AN ABSTRACT OF THE THESIS OF

Lisa Page Fredericks for the Masters of Science

in Biology presented on August 17, 1994

Title: Genetic variation in insular populations of the eastern woodrat (Neotoma floridana) in a forest-prairie mosaic

Abstract approved: [signature]

The genetic makeup of a population is strongly dependent upon the dispersal patterns among the demes within that population. Dispersal allows gene flow to occur among demes, and lack of it allows genetic drift to cause differentiation to occur among demes. A forest-prairie ecotone exists in eastern Kansas. Many of the wooded areas house insular populations of eastern woodrats (Neotoma floridana attwateri). The purpose of my study was to determine dispersal rates among these insular populations as well as to add to the knowledge of the genetics of eastern woodrats. The hypotheses were: 1) there is limited dispersal among demes; and 2) the smaller and the more distant demes are more divergent genetically than those larger or closer to the main population. Electrophoresis was performed on eastern woodrat ear tissue. Four out of 19 loci were polymorphic. Nei's genetic distance ranged from 0.000 to 0.001. With Nei's distance coefficients this low, no determination could be made concerning dispersal among demes. The genetic differentiation among demes was essentially nonexistent. Eastern woodrats are thought to

have undergone a significant bottleneck about 10,000 ybp, which resulted in reduced genetic variability in these rats in the western and northern portions of their range. With this overall low genetic variability and more recent localized bottlenecks within the patchy habitat in Kansas, there still remains little genetic diversity within the eastern woodrats of Kansas.

GENETIC VARIATION IN INSULAR POPULATIONS OF THE EASTERN WOODRAT, (*NEOTOMA FLORIDANA*) IN A FOREST-PRAIRIE MOSAIC

A Research Thesis
Submitted to
the Division of Biological Sciences
Emporia State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
L. Page Fredericks
December, 1994

A. H. Moore
Approved by Major Advisor

James M. Mayo
Approved by Committee Member

Elmer J. Fink
Approved by Committee Member

David K. Saunders
Approved by Committee Member

David K. Saunders
Approved for Major Department

John D. Schuerm
Approved for Graduate Council

ACKNOWLEDGEMENTS

Thanks go to all those who helped me with field work, collecting woodrat ears; Terri Abbett, Kelly Conrad, Jean Schulenberg, and many of the Biology 101 class. I would like to give further thanks to Terri Abbett and Jean Schulenberg for their advice concerning my thesis. I also thank the members of my committee; Drs. Elmer Finck, James Mayo, and David Saunders for their guidance and comments concerning the writing of my thesis. Special thanks to Dr. David Saunders for all his advice, help, and encouragement during my time at Emporia State University as well as with my thesis. Special thanks also to my major advisor Dr. Dwight Moore for his advice and help with many aspects of my thesis.

PREFACE

My thesis has been prepared in a style appropriate for The Southwestern Naturalist to which it will be submitted for publication.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Patterns of dispersal play a major role in determining genetic variance among populations (Lidicker and Patton, 1987; Shields, 1987). The amount and frequency of dispersal, whether successful or not, have a large impact on the genetic structure of insular populations. The genetic consequences of dispersal involve behavior, population structure, speciation, and ultimately evolution (Shields, 1987). Low levels of immigration lead to dissimilarity between populations, and high levels of immigration lead to genetically similar populations. Unsuccessful dispersal effects are important as well, and can affect levels of competition, interactions among individuals, and genetic drift (Lidicker and Patton, 1987). When emigrants carry rare alleles from small populations, whether they successfully migrate or not, the genetic makeup of the source population can be greatly altered (Lidicker and Patton, 1987).

The eastern woodrat (Neotoma floridana attwateri) in east-central Kansas represents an opportunity to study the effects of dispersal among insular populations. An ecotone exists between the oak-hickory forests of eastern Kansas and the tallgrass prairie of the Flint Hills (Jones et al., 1985). This creates a mosaic of woodland within the prairie, where some of the woodland patches provide good habitat for woodrats. To reach some of these patches, woodrats must cross a substantial area of grassland. The

intervening grassland habitat is unsuitable for woodrats and represents a "leaky" barrier to woodrat dispersal. The grasslands provide little building material for houses, little food, and insufficient cover for protection from predators.

