	4	9.36 \pm 1.26	37
Nov	12	10.35 \pm 0.48	124	11	9.08 \pm 0.95	100
Dec	54	10.26 \pm 0.33	554	39	10.75 \pm 0.31	419

APPENDIX iv (CONTINUED)

MONTH	SIGMODON PRESENT			SIGMODON ABSENT		
	N	$\bar{X} \pm S.E.$	B	N	$\bar{X} \pm S.E.$	B
Jan 1973	35	11.53 \pm 0.35	404	26	10.30 \pm 0.30	268
Feb	22	11.23 \pm 0.35	247	16	10.79 \pm 0.36	173
Mar	15	12.36 \pm 0.40	185	8	10.36 \pm 0.62	83
Apr	10	12.34 \pm 0.51	123	7	12.66 \pm 0.57	89
May	6	15.50 \pm 0.39	93	6	12.81 \pm 1.93	77
Jun	7	11.39 \pm 1.18	80	4	14.27 ²	57
Jul	6	10.94 \pm 1.11	66	4	13.38 \pm 0.38	54
Aug	2 ¹	10.82 \pm 0.78	22 ¹	5 ¹	13.16 \pm 0.93	66 ¹

¹Raw samples of first and last months of the study. These samples do not fit the density estimator (Minimum Number Known to be Alive), and were not used in the analysis.

²Monthly estimate of mean body weight taken from a single individual.

³Monthly estimate of mean weight was not obtained from live-trap sample. The estimated mean, in this case, represents a grand mean of the measured weights from the month preceding and following the month in question.

SIGMODON SEX RATIOS PER MONTH AS MEASURED FOR Ns (REITHRODONTOMYS PRESENT) AND Ks (REITHRODONTOMYS REMOVED) CONDITIONS. THE ESTIMATED MINIMUM NUMBER KNOWN TO BE ALIVE IS ALSO GIVEN.

MONTH	Ns		Ks	
	N	% MALES	N	% MALES
Feb 1972	31 ¹	58.1 ¹	29 ¹	62.1 ¹
Mar	26	57.7	21	42.9
Apr	19	47.4	17	41.2
May	34	41.2	24	58.3
Jun	30	43.3	31	41.2
Jul	22	50.0	18	61.1
Aug	8	37.5	3	66.7
Sep	18	61.1	10	50.0
Oct	38	52.6	30	36.7
Nov	40	55.0	38	42.1
Dec	38	39.5	34	38.2
Jan 1973	23	43.5	21	23.8
Feb	21	42.9	15	33.3
Mar	19	52.6	12	33.3
Apr	11	45.5	7	42.9
May	9	66.7	8	37.5
Jun	28	60.7	13	38.5
Jul	16	43.8	8	37.5
Aug	11 ¹	54.5 ¹	8 ¹	62.5 ¹

¹Raw sample data from live-trapping. These months are not used in the analysis.

APPENDIX vi

REITHRODONTOMYS SEX RATIOS PER MONTH AS MEASURED FOR Nr (SIGMODON PRESENT) AND Kr (SIGMODON REMOVED) CONDITIONS. THE ESTIMATED MINIMUM NUMBER KNOWN TO ALIVE IS ALSO GIVEN.

MONTH	Nr		Kr	
	N	% MALES	N	% MALES
Feb 1972	29 ¹	58.6 ¹	30 ¹	60.0
Mar	19	63.2	22	59.1
Apr	14	78.6	20	50.0
May	13	76.9	13	53.9
Jun	15	66.7	21	61.9
Jul	26	73.1	36	55.6
Aug	16	68.8	16	81.3
Sep	10	70.0	9	66.7
Oct	9	66.7	9	55.6
Nov	36	66.7	38	71.1
Dec	106	49.1	81	51.9
Jan 1973	71	50.7	57	54.4
Feb	45	51.1	34	52.9
Mar	29	51.7	19	57.9
Apr	16	37.5	16	56.2
May	12	50.0	13	53.8
Jun	13	47.2	10	60.0
Jul	12	50.0	10	60.0
Aug	7 ¹	71.4 ¹	11 ¹	54.5 ¹

¹Raw sample data from live-trapping. These months are not used in the analysis.

APPENDIX vii

SIGMODON MALES SURVIVORSHIP. REITHRODONTOMYS PRESENT (Ns) AND ABSENT (Ks). FREQUENCIES OF SURVIVORSHIP PER CLASS (MONTHS) WERE POOLED OVER THE NINETEEN MONTHS OF THE STUDY, EXCLUDING THOSE INDIVIDUALS KNOWN TO BE ALIVE DURING THE FIRST SAMPLING PERIOD AND THOSE KNOWN TO BE ALIVE AT THE LAST PERIOD (SEE TEXT).

