QUANTIFICATION OF SMALL MAMMAL DISPERSAL BY GENETIC AND DEMOGRAPHIC CHARACTERS

A Thesis

Presented to

the Faculty of the Department of Biology

University of Houston

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

---

by

Bradley C. Borlase

July 1976

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This study concerned the identification of dispersers in small mammal populations using genetic and demographic characters from three species of rodents, Sigmodon hispidus, Reithrodontomys fulvescens, and Oryzomys palustris. The hypotheses tested were (1) that there are no differences in the levels of heterozygosity (genetic variability) between resident and dispersing rodents and (2) that there are no correlates between movement and certain demographic parameters. A three-year Sympatric Experiment was utilized to study movement patterns and demographic parameters of Sigmodon and Reithrodontomys. Dispersers were collected along with residents at the termination of this experiment and used in the genetic analysis. A one-year Void Experiment was also utilized to collect genetic data and short term demographic data for Oryzomys and Reithrodontomys. No significant differences were found between residents and dispersers in their levels of genetic heterozygosity. No effect of heterozygosity upon distance moved was found for Reithrodontomys. Both Sigmodon and Reithrodontomys had significant positive correlations between distance moved and reproductive condition. Sex ratios were skewed towards males for Sigmodon and Reithrodontomys when analyzing animals that moved greater distances.

The number of loci necessary to detect a significant difference between two mean heterozygotic levels ($\bar{H}$) was calculated to determine the effectiveness of electrophoresis for this type of experiment. Using the data from this study, it was found that several thousand loci were necessary to detect a significant difference. A proposal is made for future dispersal studies and involves the use of environmental monotoring, movement patterns, and resource utilization over a large area and at least 2 years.

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Introduction

Evidence from several recent studies suggests that dispersal is a critical process in attaining and maintaining population structure. The importance and type of dispersal strategy required by an organism varies tremendously between organisms and becomes exceedingly difficult to quantify, especially in small mammal populations. Dispersal has been defined as 'the movement of individuals or their disseminules or propagules into, or out of the population or population area' (Odum, 1971) and as 'the movement an animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate' (Howard, 1960). Both definitions include an important quantifier of dispersal, movement, but both lack experimental applicability. Dispersal is always assumed to occur and very crude quantification has been attempted, but a working experimental definition has not been developed.

Numerous functions of dispersal have been discussed (Howard, 1960, Lidicker, 1962, 1973, 1975, Gadgil, 1971, Van Valen, 1971), the most important including genetic exchange, range expansion, population regulation and species survival from resource depletion. Lidicker (1975) proposed that dispersal acts as a regulatory mechanism for population numbers below the carrying capacity. He divides dispersal strategies into presaturation and saturation types according to the timing of emigration from a population with respect to attainment of the carrying capacity. Different dispersal strategies would have a marked effect

upon population demography and reinforce the importance of demographic quantification of dispersers.

Quantification of dispersal by these definitions in small mammal populations would require a measure of population periphery or area, enabling the discrimination between residents and dispersers. Since this dimension is extremely difficult to attain, the application of the above definitions of dispersal to field experimentation would be tenuous. Therefore, quantification of dispersal requires the use of other parameters of small mammal populations.

Demography could used to characterize residents and dispersers. The demographic characteristics that are measurable in small mammal populations include age, sex, reproduction, weight, and density, all of which have been used in dispersal studies with varying results (Stickel, 1946, Myers and Krebs, 1971, Myers, 1974, Joule and Cameron, 1975, and Krebs, et al., 1975). In addition, several studies have shown the significance of environmental variation in determining movement patterns and demographic changes (Lidicker and Anderson, 1962, Gentry, 1966, Lidicker, 1973).

Genetic characters could also be used to differentiate dispersers from residents. The effects of dispersal upon the genetic variation of a population may be positive or negative, depending upon the direction of gene flow and the advantage acquired from retaining these genes within the population. Dispersal has been considered by some as a retarder of evolution, effecting geographic variation, speciation, and

long range evolution (Mayr, 1963), and evidence has been presented that dispersers can be identified by their greater genetic variability when compared to residents. These genetic differences may involve an increase in individual heterozygosity and may be instrumental in the propensity of an individual to disperse and, hence, in determining population charcteristics (Dice and Howard, 1953, Howard, 1960, Myers and Krebs 1971, Smith, et al., 1975, Krebs, et al., 1975).

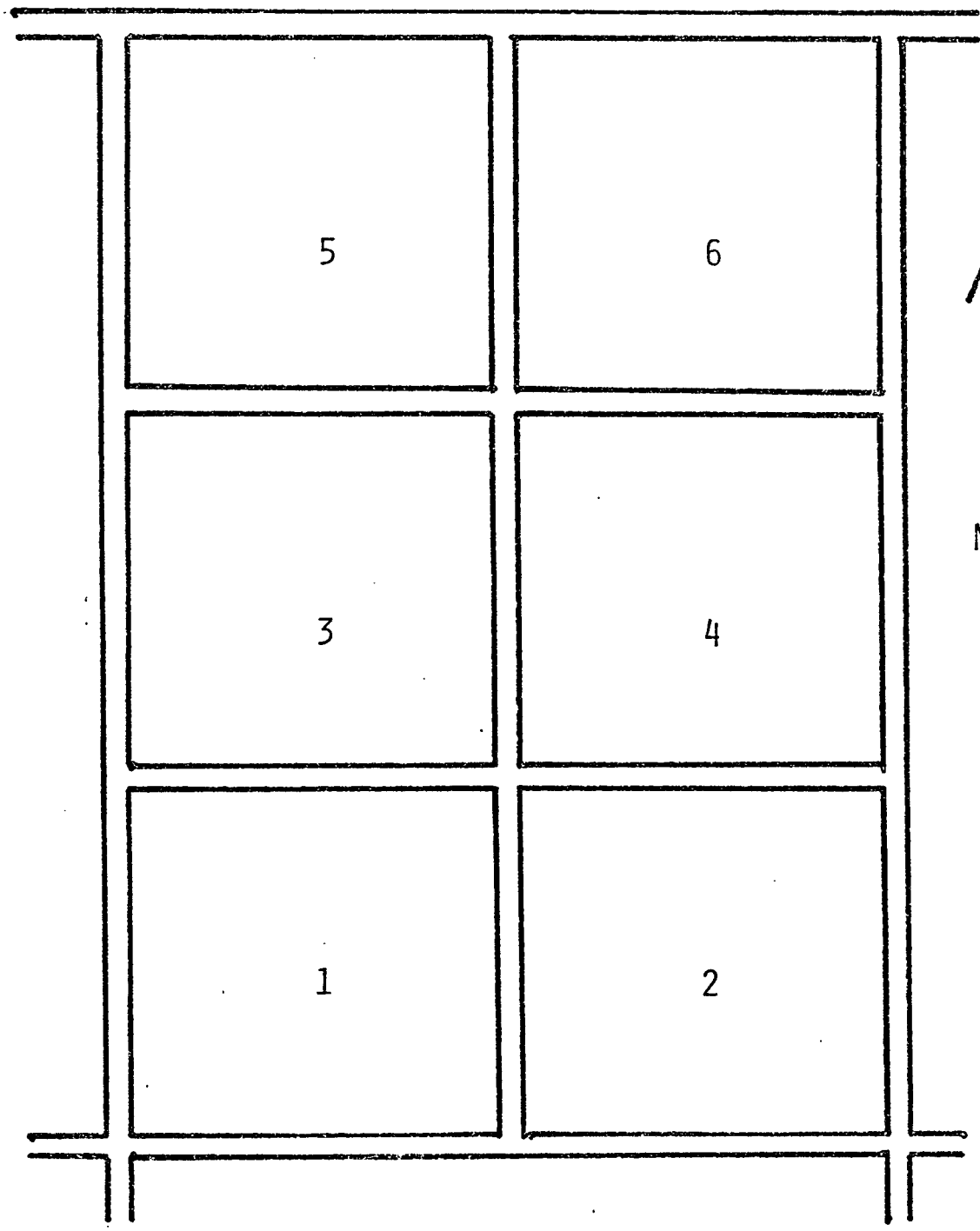
This study considered the demographic and genetic components of dispersal in three sympatric rodents, Sigmodon hispidus, Oryzomys palustris, and Reithrodontomys fulvescens. Comparison of the dispersal strategies of these three rodents was especially important and field experiments were designed to test two hypotheses: (1) that there is no genetic difference between resident and dispersing animals and (2) that there are no correlates between demographic parameters and movement patterns. These hypotheses were used to determine if demographic and/or genetic characteristics could identify dispersers and, hence, serve as a basis to define a disperser.

