Paul R. RAMSEY & Linda A. BRIESE

Effects of Immigrants on the Spatial Structure of a Small Mammal Community*

[With 2 Tables & 3 Figs.]

Experiments were performed to test effects of simulated immigration upon a community of small mammals. Intra- and interspecific contacts were induced by releasing four groups of alien cotton rats, *Sigmodon hispidus*, onto a semi-enclosed pasture. A similar, adjacent area served as a control. The sequential appearance of three species of rodents in live-trapped samples was not affected by the releases. No changes resulting from the releases were observed in rates of cumulative capture of eastern harvest mice, *Reithrodontomys humulis*, or meadow voles, *Microtus pennsylvanicus*. Increased mortality (or emigration) and decreased trappability occurred in the population of resident *Sigmodon* under treatment. Differences in initial dispersion of the »immigrants« are presented. The characteristics of migrant animals are discussed.

I. INTRODUCTION

There have been few studies of interactions between migrant and resident rodents. Calhoun (1958) reported that many introduced Norway rats emigrated from his study area, but some became incorporated into resident populations. Golley (1962) indicated that 45% of a group of introduced cotton rats remained and survived in a grass field. Introduced mice were a deterrent to homing in an enclosed population of *Peromyscus maniculatus* (Terman, 1962)). Owls preyed more upon transient than resident white-footed mice (Metzgar, 1967).

Introduction of additional animals seemed to halt the increase of a population of brown rats (Davis & Christian, 1956). Lidicker (1962) suggested that emigration may be an important aspect of population regulation during both adverse and improving conditions. The impact of migrants upon residents may be an important factor in the regulation

of populations. Possible influences of migrants upon natural populations and communities remains to be assessed.

The basic design of our experiment was to use introduced animals to simulate immigration. Specific effects of successive groups of aliens upon activity, movements and survival in alien and resident populations were then evaluated. Tests were to be conducted in winter populations of low density and negligible reproductive effort.

II. METHODS

The study was conducted near Athens, Georgia, USA on lands of the University of Georgia. This area of pastures is called Horseshoe Bend because of the configuration of the Oconee River which partially encloses them. Plots were situated in two old pastures. The fields, last grazed by cattle in the spring of 1969, had been planted with coastal bermuda and several types of bunch grasses. Grass cover was nearly uniform (20—30 cm in height) on both plots.

A grid arrangement of live traps was established in each pasture. Precensus studies involved marking and recapturing resident small mammals on the two quadrats. Control grid (A) was 0.50 ha, and the experimental plot (B), located on the floodplain, was 0.86 ha. Grid A was on a hillside and bordered by hedge on the east, hardwood forest on the north and south, and a highway on the west. Grid B was approximately 0.6 km to the west and was bounded on the north and west sides by the river and a stream and on the south by an embankment, a hedge row and a highway.

Drop-door live traps were set at 10-meter intervals on both plots. One trap was set at each of 72 stations on grid A and at each of 118 stations on grid B. Traps were checked and reset twice daily during the precensus and release periods from 26 January to 22 February 1970. For the first five days of the precensus, alternate rows of traps were set on each plot; later, all traps were operated each day. Resident animals on both plots were toe-clipped, sexed, weighed with a spring scale and released at the site of capture.

Trapping was suspended for three days (4—6 February) to minimize disturbance of resident animals on the experimental area. A small pile of brush, placed in the center of each plot, served on grid B as the site of release for alien *Sigmodon hispidus* S a y & O r d, 1825. Experiments consisted of releasing groups of 7, 7, 8 and 10 animals on 7, 13, 17 and 19 February, respectively. Individuals were sexed, weighed, and placed under the pile of brush between 16.00 and 17.00 hours. The first three groups were trapped from a field approximately 1 km from the study areas and were held for 21, 3 and 1/2 day(s), respectively. For easier identification, these animals were ear-notched as well as toe-clipped. Animals in the fourth group were known residents removed from grid A. Animals in this group were released on the afternoon of their capture. Both plots were resampled on 2 March. Removal of all animals from grid B was begun on 17 March and was continued for seven days, until heavy rains caused flooding and termination of the study.