Survival Time (Months)	Ns		Ks	
	N	cum. freq.	N	cum. freq.
1 - 2	47	57.3	41	65.1
2 - 3	14	74.4	13	85.7
3 - 4	12	89.0	4	92.1
4 - 5	1	90.2	2	95.2
5 - 6	3	93.9	<u>3</u>	100.0
6 - 7	3	97.6	<u>63</u>	
7 - 8	0	97.6		
8 - 9	1	98.8		
9 - 10	<u>1</u>	100.0		
	<u>82</u>			

APPENDIX viii

SIGMODON FEMALE SURVIVORSHIP. REITHRODONTOMYS PRESENT (Ns) AND ABSENT (Ks). FREQUENCIES OF SURVIVORSHIP PER CLASS (MONTHS) WERE POOLED OVER THE NINETEEN MONTHS OF THE STUDY, EXCLUDING THOSE INDIVIDUALS KNOWN TO BE ALIVE DURING THE FIRST SAMPLING PERIOD AND THOSE KNOWN TO BE ALIVE AT THE LAST PERIOD (SEE TEXT).

Survival Time (Months)	Ns		Ks	
	<u>N</u>	<u>cum. freq.</u>	<u>N</u>	<u>cum. freq.</u>
1 - 2	33	55.0	45	60.0
2 - 3	8	68.3	12	76.0
3 - 4	6	78.3	8	86.7
4 - 5	2	81.7	2	89.3
5 - 6	5	90.0	1	90.7
6 - 7	0	90.0	4	96.0
7 - 8	2	93.3	2	98.7
8 - 9	3	98.3	0	98.7
9 - 10	<u>1</u>	100.0	0	98.7
10 - 11	<u>60</u>		<u>1</u>	100.0
			<u>75</u>	

REITHRODONTOMYS MALES SURVIVORSHIP. SIGMODON PRESENT (Nr) AND ABSENT (Kr). FREQUENCY OF SURVIVORSHIP PER CLASS (MONTHS) WERE POOLED OVER THE NINETEEN MONTHS OF THE STUDY, EXCLUDING THOSE INDIVIDUALS KNOWN TO BE ALIVE DURING THE FIRST SAMPLING PERIOD AND THOSE KNOWN TO BE ALIVE DURING THE LAST PERIOD (SEE TEXT).

<u>Survival Time (Months)</u>	<u>Nr</u>		<u>Kr</u>	
	<u>N</u>	<u>cum. freq.</u>	<u>N</u>	<u>cum. freq.</u>
1 - 2	50	49.0	39	45.9
2 - 3	17	65.7	16	64.7
3 - 4	11	76.5	13	80.0
4 - 5	11	87.3	6	87.1
5 - 6	5	92.2	4	91.8
6 - 7	3	95.1	3	95.3
7 - 8	4	99.0	1	96.5
8 - 9	<u>1</u>	100.0	1	97.7
9 - 10	102		0	97.7
10 - 11			0	97.7
11 - 12			1	98.8
12 - 13			<u>1</u>	100.0
			85	

APPENDIX x

REITHRODONTOMYS FEMALES SURVIVORSHIP. SIGMODON PRESENT (Nr) AND ABSENT (Kr). FREQUENCY OF SURVIVORSHIP PER CLASS (MONTHS) WERE POOLED OVER THE NINETEEN MONTHS OF THE STUDY. EXCLUDING THOSE INDIVIDUALS KNOWN TO BE ALIVE DURING THE FIRST SAMPLING PERIOD AND THOSE KNOWN TO BE ALIVE DURING THE LAST PERIOD (SEE TEXT).

Survival Time (Months)	Nr		Kr	
	N	cum. freq.	N	cum. freq.
1 - 2	44	55.0	37	50.0
2 - 3	15	73.8	15	70.3
3 - 4	6	81.3	7	79.7
4 - 5	4	86.3	2	82.4
5 - 6	2	88.8	7	91.9
6 - 7	2	91.3	3	96.0
7 - 8	4	96.3	0	96.0
8 - 9	2	98.8	2	98.7
9 - 10	0	98.8	0	98.7
10 - 11	1	100.0	1	100.0
	<u>80</u>		<u>74</u>	

APPENDIX xi

SIGMODON SIZE CLASSES FROM MONTHLY SAMPLES. 0 - 59.99 (JUVENILES AND SUBADULTS), 60 - 109.99 (YOUNG ADULTS), 110+ (OLD ADULTS); AS USED BY ODUM (1955). MALES AND FEMALES ARE POOLED.