Methods

This study was conducted at the University of Houston Coastal Center, a 360 ha field station 35 miles south of Houston, Texas. The vegetation on the Texas Coastal praire consists of dense stands of Baccharis halimifolia (sea-myrtle), Andropogon glomaratus (bushy beardgrass), Solidago spp. (goldenrod), Schizachyrium scoparium (little blue stem) and other less dense herbaceous plants. Further habitat description can be found in Joule and Cameron (1974). Sigmodon hispidus (cotton rat) and Reithrodontomys fulvescens (fulvous harvest mouse) are the dominant rodents in this area with Oryzomys palustris (rice rat) next in abundance.

Two experimental designs were utilized using the same fields and trapping methods to determine if there were demographic or genetic differences between residents and dispersers. In the first experiment animals were trapped monthly from January, 1972, until January, 1975, with the technique of temporary species removal (described in detail by Joule and Cameron, 1974, 1975). Animals were removed over a three day period and were weighed, sexed, checked for reproductive condition and marked; individuals were released at the exact site of capture on the third day. Six 1.6 ha fields were used, with two fields being Sigmodon-only, two fields being Reithrodontomys-only, and two fields serving as controls (Fig. 1). Oryzomys was not perturbed in the above manner because of low capture numbers, but demographic data were collected. The fields were isolated by

Fig. 1 Diagram of experimental designs for both Void and Sympatric Experiments. For the Sympatric Experiment (1972-75), fields 2 and 5 were controls, fields 1 and 3 were Reithrodontomys-only, and fields 4 and 6 were Sigmodon-only. For the Void Experiment, field 2 was a control, fields 1 and 5 were marked populations, and field 3 was the void.


5
6
3
4
1
2
N

15m paved roads and mowed paths; each field contained a 9 x 9 grid of Sherman live-traps at 15m intervals and three of the fields contained 27 vertical traps for Reithrodontomys captures. All Reithrodontomys captured in Sigmodon-only fields and all Sigmodon captured in Reithrodontomys-only fields were considered dispersers. This phase of the experiment will be referred to as the Sympatric Experiment. Movement data were collected and the average distance moved between captures (AVED) computed for Sigmodon and Reithrodontomys to determine relations with demographic parameters. This movement data reported by Kincaid (1975). This experiment utilized a total of 567 traps and represented a total of 54,189 trapnites.

Further demographic data were collected from the Void Experiment initiated April, 1975 and terminated January, 1976. Four 1.6 ha fields were utilized, with two fields as sources of marked animals, one field a void between the marked fields, and one field as a control (Fig. 1). The void was established in April, 1975 by removal of all rodents and removal was continued in subsequent trapping periods. The void field contained a 9 x 9 grid of Sherman live traps with two ground traps at each station and 27 vertical traps. Therefore, the total number of traps for the void experiment was 432, with an additional 50 traps surrounding the periphery of the void during the last month of trapping.

Trapping for this later phase of the study was conducted over a two-night period every three weeks. Demographic data was collected on

all animals, utilizing the species removal technique. All animals captured in the void were considered dispersers while animals in the marked fields and control were considered residents. Since crossings of the road barriers is infrequent (averages 5% of the population) (Cameron, 1976), those rats which cross are probably not within their normal wandering ranges but are movers.

Animals from both experiments were used to assess the genetic component of dispersal. At the termination of the Sympatric Experiment, Sigmodon in Reithrodontomys-only fields and Reithrodontomys in Sigmodon-only fields were sacrificed and samples of the heart, kidney, liver, and blood were taken as described by Selander, et al., (1971) and stored at -68 C. until they were analyzed by horizontal starch gel electrophoresis at the Savannah River Ecology Laboratory (SREL) in Aiken, South Carolina during July and August, 1975. Included in this analysis were initial samples taken during the Void Experiment. All three species were sacrified in the Void Experiment using the technique described above.

This analysis confirmed the reported low genetic variability for Sigmodon (Johnson, et al., 1972) and it was decided to concentrate the genetic analysis on Reithrodontomys and Oryzomys because of their greater variability. Thereafter, Sigmodon was no longer sacrificed in the void but was removed to fields outside of the experimental area to maintain the void. Animals collected during the Fall, 1975, in the Void Experiment were analyzed at SREL in January, 1976. Oryzomys

was analyzed for 25 loci and Reithrodontomys for 22 loci. Average individual heterozygosity values were calculated for 180 individuals and comparisons made to determine if dispersers were more or less variable than residents.

Results

Genetic Analysis

Genetic variability for Reithrodontomys and Oryzomys was calculated by two indices, percent polymorphism and heterozygosity averaged over individuals ($\bar{H}$). Gene frequency was calculated from observed genotypes and a locus was considered polymorphic if the gene frequency of the most common allele was less than 0.95. Polymorphism was 13.6% for Reithrodontomys and 20% for Oryzomys, with the number of loci scored being 22 and 25, respectively. Polymorphic loci included Phosphoglucomutase-1, Phosphoglucomutase-2, and Alcohol Dehydrogenase for Reithrodontomys and -Glycerohposphate Dehydrogenase, Alcohol Dehydrogenase, Malate Dehydrogenase-1, Glutamic Oxalacetic Transaminase, and Glutamate Dehydrogenase for Oryzomys. Esterases were not included in the analysis because of difficulty in scoring, hence, these values are conservative due to the obvious variability within esterases. Each locus was tested for deviation from Hardy-Weinberg equilibrium by a Chi-square goodness of fit test with no sigmificant deviations being found.

Average individual heterozygosity ($\bar{H}$) values for Oryzomys and Reithrodontomys were used to determine whether genetic differences existed between dispersers and residents (Appendix 1). These values were calculated across loci and mean calculated from the individuals (Table 1) and also according to Nei and Roychoudhury (1974)(Table 5). No significant difference was found for either species with sexes

Table 1. Average individual heterozygosities ($\bar{H}$), sample size (n), and standard errors (SE), sexes pooled and separate.