Data were recorded to establish: (1) rates of appearance of species in the trapping sample; (2) dispersion of animals on the plots by species, sex and weight; (3) density by the calendar of captures method (P e t r u s e w i c z & A n d r z e j e w s k i,

1962), and (4) patterns of movement for each species in terms of the individual distances between successive captures (Davis, 1953). Densities were based on the area of the plot; no border zone was added. Factors such as sex, weight, period of confinement prior to release, and techniques of the releases could affect responses by aliens and residents. Survival of aliens on the plot, their success in establishing residence, and their movements from the point of release were examined for each group. Changes in movements and densities of resident and alien populations were also noted. The 5% level of probability was used to indicate significance.

III. RESULTS AND DISCUSSION

Most of the following analyses concern data from the experimental grid. Data from grid A are included for comparison where indicated.

A. Species Accounts

During the nine days of precensus, four species were recorded. Five more species were added in the subsequent 16 days. The number, location and period of capture for individuals of the three most abundant species appear in Table 1. Other species recorded from grid *B* and their numbers

Table 1

Numbers of the three most abundant species of small mammals live-trapped on control (A) and release (B) grids during precensus and release periods. Asterisk column includes animals from removal period.

Species	Precensus				Release				Total*
	A		B		A		B		
	♂	♀	♂	♀	♂	♀	♂	♀	
Sigmodon hispidus	11	14	20	17	11	14	25	17	68
Reithrodontomys humulis	1	0	13	12	1	0	13	11	35
Microtus pennsylvanicus	0	0	4	0	0	2	8	9	25
Total	26		66		28		83		

were as follows: *Blarina brevicauda* (Say, 1823) (3); *Oryzomys palustris* (Harlan, 1837) (3); *Cryptotis parva* (Say, 1823) (2); *Peromyscus leucopus* (Rafinesque, 1818) (1); *Rattus rattus* (Linnaeus, 1758) (2); and *Mus musculus* Linnaeus, 1758 (1). Of these species, only *Peromyscus* (1) was captured also on grid *A*.

Densities of the three abundant species declined slightly or were stable during the study. Approximately equivalent densities of 43/ha and 49/ha were obtained for *Sigmodon* in the precensus and release periods. Harvest mice, *Reithrodontomys humulis* (Audubon & Bachman, 1841) showed a decline from 35/ha to 28/ha, but mortality

due to traps accounted for this decrease. Meadow voles, *Microtus pennsylvanicus* (O r d, 1815), were never completely censused, since unmarked animals were captured during the removal period. However, 20/ha were recorded by the end of the releases of aliens. Voles were not captured until the seventh day of precensus. Most of the cotton rats (88%) and harvest mice (75%) wɛre captured prior to the first release on day 13.

Weights of male versus female cotton rats showed no significant differences on either grid A $(t=.14, df=24)$ or the hedge row of grid B $(t=.26, df=26)$. There were no differences between the pooled weights for the hedge and field animals $(t=.68, df=34)$ or for animals on the two grids $(t=.10, df=60)$.

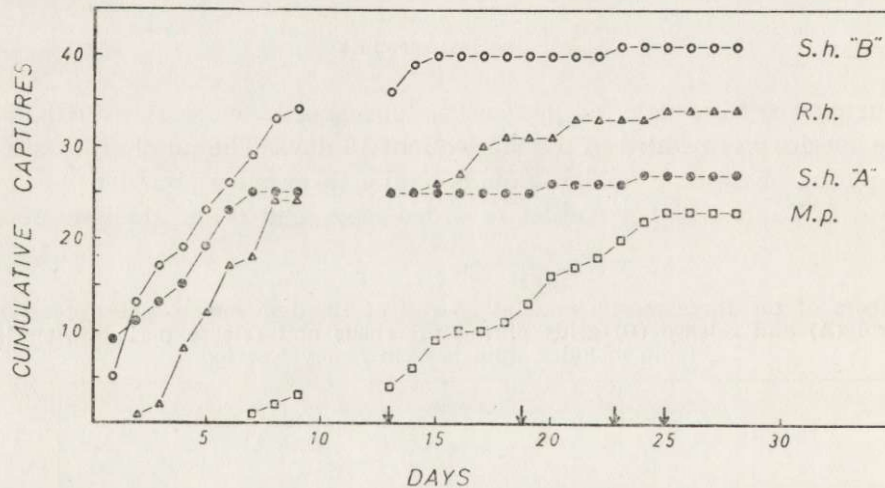Fig. 1. Cumulative captures of *Sigmodon hispidus* (S. h.) on control grid A and experimental grid B and *Reithrodontomys humulis* (R.h.) and *Microtus pennsylvanicus* (M. p.) on grid B. Trapping was suspended for days 10—12 on both grids. Arrows indicate days when alien *Sigmodon* were released on grid B.