In Kansas, woodrats construct their houses primarily of twigs (Rainey, 1956). The house is often built at the base of a tree, among limestone outcroppings, in a brush pile, or in an abandoned building (Rainey, 1956; Wiley, 1980; Jones et al., 1985). Their diet is variable, and in eastern Kansas, often consists of the leaves, seeds and fruits of trees such as Osage oranges (Maclura pomifera [Raf.] Scneid.), redbuds (Cercis canadensis L.), oaks (Quercus spp.), and green ash (Fraxinus pennsylvanica Marsh.) (Post, 1992), as well as red cedar (Juniperus virginiana L.) and rough-leaved dogwood (Cornus drummondii Meyer) (personal observation) depending upon availability. Large amounts of soybeans have also been found in woodrat caches (J. Mayo pers. comm.). However, they rarely eat grass seeds (Wiley, 1980). In the wild they obtain most or all of their water from succulent vegetation (Wiley, 1980). Owls, skunks, weasels, snakes and coyotes are all predators of woodrats (Fitch and Rainey, 1956; Wiley, 1980). With the exception of some snakes which can enter the rat's house, most predators have an easier time catching woodrats in grasslands where there is no protective cover.

Near its house, the eastern woodrat is aggressive and territorial. All woodrats invading the house are chased off or attacked (Jones et al., 1983), except when mating. Young and adults exhibit both philopatry and dispersal. The young usually leave their natal houses when they become independent of their mothers. Patterns of dispersal are irregular, however, as it may be the mother who leaves, leaving one of her young behind (Fitch and Rainey, 1956). Fitch (1958) suggested that adults may disperse to find mates. Adults and young will most often occupy vacant houses that are nearby rather than dispersing further away (Warner, 1986). However, in times of high population levels or low availability of house sites, the young and smaller adult woodrats will be forced further away from their natal sites.

Small, isolated populations, such as those experienced by endangered species, will lose all genetic variation due to drift, given adequate time (Chepko-Sade et al., 1987). A loss of genetic variation can cause reduced ability to adapt to changes in the environment (Chepko-Sade et al., 1987). For this reason, as well as for evolutionary and taxonomic analyses, genetic variation within and among species has been studied in a variety of animal species; for example: the Florida tree snail (Liguus fasciatus) (Hillis et al., 1991), the Tennessee shiner (Notropis leuciodus) (Mayden and Matson, 1992), the red-backed salamander (Plethodon

cinereus) (Highton and Webster, 1976), white-tailed deer (Odocoileus virginianus) (Mathews and Porter, 1993), and pocket gophers (Orthogeomys spp.) (Hafner, 1991).

Zimmerman and Nejtek (1977) used electrophoresis to determine evolutionary relationships among three species of woodrats, N. floridana, N. albigula, and N. micropus, from the southwestern United States. They investigated populations of N. f. attwateri from Texas, Oklahoma and Colorado, and found nine polymorphic loci out of twenty loci analyzed. Hayes and Harrison (1992) used mitochondrial DNA (mtDNA) to study the evolutionary relationships among several subspecies of woodrats from the eastern United States and found little variability in N. floridana in the western portion of its range. Except for one population in Arkansas, the nucleon diversity ($\hat{h}$) (analogous to heterozygosity in a diploid system) equalled zero. One of these populations came from about 21 km away from the populations in my study.

The genetic diversity among subpopulations of N. floridana in a small geographical area were measured to provide further genetic information on this species, which is experiencing population declines in the northeastern United States (Hayes and Harrison, 1992). Genetic analyses have indicated that the northeastern population is likely a separate species, (N. magister) (Hays and Richmond, 1993). These two groups of woodrats are closely related whether

they are separate species or subspecies. Without knowing the cause, or causes, of the decline, we should gather as much information as possible on any species before a serious decline occurs. A serious decline may never occur, but if it should, it would then be too late to gather information without further disturbing the population.

The working hypotheses of my study were: 1) there is limited dispersal among demes; and 2) the smaller or more geographically isolated demes are, the more divergent genetically they will be than those larger or closer to the main population. A better knowledge of the genetics as well as the amount and patterns of gene flow in the eastern woodrat can be helpful for conservation and management efforts (Smith et al., 1976).

MATERIALS AND METHODS

Eastern woodrats were live trapped using Tomahawk traps from mid summer to early winter in 1993-1994. After capture, the woodrats were anesthetized with ether. One ear was taken from each rat, and the rats were marked by toe clipping (ad hoc Committee on Acceptable Field Methods, 1987) for later identification. The rats were sexed, age categorized, and total length, tail length, and hind foot length measured in millimeters (see Appendix 1). They were then released at the spot of capture. Removed ears were initially placed on ice, then upon arrival at the lab, stored in an ultracold freezer at -70°C.