REITHRODONTOMYS

	Dispersers		Residents	
Sexes pooled	all	marked	all	marked
$\bar{H}$	.032	.030	.032	.034
n	91	15	89	60
SE	.039	.033	.034	.036
Male				
$\bar{H}$	.031	.021	.034	.036
n	57	11	46	35
SE	.032	.032	.055	.032
Female				
$\bar{H}$	.032	.045	.030	.031
n	34	4	43	25

ORYZOMYS

Sexes pooled				
$\bar{H}$	.053	.048	.056	.055
n	25	5	28	13
SE	.049	.052	.051	.060
Male				
$\bar{H}$	.053	.060	.058	.065
n	15	4	20	8
SE	.074	.052	.054	.071
Female				
$\bar{H}$	.052	.000	.053	.056
n	10	1	6	5
SE	.050	---	.048	.067

pooled or separate (Mann-Whitney U and Wilcoxen tests). Table 1 lists two kinds of dispersers and residents, "all" and "marked". "All" represent marked and unmarked animals whereas "marked" represent only marked animals whose point of origin and movement pattern are known. The $\bar{H}$ values were not significantly different between "all" and "marked" animals. Therefore, the "all" values were used in subsequent tests because of the larger sample sizes. Differences appeared when dispersers and residents were separated by sex, but these were not significant and were probably due to smaller sample sizes.

The values for heterozygosity and polymorphism were consistent with values found for Peromyscus, Dipodomys, Geomys, and other small mammals (Selander and Johnson, 1973, Smith, et al., 1976).

Average individual heterozygosity values for Reithrodontomys and Oryzomys were calculated according to age class, with age class determined by weight (Table 2). Reithrodontomys was separated into three age classes (in grams): juveniles (0-8.9), young adults (9-11.9) and adults (12-over). Oryzomys was separated into two age classes: juveniles and young adults (0-29) and adults (30-over). These weight classes are based upon reproductive characters with juveniles being non-reproductive. No significant differences were found for $\bar{H}$ values between residents and dispersers within or between age classes (t-test).

Individuals were grouped according to heterozygosity values and

Table 2. Average individual heterozygosities ($\bar{H}$), sample size (n), standard error (SE), and average weight (AW) for weight/age classes for Reithrodontomys and Oryzomys.

	Dispersers		Residents	
	Male	Female	Male	Female
REITHRODONTOMYS				
Juveniles				
$\bar{H}$	.000	.011	.023	.045
n	4	4	2	1
SE	.000	.032	--	--
AW	8.62	7.88	8.45	8.00
SE	.341	1.131	--	--
Young adults				
$\bar{H}$	.041	.033	.033	.024
n	31	23	33	26
SE	.045	.045	.032	.032
AW	10.76	10.28	10.58	10.44
Adults				
$\bar{H}$	.026	.030	.038	.035
n	19	6	11	14
SE	.032	.045	.032	.032
AW	12.77	13.55	13.21	13.10
SE	.695	1.140	.693	1.158
ORYZOMYS				
Adults				
$\bar{H}$	.060	.050	.060	.050
n	12	6	20	6
SE	.045	.063	.055	.045
AW	49.73	44.37	46.68	42.63
SE	16.45	12.13	10.45	7.22
Juveniles and Young adults				
$\bar{H}$	.010	.050	--	--
n	3	3	0	0
SE	.032	.045	--	--
AW	17.5	23.6	--	--
SE	.17	5.16	--	--

AVED to test the effect of heterozygosity upon movement in Reithrodontomys (Table 3). Since there were only three possible heterozygosity values (.000,.045,.090) denoting individuals heterozygous at 0, 1, and 2 loci respectively, the AVED for individual animals are lsited according to the number of heterozygous loci. The mean AVED for individuals captured 2 or more times and individuals capdured 3 or more times was computed. There were no significant differences between individuals with 0, 1, or 2 heterozygous loci (single classification ANOVA). Therefore, no effect of heterozygosity upon average distances moved was found.

Demographic Analysis

Demographic data from the Sympatric Experiment for Sigmodon and Reithrodontomys was used to determine whether there were demographic characteristics associated with movement. . The average distance moved (AVED) was computed on a monthly basis and used to estimate an animals routine movement (Kincaid, 1975). A summary of product-moment correlation coefficients between movement and demographic parameters over a 3-year period is presented for Sigmodon and Reithrodontomys, listing correlations between percent reproductive and AVED, density and AVED, and density and percent reproductive (Table 4). Density measures were transformed by $\log_{10}(Y)$ and percent reproductive by arcsin (Y) to normalize the data. There were significant correlations for all groupings for Reithrodontomys while Sigmodon AVED was correlated only with percent reproductive.

Table 3. Reithrodontomys AVED listed according to number of heterozygous loci (0,1,2). Mean AVED (individual listed for individuals captured 2 times or more and 3 times or more (*).

Number of Heterozygous Loci		
0	1	2
1.20	.72	.00
.00	.00	1.41
1.00	1.41	1.00
.00	.00	.00
1.00	.00	.00
.00	1.00	1.81*
1.00	1.41	.71*
.00	1.00	.28*
1.00	2.00	
.00	1.00	
1.00	.00	
.00	1.00	
1.41	1.41	
2.00	1.71*	
.63	.50*	
1.41	1.50*	
1.12*	1.21*	
.50*	.50*	
.50*	1.71*	
.73*	1.51*	
.71*	1.31*	
	.98*	
3 captures or more (*)		
mean AVED .712*	1.214*	.933*
SE .253	.467	.789
n 5	9	3
2 captures or more		
mean AVED .724	.996	.651
SE .574	.607	.702
n 21	22	8

Table 4. Correlation analysis for data collected over 3 years (Sympatric Experiment) with sample size (n), product-moment correlation coefficient (r), and significance level (P).

	n	r	P
REITHRODONTOMYS			
% reprod. vs $AVED_{pop}$	34	.445	.01
Density vs AVEDpop	34	-.420	.05
Density vs % reprod.	34	-.698	.01
SIGMODON			
% reprod. vs $AVED_{pop}$	34	.380	.05
Density vs AVEDpop	34	-.070	ns
Density vs % reprod.	34	.180	ns