Tests of sex ratio for cotton rats showed no differences on the various areas. Sex ratio (male : female) on grid A was .83, while that on grid B was 1.5 with a ratio of 1.4 on the hedge row and 1.8 on the field. During the release periods, the ratio ranged from 1.3—1.8 on the hedge row and 1.2—1.4 on the field.

B. Residents

C a p t u r e s & A c t i v i t y: Rates of capture of the three abundant species were examined for possible responses to inputs of aliens (Fig. 1). Cumulative captures during two periods of precensus and two periods

after releases I and II+III were used in a Friedman two-way analysis of variance by ranks (S i e g e l, 1956). Rate of capture of voles differed from that of cotton rats and harvest mice ($\chi r^2 = 48.0$, $P < .028$, $df = 2$) The delay and lag of input by voles into our samples was followed by a rather constant rate of capture. B a r b e h e n n (1958) reported that nine days were required for maximal use of feeding stations by a population of *M. pennsylvanicus*. It appears that alien animals had little effect upon the rates of capture of resident species, although harvest mice and voles may have shown stimulated input following the release of cotton rats. The rate of accumulation of voles was relatively constant, but the daily first captures declined slowly, and accumulation ceased on the 25th day. The presence of pregnant and lactating females and additional animals in the removal samples suggest that breeding activity affected the captures of voles.

It is difficult to separate the responses of animals to traps according to the influences of weather, technique or species-individual reactions. Captures of cotton rats (mostly females) increased on the fifth day as weather changed from overcast and rain to clear conditions (Fig. 1). G e n t r y, G o l l e y & M c G i n n i s (1966) found similar response in removal trapping of this species. Daily activity of voles as measured by numbers captured per day (maximum=7) decreased with increasing temperature and overcast conditions. Captures of harvest mice were likewise few, but generally were the inverse of daily numbers of voles. Harvest mice were accumulated more slowly under conditions of rain or low temperature. D u n a w a y (1968) stated that populations of eastern harvest mice show reduced activity and experience heavy mortality during the winter. Thus, the activity of each species showed some alteration with changes in weather.