Horizontal starch gel electrophoresis was performed on the ear tissue using a method similar to Dubach's (1986). Electrophoretic techniques, buffer systems and stains were modified after those described by Harris and Hopkinson (1976). Gels were prepared using hydrolyzed potato starch, either 100% from Sigma Chemical Co. (St. Louis, MO) or a 50:50 mixture of Sigma starch and Connaught starch (Toronto, Canada). In multiple locus systems, the isozyme migrating most anodally was designated "1". Alleles were scored by designating the most anodally migrating allele as "A". All other alleles at a locus were assigned alphabetic designations in order of decreasing anodal mobility. Nineteen presumptive loci were resolvable on three buffer media. Esterase-1, -2 (ES-1, -2; 3.1.1.1), purine

nucleoside phosphorylase (NP; 2.4.2.1), peptidase glycyl-leucine (PEPgl; 3.4.11), peptidase leucyl-glycyl-glycine (PEPlgg; 3.4.11), and xanthine dehydrogenase (XDH; 1.2.3.2) were resolvable using lithium hydroxide (ph 8.2) buffer. Lactate dehydrogenase-1, -2 (LDH-1, -2; 1.1.1.27), malate dehydrogenase-1, -2 (MDH-1, -2; 1.1.1.37), and malic enzyme (ME; 1.1.1.40) were resolvable using tris citrate (ph 6.7) buffer. Creatine kinase-1, -2 (CK-1, -2; 2.7.3.2), general protein (GP), glucose phosphate isomerase (GPI; 5.3.1.9), glucose-6-phosphate dehydrogenase (GD; 1.1.1.49), isocitrate dehydrogenase (IDH; 1.1.1.42), and phosphoglucomutase-1, -2 (PGM-1, -2; 2.7.5.1) were resolvable using tris citrate (ph 8.0) buffer.

F-statistics (Wright, 1965, 1978; Nei, 1977) were performed to determine levels of inbreeding. Coefficients for Nei's (1972) genetic distance and Rogers' (1972) similarity were used to compare populations on the basis of gene frequencies. All statistics were performed using the BIOSYS-1 package of Swofford and Selander (1981).