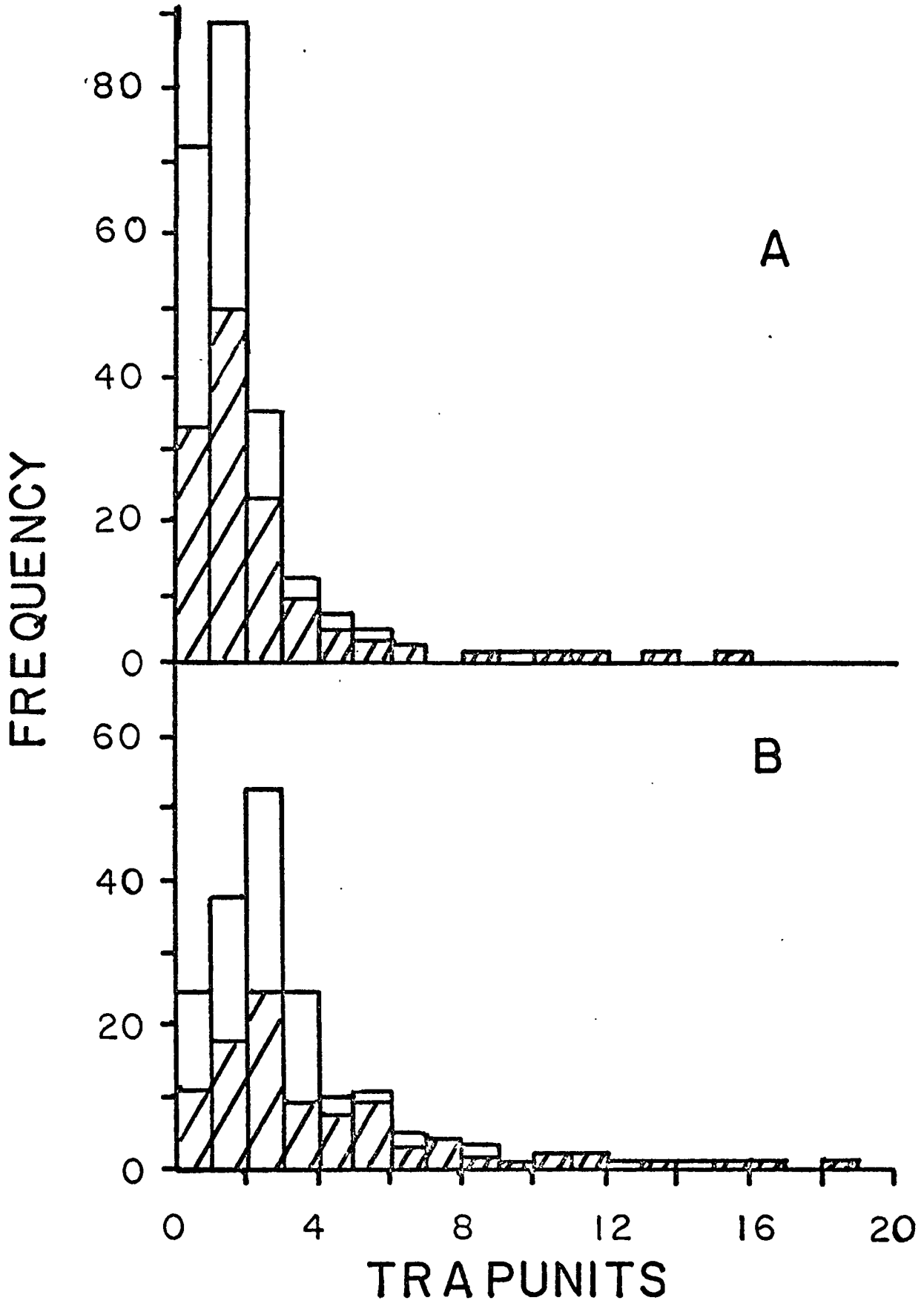
Demographic correlates with movement could not be assessed for Oryzomys because to low individual recaptures invalidated computations of AVED.

Knowledge of the distribution of movement is necessary to develop an experimental or working definition of a disperser. Figure 2 is a frequency distribution of the AVED (in trapunits) between recaptures for both species, by sex. Sigmodon moving 6 or more trapunits significantly deviated from a 1:1 sex ratio (X^2, $P<.01$), with males dominant. Reithrodontomys moving 4 or more trapunits deviated significantly from a 1:1 sex ratio (X^2, $P<.05$), with males also dominant. Reithrodontomys deviated from a 1:1 sex ratio also when considering all animals (X^2, $P<.05$), but Sigmodon did not. Such a skewed sex ratio for Reithrodontomys is not unusual (Fisler, 1971, Joule and Cameron, 1975). Those animals with longer movement distances,i.e. greater AVED, comprised 7% of the total number of animals and are skewed statistically toward males for both species. Therefore, either males move longer distances or males have a greater recapture propensity.

Analysis of the effect of the void field was necessary to determine if the void acted as a "magnet" for any of the three species. In an independence test of fields and species, no significant deviation from independence was found for unmarked animals from any of the fields. Therefore, the void was not attracting unmarked animals in a greater proportion than the marked fields.

Sex ratios for each species in the void experiment were tested to

Fig. 2 Graph of the average distance moved (Trapunits) and the number of animals moving this distance (Frequency) for Reithrodontomys (A) and Sigmodon (B). Each trapunit represents 15 meters. The hatched areas represent males and the clear areas represent females.


FREQUENCY
80
60
40
20
0
A
60
40
20
0
B
0
4
8
12
16
20
TRAPUNITS

determine if they deviated significantly from a 1:1 in the marked and void fields. No significant differences were found for Sigmodon or Oryzomys in any of the three fields tested (G_7-test). Reithrodontomys had significant deviations from a 1:1 in the void and one marked field (G_7-test, $P < .05$); these fields were skewed towards males.

Total number captured was similarly analyzed to determine if the number of animals captured in each of the three fields was independent of field and time, with sexes tested together and separately. No significant deviation from independence was found for Sigmodon or Reithrodontomys, but a significant deviation was found for Oryzomys with sexes pooled ($G_{10}=28.35$, $P < .01$) and in males ($G_{10}=21.38$, $P < .05$). Therefore, for Oryzomys, the capture of males was not independent of field and time and could be attributed to one of the marked fields. From these results, it is shown that the void acted the same as any of the other fields, having virtually no effect.

Reproductive condition was tested in all three species to determine if there was a dependence of reproductive condition and field, using all four fields. No significant deviation from independence was found for Sigmodon or Reithrodontomys, but a significant deviation was found for Oryzomys males ($G_3=9.38$, $P < .05$) and could be attributed to a lack of reproductive condition in one of the marked fields. Therefore in none of the three species was the void field inhabited by a dependent or greater amount of reproductive animals than any of the other fields. This suggests that animals

that are movers are not reproductively different from animals that move less.

Reproductive condition was also tested to determine if it was independent of season and field. No significant deviation from independence was found for Sigmodon and Reithrodontomys, but Oryzomys males that were non-reproductive (testes not descended, TND) deviated from independence (G_6=14.18, $P<.05$). Therefore, only Oryzomys males that were TND were not independent of field and season. This was attributed mainly to the first trapping season (spring) by testing for non-significant subsets and not to an effect of the void field.

To determine if differences existed between fields when weights were pooled, each species was subjected to a single classification ANOVA with sexes pooled, testing for differences between fields through time. No significant differences were found between fields for any of the three species.

Discussion

Increasing knowledge of the role of dispersal in small mammal populations suggests the necessity for a comprehensive approach to an analysis of dispersal, including its causes and effects (Metzger, 1971, Schroeder and Rosenzweig, 1975, Lidicker, 1975). An inherent part of such an analysis requires precise definitions, especially of dispersers. Most definitions of dispersal, however, do not offer a working or testable definition due to their simplicity or inclusion of unquantifiable parameters, i.e., population periphery or point of origin. The precise determination of emigration and immigration is very difficult without a complex analysis. The most important components include daily and seasonal movement patterns of each individual within a population, defined here as the total number of individuals within the experimental area, and the effect of environmental fluctuations and resource availability upon these movement patterns.

Such a multivariate approach has yet to be undertaken, but some of the components have been independently investigated. Rates of invasion of new habitat are a function of resource utilization for Peromyscus polionotus and Mus musculus (Gentry, 1966) and also for Microtus californicus (Lidicker and Anderson, 1962). Lidicker (1973) has shown the importance of weather in determining the reproductive season and, concomitantly, population fluctuations. Other studies

considered genetic (Tamarin and Krebs, 1969, Myers and Krebs, 1971) and demographic (Myers and Krebs, 1971, Joule and Cameron, 1975) chaacterization of dispersal.