There were, however, indications of interaction between aliens and residents. These indications were from changes in »trappability« and in the composition and size of various segments of the population of resident cotton rats. There was a gradual decrease in the ratio of captured cotton rats to the total number known to be present (Fig. 2). A similar decline in this index of activity did not occur on grid *A* between the 13th and 25th days. Calculated linear regression coefficients for these ratios were significantly different from zero for animals on grid *A* ($b = .022$, $t = 2.206$, $P < .05$) and grid *B* ($b = -.014$, $t = 2.815$, $P < .025$). Regression coefficients for the two lines were significantly different ($t = 3.50$, $P < .005$). Trappability of rats on grid *A* decreased and recovered, after 11 animals were removed on day 25. Except for days 19—21 and 28, trends in trappability of cotton rats on the two areas were similar. After the 2nd and 4th releases, rats on grid *B* showed lower ratios.
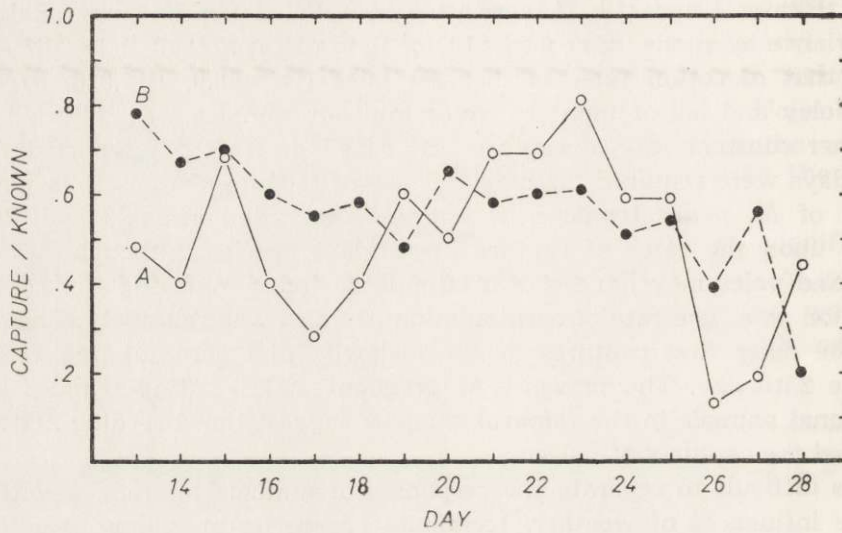
Fig. 2. Ratios of daily capture of resident *Sigmodon hispidus* per number known to occur on control (*A*) and experimental (*B*) grids. Eleven animals were removed from the control on day 25. Regression lines for the ratios from days 13—25 were calculated for control ($Y = .396 + .022\,X$) and experimental ($Y = .699 - .014\,X$).
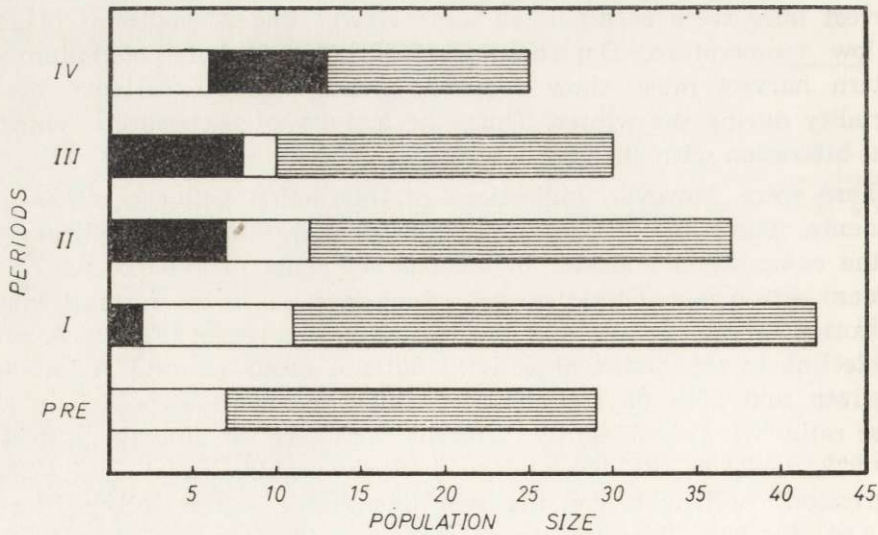
Fig. 3. Number of *Sigmodon hispidus* captured on experimental grid during precensus (*PRE*) and periods which followed releases of aliens. Superimposed bars indicate total numbers of field (open), alien (shaded) and hadge (striped) animals.

There also were changes in the numbers and composition of resident cotton rats on grid B. During the interval between releases I and III, the total population increased as aliens established residence and natural immigration occurred (Fig. 3). The increase after the precensus included undetected residents. After the third release, total numbers dropped, and there was a reversal in the kind of field residents. By the end of the fourth interval, although total numbers remained stable, the ratio of established aliens to prior residents had changed. Numbers of peripheral (hedge row) and field residents decreased. Mortality of field residents (or aliens) was observed in the form of patches of fur; skulls of cotton rats were found in owl pellets under nearby trees. There was marked stability in total numbers until the third release and a change in the composition of the population on grid B.

D i s p e r s i o n: Although grid B was more mesic than grid A, the three abundant species were found on both plots. Individuals were captured at 62 stations on grid B. The numerical ratio of the three species on all of plot B was $2.5 : 1.4 : 1.0$ (Table 1). Captures at the 62 stations should have been partitioned according to this ratio if habitat and dispersion of the species were uniform. Capture of a single species (41 stations), two species (17) and three species (4) did not follow the prescribed ratio or order ($\chi^2 = 9.79$, $P < .01$, $df = 2$). These calculations were derived from the 87 total sites of capture of the three species in the three combinations. Cotton rats, harvest mice and voles accounted for 39%, 51% and 10%, respectively, of exclusive stations. For all three classes of stations, these species appeared in 39%, 44% and 17% of the captures. There were fewer captures of cotton rats and more of harvest mice than expected. These data reflect the wider utilization of available habitat by harvest mice, since cotton rats and voles appeared restricted to matted and bunched grasses. If stations along the hedge row are excluded (at which only cotton rats were captured), the percentages for harvest mice increase in both comparisons. Exclusion from traps was not demonstrated apart from restriction to particular microhabitats.