STUDY AREA

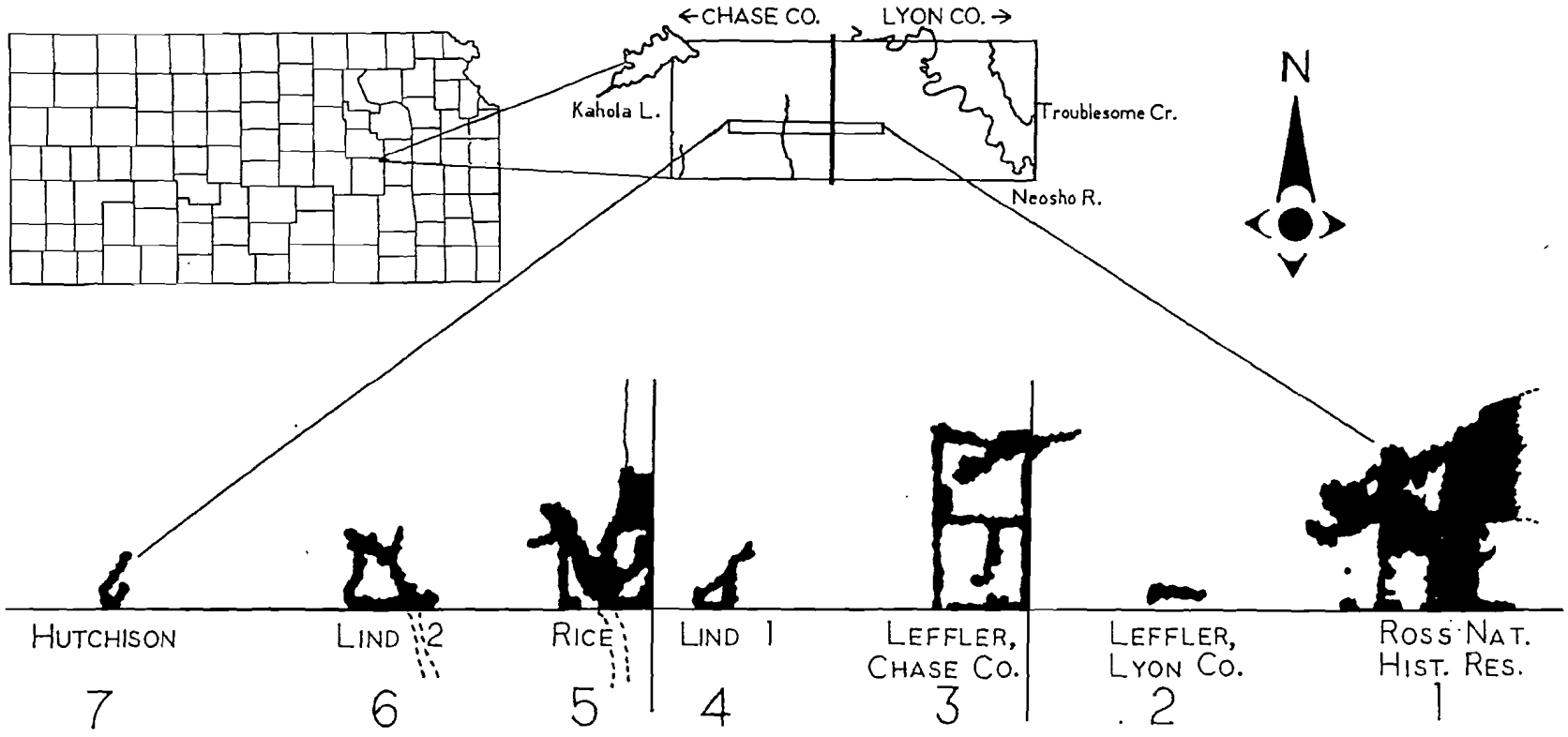
Eastern woodrats were live trapped from seven subpopulations in eastern Kansas (Fig. 1). These populations were assumed to be insular, or temporarily isolated but with some immigration, as characterized for other species by Chesser (1983). One aspect of my study was to determine the validity of this assumption. The names, legal descriptions and area of each woodlot, and the number of animals from which tissue was taken (indicated by the number in parentheses) are presented below. The approximate area of each woodlot was measured from current county soil survey maps and converted to hectares. Ross Natural History Reservation (Ross): SW 1/4, Sec 8, T 18S, R 10E; approximate area = 50 ha, (17). Leffler, Lyon Co.: S 1/2, Sec 7, T 18S, R 10E; approximate area = 2 ha, (4). Leffler, Chase Co.: E 1/2, Sec 12, T 18S, R 9E; approximate area = 32 ha, (18). Lind 1: E 1/2, Sec 12, T 18S, R 9E; approximate area = 32 ha, (4). Rice: SE 1/4, Sec 11, T 18S, R 9E; approximate area = 21 ha, (9). Lind 2: SW 1/4, Sec 11, T 18S, R 9E; approximate area = 2 ha, (6). Hutchison: E 1/2, SW 1/4, Sec 10, T 18S, R 9E; approximate area = 2 ha, (3). The minimum distances between each woodlot containing a subpopulation examined in my study are: Ross to Leffler, Lyon Co. = 0.58 km; Leffler, Lyon Co. to Leffler, Chase Co. = 0.54 km; Leffler, Chase Co. to Lind 1 = 0.78 km; Lind 1 to Rice = 0.18 km; Rice to Lind 2 = 0.46 km;

Lind 2 to Hutchison = 0.94 km.

The study area, as well as each of the seven sites, includes both grassland and woodland. The dominant grasses are big bluestem (Andropogon gerardii, Vitman.), little bluestem (Andropogon scoparius, Michx.), and Indian grass (Sorghastrum nutans, [L.] Nash). Between each site is primarily grazed grassland, and within each site is mixed deciduous trees with a few red cedars. On the Ross, red cedars are more abundant with lesser numbers of honey locust (Gleditsia triacanthos), elm (Ulmus spp.), small Osage orange, russian olive (Elaeagnus angustifolia), hickorys (Carya spp.), oaks (Quercus spp.), hackberry (Celtis occidentalis), green ash (Fraxinus pennsylvanica), and in low lying, wetter areas cottonwood (Populus deltoides) and black willow (Salix nigra). Wild plum (Prunus americana) and rough-leaved dogwood thickets occur on portions of the Ross as well. The majority of trees on the sites in Chase Co. are Osage oranges, though along the riparian corridors cottonwoods are the predominant tree. Hedge (Osage orange) rows occur on at least two sides of the Leffler, Chase Co.; Lind 2; and Rice sites, each of which includes a portion of a riparian corridor. On the Rice site, cottonwoods interspersed with rough-leaved dogwoods predominate. The Lind 1 site consists of Osage oranges, honey locusts, black willows, and other deciduous trees situated around a pond. All of the sites, except Leffler, Lyon Co. and Hutchison,