The possibility of a genetic component to dispersal has been discussed (Howard, 1960) but few experiments have tested the hypothesis that certain genotypes are predisposed toward long distance movement, i.e., dispersal (Myers and Krebs, 1971, Smith, et al., 1975). The present experiment verified the hypothesis that there are no genetic differences between dispersers and residents in Reithrodontomys and Oryzomys. These findings are based upon assessment of genetic heterozygosity at 22 loci for Reithrodontomys and 25 loci for Oryzomys; in addition, individual sample size for both dispersers and residents was essentially equal and large, narrowing the possibility of sampling error affecting the genetic measurements. The lack of significant differences between residents and dispersers, however, does not mean that a genetic component does not exist, only that the genetic variability was not detected by eletrophoretic technique. Nei and Roychoudhury (1974) had determined that when using electrophoresis, the most important component is not individual sample size, which is a persistent problem in mammal studies, but instead locus sample size. Variance estimates for heterozygosities of dispersers and residents were determined according to Nei and Roychurdhury (1974) and are listed in Table 5. These results substantiate the hypothesis that no differences exist between residents and dispersers.

Table 5. Number of loci (r), average individual heterozygosity ($\bar{H}$), and standard errors (SE), calculated according to Nei and Roychoudhury (1974).

	REITHRODONTOMYS		
Dispersers	r = 22	$\bar{H}$ = .032	SE = .054
Residents	r = 22	$\bar{H}$ = .032	SE = .062
	ORYZOMYS		
Dispersers	r = 25	$\bar{H}$ = .052	SE = .079
Residents	r = 25	$\bar{H}$ = .055	SE = .103

Genetic characterization shows that percent polymorphism and average individual heterozygosity values in Reithrodontomys and Oryzomys is consistent with polymorphic and heterozygotic levels measured in other rodents (Smith, et al. 1976). The lack of deviation from Hardy-Weinberg equilibrium was not surprising when considering the sample necessary to determine a significant deviation. It is important to note, however, that small mammal populations violate every assumption of the Hardy-Weinberg equilibrium and that the finding of such a deviation may only be an artifact of a violation of these assumptions. Significant departures from Hardy-Weinberg equilibrium have been reported for other small mammal populations (Microtus) (Myers and Krebs, 1971, Krebs, et al., 1975). Therefore, the finding of these departures or the lack of such findings does not offer strong evidence for or against a genetic component to dispersal.

Myers and Krebs (1971) reported association between dispersal propensity and genetic heterozygosity at two loci (LAP and Tf) for Microtus pennsylvanicus and ochrogaster. In their experiment, control (A,I,F) and removal (dispersal) (J,K) fields were used; field J was not used due to low sample size. Significant differences were found during periods of population decrease between resident and disperser Microtus pennsylvanicus males at the transferrin phenotype during winter 1968-69 and summer 1969; heterozygotes were more abundant in the dispersal fields. These results were not replicated during

population declines in winter 1969-70 or summer 1970. The heterozygote excess that existed initially had vanished by the end of the experiment. Therefore, the significant difference found early in this study may have been a function of the effects of non-random or incomplete removal of animals from a population. When comparing only field A (control) and K (dispersal), no significant differences can be found in the number of heterozygotes. Field A is farther from K (the dispersal field) than the other fields (I and F). This illustrates again that the effect found was probably due to removal biases, not differential dispersal between genotypes.

Significant differences were found between resident and disperser Microtus pennsylvanicus females in the transferrin phenotypes during fall 1969 and summer 1970, between control (I and F) and dispersal (K) fields, but not between fields A and K. These differences occurred during periods of low density just before an increase, but are not replicated during any other similar phase. For this reason and the lack of significant differences between fields K (removal) and A (control), these results are unclear.

Similar results were obtained for the LAP phenotypes for males. Significant differences between dispersers and residents occurred in the first winter between I and F (control) and K (removal), but these differences were not replicated during the same season the next year or during a similar population phase; also, there were no significant differences between field A (control) and field K (dispersal), illustrating again the results may have been due to non-random removal

and not differential dispersal.

There is a lack of heterozygotes in the dispersal field for both Tf and LAP for Microtus ochrogaster males (Table 13 Myers and Krebs, 1971); differences between the total number of animals captured in each field were large. Therefore, these differences or shortage of heterozygotes may be a function of sample size rather than differential dispersal and they may also be due to pooling over years. Large deficiencies begin to appear in males between dispersal fields (J and K) at the LAP phenotype, but a comparison of the sample sizes suggests the reason for this difference.

There is some evidence for a genetic component to dispersal. Tsakas and Krimbas (1970) have found differences in genotype and mobility patterns in the olive fruit fly (Dacus oleae). They found consistently greater mobility in adult flies that were heterozygous at an esterase locus, with selection for heterozygotes occurring due to the necesssity for escape from an organophosphate pesticide. These genetic differences are not great, however, and since electrophoresis can detect a maximum of 50 to 75% of the genetic variability within an organism (Selander, 1976), any genetic differences that distinguish dispersers and residents would be difficult to detect. Therefore, the use of electrophoresis to find a genetic characteristic of dispersal requires considerable good fortune in finding an enzyme locus that is linked to other loci that are involved in the mobility of the organism.

Another problem arising from a genetic analysis of dispersal is that even if the variability within an individual could be adequately measured, the effect of pleiotropy and epistasis could not. These effects upon the development of an organism are undoubtedly great and will influence the phenotype of the individual, which will effect individual movement patterns. Genetic differences between residents and dispersers may not exist, but instead, disperser differences may be caused by epistatic and pleiotropic effects due to gene interactions or the lack of interaction.

Determination of the sample size (locus and individual) needed to detect a significant difference between residents and dispersers may be used to assess the usefulness of electrophoresis in this type of experiment and also the size of the differences necessary for the number of loci used in this experiment. Table 6 lists the number of loci necessary to detect a significant difference at the .05 level 80% of the time depending upon the difference between the means (δ) and the standard error of all individuals (σ). The appropriate formula is:

$$r \geq 2 \left(\frac{\sigma}{\delta}\right)^2 \left(t_{\alpha\nu} + t_{2(1-P)\nu}\right)^2$$

(Sokal and Rolf, 1969). This equation yields the number of loci (r) necessary to detect a true difference between two means (dispersers and residents) with a probability of certainity of .80 at the .05 level; this value is tabeled according to difference required between the two means (δ) and the standard error (σ) (Table 6). By comparing the results of this experiment with Table 6, the number of loci

Table 6. The number of loci necessary to detect differences 80% of the time at the .05 level, using the difference between the means (δ) and the standard error (σ).

δ \ σ	.050	.070	.080	.100
.001	40898	80160	104698	163592
.005	1636	3206	4188	6544
.010	409	802	1047	1636
.020	102	200	262	409
.040	26	50	65	102
.080	6	13	16	26
.100	4	8	10	16

necessary to detect a true difference between residents and dispersers can be computed. Therefore, for Oryzomys, the difference between dispersers and residents is .003, with an average standard error of .08 (Table 5). From Table 6, over 4000 loci would be necessary to detect a true difference 80% of the time. In order to determine differences between residents and dispersers when the difference (δ) is equal to .02, six times greater than the results of this study, and a standard error equal to the one of this experiment, 10 times the number of loci used would be necessary to make these differences significant 80% of the time. Using the reverse approach, the mean differences necessary to detect a significant difference 80% of the time using 22 loci and the same standard error, would be approximately .08, which is 27 times the difference obtained in this experiment. Therefore, the use of electrophoresis to assess differences in heterozygosity between residents and dispersers is inadequate because of the large number of loci required.