M o v e m e n t s: Average distance between successive captures for cotton rats appeared to change from the precensus through the release periods. For example, males showed a decline in average movements from 19.1 ± 2.2 m ($\pm$ SE) during precensus to 12.1 ± 1.5 during an equal interval after the second release. Females of this species showed reduced movements from 16.7 ± 2.0 to 12.0 ± 2.7 for the same times. Fewer recaptures (< 20) were obtained for each sex of the other species. However, similar values for male and female harvest mice were 12.1 ± 3.8 and 10.1 ± 5.9 (precensus) and 12.1 ± 3.5 and 23.5 ± 10.9 (release). Calculated

through the first release of aliens, the average movements of male and female voles were 17.8 ± 11.1 and 9.7 ± 8.6, respectively.

A Kolmogorov-Smirnov two-sample test (Siegel, 1956; D is the resulting statistic with $df=2$) was applied to the frequency distributions of distances between captures. The calculations revealed that male cotton rats moved further than females on grid A ($D=.402$, $\chi^2=11.77$, $P<.01$). Exclusive of period IV, when animals were removed from grid A, females on grid B moved further than those on grid A during the precensus and total periods ($D=.411$, $\chi^2=11.36$, $P<.01$ and $D=.208$, $\chi^2=10.45$, $P<.01$). Thus, distinctions can made between movements by rats on the control and treatment plots. Analysis of grouped frequencies on grid B for release periods I, II, and III+IV in a contingency table showed no changes with treatment ($\chi^2=3.23$, $P<.70$, $df=6$).

Table 2

Permanence of four groups of alien *Sigmodon* on experimental grid B. Day 28 was three days after the fourth release. Removal of animals by live-trapping was begun on day 51.

	Groups			
	I	II	III	IV
Number Released ♂	1	4	3	5
♀	6	3	5	5
Days of Exposure Until Removal	37	31	27	25
Per Cent Remaining to Day 28	83.3	85.7	37.5	80 0
Per Cent Remaining to Day 51	43.0	0.0	12.5	20.0
Number Lost Per Day of Exposure	0.11	0.23	0.26	0.32

C. Aliens

A summary of the observations of aliens is presented in Table 2. Of the 32 animals released, 28 were recaptured at least once. Nineteen were recaptured three or more times (present for at least 1.5 days) and were considered to have established residence. Group III apparently had least success in establishing residence. Whether affected by prior residents or other aliens, the groups were ordered initially in their permanence: III<IV<I<II. After approximately one month, group II had disappeared from the area. The loss through mortality or emigration per day of exposure was the reverse of the duration of exposure for each group. Successive groups appeared either more susceptible to mortality or more prone to leave the area. Contrary to Orr (1966), prolonged confinement of animals may cause more sedentary habits when they are re-

leased. Perhaps this explains the success of group I in our experiments Movements & Dispersion: We have applied the K & S two-
-sample test to the cumulative frequency distributions of distances between captures for residents and aliens from the first release to the end of the experiment. Our assumption was that the movements by each successive group would follow a continuum established by the first group. No difference was detected between these two distributions $(D=.084,\ \chi^2=2.52,\ P<.20)$.

First captures for individuals of each group showed that direction of movements was essentially random $(\chi^2=1.16,\ P<.70,\ df=3)$. This is important to the assumption that movements approach a normal bi-variate ditribution such that all captures could be summed in concentric annuli from the site of release.

Each group showed a characteristic distribution about the site of re-lease. Frequency tables of the observed recaptures versus the zones (10 m) of recapture were used to illustrate the occupation of the surround-ing habitat by aliens. This method was used by F r e n c h, T a g a m i & H a y d e n (1968) to describe the dispersive movements of desert rodents. The mean distance moved, number of recaptures, and variance of the distances were computed. Dispersion is described by the ratio of the fourth moment about the mean distance to the square of the second moment. This measure of kurtosis will approximate 3.0 for a normal distribution (S n e d e c o r & C o c h r a n, 1967). A correction for animals which might huddle at the release site was applied to data for group I. The effects of confinement were evident for these animals as judged by the nearness of their first captures to the site of release.