have areas of relatively compact woods. The Hutchison site is situated within a gently sloping grassland at the edge of the Flint Hills. Osage orange trees are scattered along a shallow ravine that ends in a small pond sparsely surrounded by cottonwoods. The Leffler, Lyon Co. site lies within a grassy pasture, with low rocky outcrops, a few small bushes, and no trees.

Figure 1. Names and locations of the seven subpopulations of Neotoma floridana sampled from Lyon and Chase counties, Kansas. Subpopulations were numbered consecutively from east to west.


←CHASE CO.
LYON CO.→
Kahola L.
Troublesome Cr.
Neosho R.
N
HUTCHISON
7
LIND 2
6
RICE
5
LIND 1
4
LEFFLER, CHASE CO.
3
LEFFLER, LYON CO.
2
ROSS NAT. HIST. RES.
1
0.3 km = 1 cm

RESULTS

Rogers' genetic similarities between pairs of populations ranged from 1.000 to 0.986 (Table 1). Nei's genetic distances were very low, 0.001 and 0.000 (Table 1). Of the 19 presumptive loci examined, four were polymorphic; malate dehydrogenase-1, purine nucleoside phosphorylase, peptidase glycyl-leucine, and phosphoglucomutase-2 (Table 2). Sample sizes at each site ranged from three to eighteen individuals. Some sites were too small to house many woodrats, and woodrat populations appeared to be low as there were empty houses on all sites (personal observation). Figure 2 shows graphically the allele frequencies of the polymorphic loci for each subpopulation. Two of the seven sites have three polymorphic loci, with NP and MDH-1 common to both. NP is polymorphic in four of the sites, in two of which NP is the only polymorphic locus. Three of the sites have no polymorphic loci. The mean F_{ST} value across all loci was 0.062 for the seven subpopulations. This value indicates some level of inbreeding, but is not statistically different from zero, probably due to small sample size. The other F-statistics obtained are unreliable, probably for the same reason (Appendix 2).