Demographic analysis indicated significant positive correlations between percent reproductive and average distance moved for both Sigmodon and Reithrodontomys, indicating movement increases during reproductive seasons. Increased levels of movement during reproductive seasons have previously been correlated (Christian, 1962), along with increase in aggression levels. This increase in movement during breeding seasons has been attributed to a decrease of available breeding sites during the breeding season (Murray, 1967). Murray

contends that if juvenile mortality is 40%, a shortage of available breeding sites during the breeding season will cause a concomitant increase in movement to locate vacant breeding sites. Precise breeding sites for Sigmodon or Reithrodontomys are unknown. If males are territorial during reproductive season, the importance of an analysis of movement patterns during both reproductive and non-reproductive seasons becomes obvious.

Sex ratios for dispersing rodents have been discussed (Stickel, 1946, Myers and Krebs, 1971, Krebs, et al., 1975, O'Farrell, 1975). Males are almost always the dominant movers into voids or they have greater movement patterns. Sex ratios of long distance movers from the Sympatric Experiment (the last 7% of the distribution) deviated significantly from a 1:1 sex ratio (Fig. 2); there were significantly more male long distance movers for both Sigmodon and Reithrodontomys, a phenomena consistent with the papers of Stickel (1946) and O'Farrell (1975). Sigmodon males were the predominant long distance movers, but were equal in numbers (1:1) over the three years of the Sympatric Experiment, indicating a definite effect of sex upon movement. The data for Reithrodontomys is confounded by the fact that the sex ratio for the entire population over three years was close to 2:1, with males in higher proportion than females. This result has also been reported by Fisler (1971) and Joule and Cameron (1976).

Further analysis of sex ratios in the Void Experiment, however, revealed no differences in Sigmodon or Oryzomys from a 1:1 sex ratio

in either void or marked fields, but Reithrodontomys sex ratio was skewed towards males. The finding that longer distance movers are skewed towards males was not surprising, but the lack of deviation from a 1:1 sex ratio for Sigmodon and Oryzomys in the void field was. This lack of deviation in the Void Experiment may be due to the rareness of long distance movers or they were not picked up in 1 plot over short time periods. This contrast of data from a three year experiment and a one year experiment points out the importance of longer studies and an analysis of movement patterns as oppossed to a void field.

The initial assumption of this experiment was that all animals within the void were dispersers and if the analysis of the data from the three year Sympatric is correct, then more males should be collected in the void field. Since Reithrodontomys populations are skewed towards males normally, the conclusion may be that the void field was not collecting dispersers. These findings are consistent with the conclusion of Joule and Cameron (1975), that animals moving into voids are a template of the surrounding population. Heterogeneity in sex ratios occurs only within the summer season for both Microtus pennsylvanicus and ochrogaster (Myers and Krebs, 1971), but these differences are not significant through seasons. Similar results are found in the voids utilized by Microtus townsendii (Krebs, et al., 1975). These results suggest that voids collect animals having greater ranges or movement patterns, but that these animals do no differ from

individuals in the surrounding fields.

Reproductive condition may be related to propensity for dispersal (Howard, 1960, Murray, 1967, Metzger, 1971, Myers and Krebs, 1971, Krebs, et al., 1975). Reproductive condition was independent of field and season for all three species in the void experiment, but a positive correlation was found for percent reproductive and AVED. If reproductive rediness is related to increased movement and if the void field was collecting dispersers, then a dependency between these variables should have been found in the void field. Since a dependency between reproduction and presence of dispersers in the void field was not found, two conclusions are possible: either the void field was not collecting dispersers or movement and reproduction are not correlated for these species. Evidence not supporting the latter has already been discussed. Dependency or a dominance of animals in breeding condition with field found (Myers and Krebs, 1971), with dependency due to the void field (K). Closer examination of the data shows significant heterogenity among the control fields for males Microtus pennsylvanicus and ochrogaster and female Microtus ochrogaster when considering the proportion of subadults in breeding condition (Table 6 and 7, Myers and Krebs, 1971). If field A (control) was considered as a removal field, the same differences could be shown as were found for the void fields. Therefore, the possibility exists that removal fields or void fields were not collecting dispersers or that dispersers are equal to residents demographically.

Demographic analysis showed that reproductive condition was independent of the void field and season, meaning a certain proportion of animals are always in reproductive condition. Sex ratios did not differ in the void and there were no significant differences in weights between void animals and residents. The number of unmarked animals captured in the void was independent, negating the thesis that removal fields act as "magnets". These results suggest that: dispersers do not differ demographically from residents (consistent with Joule and Cameron, 1975), void fields do not collect the long distance movers, or both.

From these conclusions, a new approach to the study of dispersal will be proposed. It seems obvious from the results of this experiment and other studies that consistent attributes do not separate dispersers from residents, at least for Sigmodon and Reithrodontomys. Genetic or demographic characters may not differentiate residents, or the animals that do not leave a population, from dispersers, or animals that are long distance movers. Whether or not dispersers were different from resident animals cannot be shown from the evidence at hand. Obviously, the phenomenon of dispersal is important in maintaining population structure and gene flow, but characterization of dispersers has not been successful.

The analysis of dispersal or long distance movement and its effects upon population structure is one of the most important questions concerning small mammal populations, but is also one of the most difficult to answer. From this and similar studies concerning

dispersal, four conclusions can be presented as a stepping-stone to further analysis, and perhaps an aid in acquiring more significant results. First, genetic characterization of small mammals using heterozygosity level or deviation from Hardy-Weinberg equilibrium is questionable at best and may be non-productive. Second, demographic characterization offers contradictory and inconsistent data, due to the different dispersal strategies between rodents. Third, the use of void fields for the study of dispersal assumes that a void is inhabited by long distance movers, an assumption that is validated only by a knowledge of the recapture history of the animal. Fourth, the study of dispersal requires a detailed study of movement patterns, environmental fluctuations, and resource utilization over a significant time interval and a large study area.

In order to quantify dispersal, a knowledge of three factors is necessary: daily and seasonal movement patterns, physical and biotic environmental heterogeneity, and patterns of resource utilization. The analysis of movement requires the utilization of telemetry or daily trapping, neither of which are without problems. The attachment of electronic devices to rodents undoubtly affects their behavior, as would daily trapping and I can offer no directions from this maze of problems, but environmental monotoring and resource utilization along with weekly or biweekly trapping over a significant amount of time (2 years) and a large area, would definitely yield significant results. This experiment would require the cooperation of many researchers and

perhaps a joint effort from several universities. A continuation of short term studies or small area studies would not be advised as this would lead only to more confounding results.

It may be suggested, therefore, that "dispersers" are unable to be characterized because they are not different from other members of the population. Dispersal may be synonymous with long distance movement (reflected by a large AVED) and AVED may be useful in elucidating the contribution of such movement to population structure. The probability of dispersal may be distributed equally between all members of a population and is affected by resources and environment. It may be also suggested that for each species of animal or for each differing geographic location, differing dispersal strategies may be utilized by small mammals and general rules concerning these strategies may be found.

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APPENDIX 1.