The mean distance, as well as the variance, increased for the first three releases. The fourth group had a relatively greater variance and a mean near that of group I. The observed distributions resembled a normal curve for group II only. Other distributions were leptokurtic (I & IV) and platykurtic (III).

The primary objective of this report is to evaluate the possible in-teractions between alien and resident animals. The decline in trappability of cotton rats on grid B as opposed to an increase on grid A and the changes in numbers of cotton rats on grid B are indicative of these inte-ractions. Further, the decreases in trappability, numbers, and movements were each observable at days 18—21 or following the second release. The resultant dispersion of group III indicated that all vacant habitat had been filled or a critical level of effect had been reached. These findings indicate that development of significant interaction is density-
-dependent. Our evidence is restricted to intraspecific interactions between aliens and residents and among the groups of aliens. A social

hierarchy has been demonstrated for populations of cotton rats (W o l f e & S u m m e r l i n, 1968). If interspecific interactions occurred, the evidence was confounded by other factors.

Our experiment can be compared to other attempts to ascertain social behavior in natural rodent populations. These studies have utilized trapping, a technique which is subject to bias and indirect in its approach to behavioral phenomena. C a l h o u n (1964) described a dominant or *alpha* species in small-mammal communities by three characteristics. These traits were more rapid removal of 50% of the population, larger home ranges, and lower density. By these requirements in his hypothesis of interspecific hierarchies, cotton rats represented the dominant species of the open pasture as shown by live-trapping. Sequential inputs of the supposed dominant species did not alter noticeably the accumulation of the other species. C a l h o u n (1964) also described delayed and seconda-ry inputs by individual species as a reflection of the dominant-subordi-nate relationship among species. Seven and 13 days of live-trapping were required in our study to detect voles on grids B and A, respectively. Variable inputs have been observed in other studies by removal (G e n t r y, G o l l e y & S m i t h, 1971). Similar data were obtained in another study by live-trapping, and an alternative explanation of species-specific neophobia was offered (F a u s t, S m i t h & W r a y, 1971).

B a r b e h e n n (1958) suggested the poor relevance of removal-trapping to the detection of social interaction. Apparently, C a l h o u n (1964) has given accurate accounts of several random responses by rodents to the technique of removal. Samples of populations by live-trapping may contain a majority of dominants which are prone to enter traps (A n-d r z e j e w s k i, P e t r u s e w i c z & W a s z k i e w i c z-G l i w i c z, 1967). Initial samples by removal may also contain a preponderance of dominants, and normal behavior of the remaining animals may be lost in a readjustment of intraspecific hierarchies. Thus, live-trapping is the preferred method if individual responses to traps can be eliminated as a variable. Sufficient time must be allowed to insure capture of every important species. S m y t h (1968) found that natural immigration pre-cluded definitive answers in his field experiment with populations of *Clethrionomys*.

Spatial reorganization must also occur when there is exchange between populations. Changes in seasonal hierarchies have been observed in populations of *Apodemus* (B r o w n, 1969). Further, groups of migrants may differ in the quality of their respective members depending on the environmental conditions under which exchange is initiated (L i d i c k e r, 1962). In populations where social hierarchies exist, emigration could

be either a negative response to increasing demand by dominants for reproductive space or a positive response by subordinates to possibly greater reproductive potential elsewhere.

REFERENCES

1. Andrzejewski R., Petrusewicz K. & Waszkiewicz-Gliwicz J., 1967: The trappability of *Clethrionomys glareolus* (Schreber, 1780) and other ecological parameters obtained by the *CMR* capture method. Ekol. pol. A, *15*: 709—725.

2. Barbehenn K. R., 1958: Spatial and population relationships between *Microtus* and *Blarina*. Ecology, *39*: 293—304.

3. Brown L. E., 1969: Field experiments on the movements of *Apodemus sylvaticus* L. using trapping and tracking techniques. Oecologia, *2*: 198—222.

4. Calhoun J. B., 1948: Mortality and movement of brown rats (*Rattus norvegicus*) in artificially supersaturated populations. J. Wildl. Mgt., *12*: 167—172.

5. Calhoun J. B., 1964: The social use of space [In: »Physiological Mammalogy«, Eds. Mayer W. & Van Gelder R. G.] Vol. *1*: 1—187. Academic Press, New York.