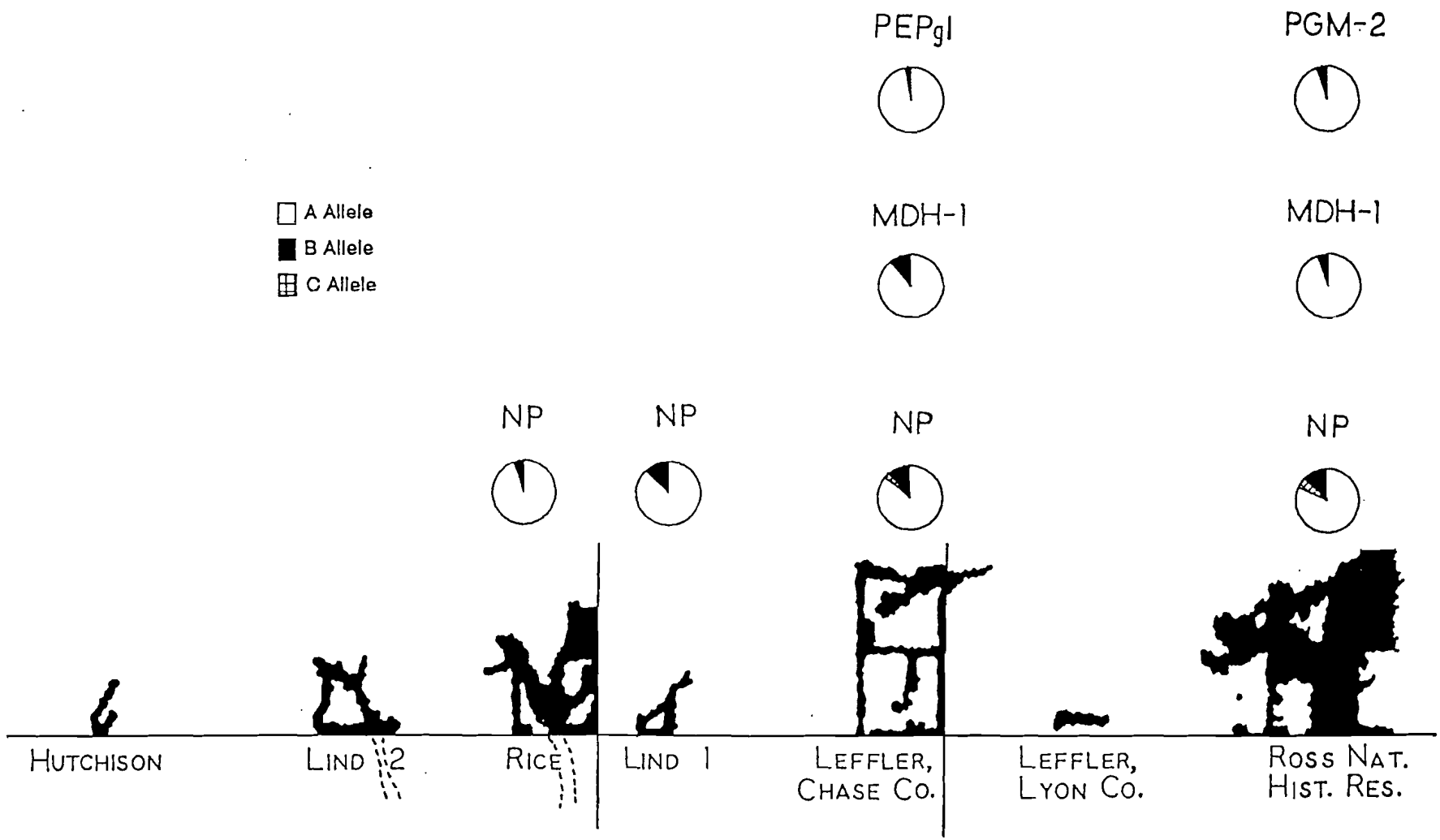
Table 1. Matrix of genetic similarity and distance coefficients. Above diagonal, Rogers' (1972) genetic similarity; below diagonal, Nei's (1978) unbiased genetic distance for seven subpopulations of Neotoma floridana in east-central Kansas.

Population	1	2	3	4	5	6	7
1 ROSS NAT HX RES		0.986	0.991	0.991	0.988	0.986	0.986
2 LEFFLER LYON CO	0.001		0.986	0.993	0.997	1.000	1.000
3 LEFFLER CHASE CO	0.000	0.001		0.991	0.989	0.986	0.986
4 LIND 1 CHASE CO	0.000	0.000	0.000		0.996	0.993	0.993
5 RICE CHASE CO	0.000	0.000	0.000	0.000		0.997	0.997
6 LIND 2 CHASE CO	0.001	0.000	0.001	0.000	0.000		1.000
7 HUTCHISON CHASE	0.001	0.000	0.001	0.000	0.000	0.000	

Table 2. Allele frequencies for the polymorphic loci of *Neotoma floridana* from seven subpopulations in east-central Kansas. All other loci were monomorphic. (N) is the number of animals sampled in each subpopulation. See Figure 1 for the designation of each of the numbered populations.

Locus	Subopulation						
	1	2	3	4	5	6	7
MDH-1							
(N)	17	4	18	4	9	6	3
A	0.941	1.000	0.889	1.000	1.000	1.000	1.000
B	0.059	0.000	0.111	0.000	0.000	0.000	0.000
NP							
(N)	17	4	18	4	9	6	3
A	0.824	1.000	0.861	0.875	0.944	1.000	1.000
B	0.118	0.000	0.111	0.125	0.056	0.000	0.000
C	0.059	0.000	0.028	0.000	0.000	0.000	0.000
PEPGL							
(N)	17	4	18	4	9	6	3
A	1.000	1.000	0.972	1.000	1.000	1.000	1.000
B	0.000	0.000	0.028	0.000	0.000	0.000	0.000
PGM-2							
(N)	17	4	18	4	8	6	3
A	0.941	1.000	1.000	1.000	1.000	1.000	1.000
B	0.059	0.000	0.000	0.000	0.000	0.000	0.000

Figure 2. Pie charts of allele frequencies of polymorphic loci of Neotoma floridana for each subpopulation from Lyon and Chase counties. Actual allele frequencies are given in table 1.