Reithrodontomys dispersers

Species	Sex	Toe Number	GOT 1	GOT 2	GDH 1	GDH 2	SDH 1	MDH 1	MDH 2	IDH 1	IDH 2	LDH 1	LDH 2	ADH 1	PGM 1	PGM 2	PGI 1	PGI 2	GPD 1	IPO 1	6PGD 1	A1 1	G-6-P 1	Hb 1	$\bar{H}$	AVED (captures)
R	F		M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	.000	
R	M														FM										.045	
R	F														M										.000	
R	M														FM	FM									.090	
R	M														M	M									.000	
R	M															F									.000	
R	F															M									.000	
R	F																								.000	
R	M													MS											.045	
R	F													M											.000	
R	F																								.000	
R	M														FM										.045	
R	?														FM	FM									.090	
R	F													FM	FM	M									.090	
R	F													M	M										.000	
R	F																								.000	
R	F																								.000	
R	F														FM	FM									.090	
R	M													FM	M	M									.045	
R	F													M	FM										.045	
R	F														M										.000	
R	M																								.000	
R	F																								.000	
R	F	1-6-50													FM										.045	.00 1
R	M														M										.000	
R	M																								.000	
R	F																								.000	
R	M													MS			MS								.090	

Species	Sex	Toe Number	GOT 1	GOT 2	GDH 1	GDH 2	SDH 1	MDH 1	MDH 2	IDH 1	IDH 2	LDH 1	LDH 2	ADH 1	PGM 1	PGM 2	PGI 1	PGI 2	GPD 1	IPO 1	6PGD 1	Al 1	G-6-P 1	Hb 1	$\bar{H}$	AVED (captures)
R	M		M	M	M	M	M	M	M	M	M	M	M	M	F	M	M	M	M	M	M	M	M	M	.045	
R	M													MS	M	FM	FM	FM							.180	
R	M	1-30-80												MS		FM	M	M							.090	
R	F													M		M									.000	
R	M																								.000	
R	M															FM									.045	
R	M														FM	FM									.090	
R	M													FM	M	M									.045	
R	M	1-7-90												M		FM									.045	
R	M															M									.000	
R	M																								.000	
R	M	3-4-5													F										.000	
R	M														M										.000	
R	M													FM											.045	
R	M													M		FM									.045	
R	M															M									.000	
R	F																								.000	
R	M																								.000	
R	M	1-7-80														FM									.045	1.41 (2)
R	M															M									.000	
R	M													FM											.045	
R	M	7-20-90												M											.000	
R	M																								.000	
R	M																								.000	
R	F	1-30-100															MS								.045	
R	M	40															M								.000	2.00 (2)
R	F	1-70																							.000	.63 (2)
R	M	1-10-80																							.000	1.41 (2)

Species	Sex	Toe Number	GOT 1	GOT 2	GDH 1	GDH 2	SDH 1	MDH 1	MDH 2	IDH 1	IDH 2	LDH 1	LDH 2	ADH 1	PGM 1	PGM 2	PGI 1	PGI 2	GPD 1	IPO 1	6PGD 1	Al 1	G-6-P 1	Hb 1	H	AVED (captures)
R	M	2-4-7																							.000	
R	F									FM					FM										.090	
R	F									M					FM										.045	
R	M			FM											FM										.090	
R	F			M											M										.000	
R	M	3-7-90																							.000	
R	F																								.000	
R	F													MS	FM										.090	
R	F													M	M										.000	
R	M			FM																					.045	
R	F			M																				MS	.045	
R	M									FM														M	.045	
R	M									M					FM										.045	
R	F									FM					M		FM								.090	
R	M									M							M				MS				.045	
R	F	3-6-8		MS																	M		MS		.090	
R	M			FM						FM													M		.090	
R	F			M						M					F										.000	
R	M		MS												M										.045	
R	M		M	MS																					.045	
R	M			M											FM										.045	
R	M	3-7-20													M										.000	
R	M														F										.000	
R	M														M		FM								.045	
R	F																M								.000	
R	M																								.000	
R	M																								.000	
R	M																								.000	

Species	Sex	Toe Number	GOT 1	GOT 2	GDH 1	GDH 2	SDH 1	MDH 1	MDH 2	IDH 1	IDH 2	LDH 1	LDH 2	ADH 1	PGM 1	PGM 2	PGI 1	PGI 2	GPD 1	IPO 1	6PGD 1	Al 1	G-6-P 1	Hb 1	H	AVED (captures)
R	M													MS											.045	
R	F													M											.000	
R	M		MS																						.045	
R	F		MS																						.045	
R	F		FM																						.045	
R	F		MS											MS	FM						MS				.180	
R	M		M											MS	M						M				.045	

APPENDIX 2.

Reithrodontomys residents

Species	Sex	Toe Number	GOT 1	GOT 2	GDH 1	GDH 2	SDH 1	MDH 1	MDH 2	IDH 1	IDH 2	LDH 1	LDH 2	ADH 1	PGM 1	PGM 2	PGI 1	PGI 2	GPD 1	IPO 1	6PGD 1	Al 1	G-6-P 1	Hb 1	Ā	AVED	(captures)
R	M	3-6-100	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	.000		
R	M	3-20-30								FM							FM								.090		
R	M									M							M						MS		.045		
R	M	3-7-50																					M		.000		
R	M	4-5-40													FM								S		.045		
R	M														FM								M		.045		
R	M	3-8-40													M										.000		
R	F																								.000		
R	F	3-30-70																							.000		
R	F	3-7-60												MS											.045		
R	M	3-20-90												M											.045		
R	M	3-7-10																							.000		
R	M	3-8-90																FM							.045		
R	F	1-7-30												FM				M							.045	2.00	(2)
R	M	2												M	FM										.045	1.31	(4)
R	M	1-30-50													M										.000	1.00	(2)
R	F	8-10		MS																					.045	.98	(4)
R	M	2-5-50		M																					.000		
R	F	1-7-60																							.000	.00	(2)
R	F													MS											.045		
R	M													M	FM										.045		
R	M	1-7-70												MS	M										.045	1.00	(2)
R	F	2-3-20												M	FM	FM									.090	1.00	(2)
R	M	1-7-100													M	FM									.045	.00	(2)
R	F	1-8-40													FM	M									.045	1.00	(2)
R	M	1-2-100													M										.000	.71	(3)
R	M																								.000		
R	F															FM									.045		

Species	Sex	Toe Number	GOT 1	GOT 2	GDH 1	GDH 2	SDH 1	MDH 1	MDH 2	IDH 1	IDH 2	LDH 1	LDH 2	ADH 1	PGM 1	PGM 2	PGI 1	PGI 2	GPD 1	IPO 1	6PGD 1	A1 1	G-6-P 1	Hb 1	Ñ	AVED	(captures)
R	M	1-5-8													FM	FM									.090	.00	(2)
R	M	1-40-50													M	M									.000	1.00	(2)
R	M	1-40-60																							.000	.00	(2)
R	M	100												FM		FM									.090	.00	(2)
R	M	2-5-90												MS	FM	FM									.135		
R	F	1-5-10												M	M	M									.000	1.41	(2)
R	M	70													FM	FM									.090	1.81	(8)
R	F														FM	FM									.090		
R	M														M	M									.000		
R	F	1-4-8																							.000	.50	(3)
R	F	1-5-6												MS											.045	.00	(2)
R	F													M											.000		
R	F																MS								.045		
R	F			MS													M								.045		
R	F	1-6-8	M																						.000	.00	(2)
R	F	8-30	MS																						.045	.00	(2)
R	M	1-50-60	M														MS								.045	.00	(2)
R	F	1-50-80													FM	FM	M								.090	.00	(2)
R	M														M	M	MS								.045		
R	F	1-8-70															M								.000	1.00	(2)
R	F	1-60-70												MS	FM										.090	.00	(2)
R	F														FM										.045		
R	M	7		MS											M										.045	1.71	(11)
R	M	1-3-50	M																						.000	.50	(3)
R	M	1-60-100															MS								.045	1.41	(2)
R	M																M								.000		
R	M			MS											FM										.090		
R	M	7-20		MS											M										.045	1.51	(7)