6. Davis D. E., 1953: Analysis of home range from recapture data. J. Mamm., *34*: 167—172.

7. Davis D. E. & Christian J. J., 1956: Changes in Norway rat populations induced by introduction of rats. J. Wildl. Mgt., *20*: 378—383.

8. Dunaway P. B., 1968: Life history and population aspects of the eastern harvest mouse. Amer. Midl. Nat., *79*: 48—67.

9. Faust B. F., Smith M. H. & Wray W. B., 1971: Distances moved by small mammals as an apparent function of grid size. Acta theriol. *16*: 161—177.

10. French N. R., Tagami T. Y. & Hayden P., 1968: Dispersal in a population of desert rodents. J. Mamm., *49*: 272—280.

11. Gentry J. B., Golley F. B. & McGinnis J. T., 1966: Effect of weather on captures of small mammals. Amer. Midl. Nat., *75*: 526—530.

12. Gentry J. B., Golley F. B. & Smith M. H., 1971: Yearly fluctuations in small mammal populations in a southeastern United States hardwood forest. Acta theriol., *16*: 179—190.

13. Golley F. B., 1962: Mammals of Georgia. Univ. of Georgia Press: 1—218, Athens.

14. Lidicker W. Z., 1962: Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. Amer. Nat., *96*: 29—33.

15. Metzgar L. H., 1967: An experimental comparison of screech owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). J. Mamm., *48*: 387—391.

16. Orr H. D., 1966: Behavior of translocated white-footed mice. J. Mamm., *47*: 500—506.

17. Petrusewicz K. & Andrzejewski R., 1962: Natural history of a free--living population of house mice (*Mus musculus* Linnaeus) with particular reference to groupings within the population. Ekol. pol. A, *10:* 85—122.

18. Siegel S., 1956: Nonparametric statistics for the behavioral sciences. McGraw Hill: 1—312, New York.

19. Smyth M., 1968: The effects of the removal of individuals from a population of bank voles *Clethrionomys glareolus.* J. anim. Ecol., *37:* 167—183.

20. Snedecor G. W. & Cochran W. G., 1967: Statistical methods. Iowa St. Univ. Press: 1—593, Ames.

21. Terman C. R., 1962: Spatial and homing consequences of the introduction of aliens into semi-natural populations of prairie-deermice. Ecology, *43:* 216—223.

22. Wolfe J. L. & Summerlin C. T., 1968: Agonistic behavior in organized and disorganized cotton rat populations. Science, *160:* 98—99.

Savannah River Ecology Laboratory,   Department of Zoology,
Drawer E,   or   University of Georgia,
Aiken, South Carolina, USA, 29801.   Athens, Georgia, USA, 30601.

Paul R. RAMSEY i Linda A. BRIESE

WPŁYW IMIGRANTÓW NA STRUKTURĘ PRZESTRZENNĄ ZESPOŁU DROBNYCH SSAKÓW

Streszczenie

Na dwóch pół-ogrodzonych pastwiskach (Tabela 1) prowadzono inwentaryzację populacji *Sigmodon hispidus* (S a y & O r d, 1825), *Reithrodontomys humulis* (A u d u b o n & B a c h m a n, 1841) i *Microtus pennsylvanicus* (O r d, 1815). Na jednym z pastwisk wypuszczono cztery grupy liczące 7, 7, 8 i 10 osobników (*Sigmodon*. Tempo wyłowu tych trzech gatunków nie zostało wyraźnie zmienione przez obecność osobników wprowadzonych (Ryc. 1). Łowność (Ryc. 2) oraz liczebność (Ryc. 3) miejscowych osobników *Sigmodon* zmniejszyła się na terenie doświadczalnym. Grupy osobników wprowadzonych wykazały wyraźne uszeregowanie przeżywania (Tabela 2). Kolejne grupy wykazały większe straty w przeliczeniu na dzień ekspozycji. Kierunki początkowych przemieszczeń osobników wprowadzonych były losowe. Każda grupa posiadała charakterystyczną dyspersję. Klasy częstotliwości odległości pomiędzy kolejnymi złowieniami nie ujawniły żadnych zmian w pomieszczeniach osobników miejscowych. Doświadczenie nie udowodniło międzygatunkowej hiererchii społecznej.