PEPgl
PGM-2
A Allele
B Allele
C Allele
MDH-1
MDH-1
NP
NP
NP
NP
HUTCHISON
LIND 2
RICE
LIND 1
LEFFLER, CHASE CO.
LEFFLER, LYON CO.
ROSS NAT. HIST. RES.

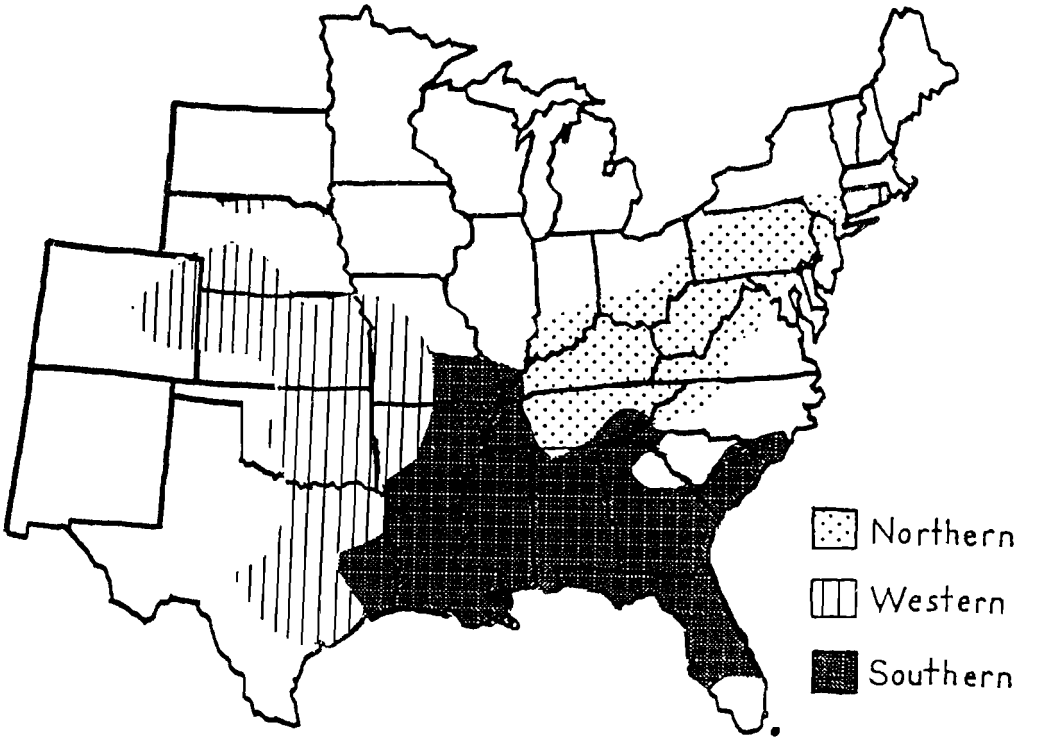
DISCUSSION

My data indicate that there is little genetic variability among, or within, the subpopulations of the eastern woodrat in my study. Nei's (1972) genetic distance and Rogers' (1972) genetic similarity show almost no differentiation among any of the subpopulations. From these results, my first hypothesis concerning woodrat dispersal can neither be accepted nor rejected. The second hypothesis of genetic differentiation among demes is, however, rejected. Therefore, these are probably not insular deems, unless there has been insufficient time for differentiation to have occurred.

Of the nine polymorphic loci found in N. f. attwateri by Zimmerman and Nejtek (1977), the most variable loci were found in blood. As ear tissue lacks sufficient blood, I was unable to analyze those loci and do a comparison. I did compare one protein, an esterase, for which the population in this study was monomorphic.

Hayes and Harrison (1992) found little mtDNA variability between eastern woodrats in the central United States. Their data indicated that three lineages of N. floridana, a northern, southern, and western, exist and diverged from each other only recently (Fig. 3). The northern lineage, however, may have diverged sufficiently to be considered a different species, N. magister (Hays and Richmond, 1993). Woodrats from the central United States,

Figure 3. Map of the distribution of the eastern woodrat (Neotoma floridana). The distribution of Hays and Harrison's (1992) three lineages are indicated (from Hays and Harrison, 1992).