Species	Sex	Toe Number	GOT 1	GOT 2	GDH 1	GDH 2	SDH 1	MDH 1	MDH 2	IDH 1	IDH 2	LDH 1	LDH 2	ADH 1	PGM 1	PGM 2	PGI 1	PGI 2	GPD 1	IPO 1	6PGD 1	A1 1	G-6-P 1	Hb 1	R	AVED	(captures)
R	M	1-70-80													F	MFM									.090	1.41	(2)
R	F	1-10-50													M	M									.000	1.00	(2)
R	F																								.000		
R	M	1-30-70	MS												F	M									.090	.71	(3)
R	F	81		M											M										.000	.73	(8)
R	F	20-100													F	MFM									.090	.28	(3)
R	F	1-4-60													M	M	MS								.045	1.00	(2)
R	M	1-4															M								.000	.00	(2)
R	F																								.000		
R	M																								.000		
R	F														F	M									.045		
R	F														F	M									.045		
R	F														F	M									.045		
R	F														M										.000		
R	M	1-3-90																							.000	1.12	(3)
R	F	80																							.000	1.20	(2)
R	M																								.000		
R	M	1-5-30																MS							.045	1.41	(2)
R	F																	M							.000		
R	F																								.000		
R	F	1-3														F	M								.045	.72	(2)
R	M	20-30-60												MS		M									.045	1.71	(3)
R	F	3-80												MS											.045	.50	(4)
R	M	1-4-5												M	F	M									.045	1.50	(3)
R	F	1-6-7													M										.000	.00	(2)
R	M	1-20-50																							.000	1.00	(2)
R	F													FM		FM									.090		
R	M	1-60												M		M									.000	.00	(2)

Species	Sex	Toe Number	GOT 1	GOT 2	GDH 1	GDH 2	SDH 1	MDH 1	MDH 2	IDH 1	IDH 2	LDH 1	LDH 2	ADH 1	PGM 1	PGM 2	PGI 1	PGI 2	GPD 1	IPO 1	6PGD 1	A1 1	G-6-P 1	Hb 1	Π	AVED	(captures)
R	M																								.000		
R	F															FM									.045	1.21	(7)
R	F	1-6-90														M									.000	1.00	(2)
R	M	1-4-90													FM										.045	.50	(3)
R	F														M										.000		

APPENDIX 3.

Oryzomys dispersers

Species	Sex	Toe Number	GOT 1	GOT 2	GDH 1	GDH 2	SDH 1	MDH 1	MDH 2	IDH 1	IDH 2	LDH 1	LDH 2	ADH 1	PGM 1	PGM 2	PGI 1	PGI 2	GPD 1	IPO 1	6PGD A1 1	G-6-P Hb 1	AP 1	Pept. 1	Pept. 2	H
O	F		M	M	M	MS	M	M	M	M	M	FM	M	M	M	M	M	M	FM	M	M	M	M	M	M	.12
O	F					FM						F		FM					F							.08
O	M					M						F		M					MS							.04
O	M											M				MS			M							.04
O	M											FM		FM		MS			MS							.16
O	M									FM		M	F	M		M			M							.04
O	M					FM				M		FM	M						MS							.12
O	F					M		FM		FM		M	F		FM				F							.12
O	M	3316						M		M		FM	M	FM	M				FS							.12
O	F											F		M					M							.00
O	M			MS								M														.04
O	M			M				FM									FM									.08
O	M							M									M									.00
O	F							MS									MS									.08
O	M			MS				M									M									.04
O	M	2-8-40		MS																						.04
O	F			M																						.00
O	M																									.00
O	F			MS				MS									MS									.12
O	M			M				M									M									.00
O	F			S																						.00
O	M	4-30		MS				F				FM					F									.08
O	F			MS				M				M					M									.04
O	F	1-2		M																						.00
O	M	4-100																								.00

APPENDIX 4.

Oryzomys residents

Species	Sex	Toe Number	GOT 1	GOT 2	GDH 1	GDH 2	SDH 1	MDH 1	MDH 2	IDH 1	IDH 2	LDH 1	LDH 2	ADH 1	PGM 1	PGM 2	PGI 1	PGI 2	GPD 1	IPO 1	6PGD 1	A1 1	G-6-P 1	Hb 1	AP 1	Pept. 1	Pept. 2	$\bar{H}$
O	M		M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	MS	M	M	M	M	M	M	M	M	.04
O	M	4-60																	M									.00
O	M																		MS									.04
O	M													MS					M									.04
O	M													M														.00
O	M																											.00
O	M			FM																								.04
O	M			M															MS									.04
O	F					FM								FM					MS									.12
O	F	4-70				M								FM					MS									.08
O	F	4-6												M					M									.00
O	M	8				FM								FM					MS									.12
O	M					FM								FM					MS									.12
O	M	3				FM						FM		FM					M									.12
O	M	5-20				M						M		M														.00
O	?																											.00
O	F	4-90										FM																.04
O	M					MS						M		MS					MS									.12
O	M			FM		M								M					MS									.08
O	M			M															MS									.04
O	M																		MS									.04
O	M	5-80																	M									.00
O	?													MS					MS									.08
O	F	40-50		F										M					M									.00
O	M	30-100		F																								.00
O	M	foot		MS				MS				FM					MS												.16
O	F	30-80	FMM					S				FM					S												.08
O	F	40-70		MS				FM		FM		M					M												.12

APPENDIX 5.

Gel and Tissue types used

in *Oryzomys* electrophoresis.

		Gel Type				
System (loci no.)		TM+	TC 8.0	PGI-Phos	LiOH	TC 6.7	P+
Peptidase	(2)	Liver					
6 PGD	(1)	Liver					
GOT*	(2)		Liver				
IDH	(2)		Liver			Heart Kidney	
GDH*	(2)		Liver				
PGI	(2)			Liver			Liver
PGM	(2)			Liver			Liver
GPD*	(1)			Liver	Liver		Liver
SDH	(1)			Liver	Liver		Liver
ADH*	(1)			Liver			Liver
A1	(1)				Liver		
MDH*	(2)					Heart Kidney	
LDH	(2)					Heart Kidney	
IPO	(1)						Liver
G-6-P	(1)						Liver
AP	(1)		Liver				
Hb	(1)				Liver		

*Polymorphic at the .05 level

APPENDIX 6.

Gel and Tissue types used

in *Reithrodontomys* electrophoresis.

Gel Type

System (loci no.)		LiOH	TC 8.0	TC 6.7	P+	TM+	PGI-Phos
SDH	(1)	Liver	Liver				
PGI	(2)						Liver
PGM*	(2)						Liver
LDH	(2)			Heart Kidney			
IDH	(2)			Heart Kidney			
MDH	(2)		Liver	Heart Kidney			
GOT	(2)		Liver				
GDH	(2)		Liver			Liver	
GPD	(1)	Liver			Liver		
G-6-P	(1)				Heart Kidney		
ADH*	(1)						Liver
6-PGD	(1)					Liver	
IPO	(1)				Liver		
Hb	(1)	Liver					
Al	(1)	Liver					

*Polymorphic at the .05 level