Month	<u>REITHRODONTOMYS PRESENT (N_S)</u>				<u>REITHRODONTOMYS ABSENT (K_S)</u>			
	<u>% of Monthly sample</u>				<u>% of Monthly sample</u>			
	<u>0 - 59.99</u>	<u>60 - 109.99</u>	<u>110+</u>	<u>Total</u>	<u>0 - 59.99</u>	<u>60 - 109.99</u>	<u>110+</u>	<u>Total</u>
Feb 1972	13.3	70.0	16.7	30	3.5	62.1	34.4	29
Mar	0.0	64.0	36.0	25	0.0	58.8	41.2	17
Apr	0.0	46.7	53.3	15	0.0	35.7	64.3	14
May	41.9	9.7	48.4	31	36.4	18.2	45.4	22
Jun	39.3	21.4	39.3	28	42.4	21.2	36.4	33
Jul	4.8	61.9	33.3	21	38.9	16.7	44.4	18
Aug	0.0	62.5	37.5	8	33.3	66.7	0.0	3
Sep	29.4	41.2	29.4	17	37.5	25.0	37.5	8
Oct	14.3	54.3	31.4	35	20.7	48.3	31.0	29
Nov	34.2	44.7	21.1	38	48.7	37.8	13.5	37
Dec	32.4	58.8	8.8	34	65.5	34.5	0.0	29
Jan 1973	19.1	80.9	0.0	21	52.9	47.1	0.0	17
Feb	5.0	85.0	10.0	20	18.2	54.5	27.3	11
Mar	0.0	68.4	31.6	19	0.0	33.3	66.7	9
Apr	0.0	20.0	80.0	10	0.0	28.6	71.4	7
May	25.0	0.0	75.0	8	42.9	14.3	42.9	7
Jun	59.3	11.1	29.6	27	61.5	7.7	30.8	13
Jul	18.8	37.5	43.7	16	0.0	75.0	25.0	8

APPENDIX x11

REITHRODONTOMYS SIZE CLASSES TAKEN FROM MONTHLY RAW DATA. 0 - 8.99 (JUVENILES AND SUBADULTS), 9 - 11.99 (YOUNG ADULTS), 12+ (OLD ADULTS). TOTAL IS THE RAW CAPTURE SAMPLE PER MONTH. MALES AND FEMALES ARE POOLED.

Month	<u>SIGMODON PRESENT (N_r)</u>				<u>SIGMODON ABSENT (K_r)</u>			
	<u>% of Monthly sample</u>				<u>% of Monthly sample</u>			
	<u>0 - 8.99</u>	<u>9 - 11.99</u>	<u>12+</u>	<u>Total</u>	<u>0 - 8.99</u>	<u>9 - 11.99</u>	<u>12+</u>	<u>Total</u>
Feb 1972	3.6	53.6	42.9	28	0.0	33.3	66.7	9
Mar	5.9	47.1	47.1	17	0.0	52.3	47.6	21
Apr	0.0	18.2	81.8	11	0.0	33.3	66.7	15
May	0.0	0.0	100.0	7	0.0	22.2	77.8	9
Jun	8.3	25.0	66.7	12	11.1	27.8	61.1	18
Jul	20.0	44.0	36.0	25	18.8	46.9	34.4	32
Aug	0.0	38.5	61.5	13	0.0	27.3	72.7	11
Sep	0.0	100.0	0.0	4	0.0	0.0	100.0	3
Oct	33.3	33.3	33.3	3	16.7	33.3	50.0	6
Nov	35.5	45.2	19.3	31	25.7	54.3	20.0	35
Dec	21.1	58.7	20.2	104	18.9	52.7	28.4	74
Jan 1973	1.5	66.2	32.4	68	14.3	71.4	14.3	49
Feb	5.0	67.5	27.5	40	4.0	68.0	28.0	25
Mar	0.0	44.0	56.0	25	0.0	76.9	23.1	13
Apr	0.0	40.0	60.0	10	0.0	18.2	81.8	11
May	0.0	12.5	87.5	8	12.5	0.0	87.5	8
Jun	11.1	33.3	55.6	9	16.7	16.7	66.7	6
Jul	14.3	42.9	42.9	7	0.0	57.1	42.9	7