Northern
Western
Southern

including Kansas, are part of the western lineage. Hayes and Harrison (1992) proposed that Neotoma experienced a period of rapid expansion during the early Pleistocene. Birney (1976) suggested that N. floridana dispersed from Mexico and the southwestern United States, first eastward into the southeastern United States during the Wisconsin glaciation, and then northward along the east coast and also into the midwest and central plains after the glaciers had receded. Such a rapid, recent expansion would allow insufficient time for much detectable genetic change to occur within the lineages. Hayes and Harrison (1992) suggest that the three lineages occupied different refugia in the southeastern United States during the Pleistocene, perhaps creating a genetic bottleneck. Only the southern lineage has much mtDNA variability.

The electrophoretic data in my study showed little genetic variability either within individuals or within or among demes in Kansas, and supported Hayes and Harrison's (1992) lack of variability of mtDNA in the western lineage. As mtDNA evolves faster than that of nuclear DNA in mammals (Moritz et al., 1987) it is not surprising that with little mtDNA variability there is also little nuclear DNA variability.

A bottleneck probably occurred in N. floridana during the last glacial period, ending about 12,000 ybp (Wright, 1970), during which the progeners of the three lineages

occupied their own refugia (Hayes and Harrison, 1992). A prolonged bottleneck, with few founders, usually results in decreased genetic variability within the bottlenecked population (Leberg, 1992). Such a bottleneck strongly affects genetic variability in other mammalian species, for example: the northern elephant seal (Mirounga angustirostris) (Bonnell and Selander, 1974), the cheetah (Acinonyx jubatus) (O'Brien et al., 1987), and the American plains bison (Bos bison) (McClenaghan et al., 1990). These are all large mammals with low reproductive potential, but the eastern woodrat, even though it is much smaller, also has a fairly low reproductive potential (Rainey, 1956). The northern elephant seals, bison, and the southern populations of cheetah underwent at least one bottleneck within the last century, for the seals and bison it was severe. These two species have since rebounded numerically, but with very little and perhaps no genetic variability within the species (O'Brien et al., 1987; McClenaghan et al., 1990). The cheetah probably underwent a severe bottleneck followed by inbreeding approximately 10,000 ybp when many mammalian species became extinct (Menotti-Raymond and O'Brien, 1993), and has not recovered either numerically or genetically. There has been little genetic variability added since the first bottleneck in the cheetah and the southern population lost even more variation during the second bottleneck. A similar scenario could be applied to populations of the

eastern woodrat in Kansas.

Approximately 23,000 to 12,000 ybp, eastern Kansas is thought to have been covered by a spruce forest which extended eastward to the Atlantic coast, southward to at least the northern edge of Georgia, and northward into Canada (Wright, 1970). About 12,000 ybp, in Kansas (9,000 ybp further north), climatic changes associated with the retreating glaciers occurred such that the spruce forest gave way to, for a short time, deciduous forests, and then to grassland. Then about 4,000 - 5,000 ybp deciduous forests began creeping back into the grassland (Wright, 1970). The woodrat may have followed the forest expansion.

Until the middle of the last century, around the 1860's, there were almost no trees in east-central Kansas except along rivers and streams (Andreas, 1883; French, 1929). The rest of the land was covered predominately with tall prairie grasses, especially big bluestem (French, 1929). Wild fires occurred with sufficient frequency to prevent the encroachment of trees into the prairie. After the advent of European settlers in the area, trees were planted, both around homes and as hedge rows. Several droughts of note occurred in the past 150 years which killed many of the trees that had grown here. One such drought occurred in the mid 1860's (French, 1929) and a second, more severe, occurred in the 1930's (Richmond, 1974).

Chase County, Kansas has a very similar history to Lyon

County. Prior to the arrival of European settlers, at least as far back as the early 1700's, tallgrass prairie comprised the vast majority (92%) of the habitat, with trees (8%) being almost totally confined to river and stream beds (Andreas, 1883). These grasslands were maintained by natural and Indian-set fires (French, 1929). The European settlers, who came in the late 19th century, used the land for pasture and farming, and the farmers planted the Osage orange hedge rows to keep the cattle out of their grain.

In the 1950's, there were few trees on the Ross Natural History Reservation (Spencer, 1979). In the mid 1950's, prior to the land becoming the Ross Natural History Reservation, most of it was either tallgrass prairie or cropland (Spencer, 1979). Woody patches along creeks, hedgerows, and plantings around the few buildings comprised the only trees (Spencer, 1979). More recently, trees have been allowed to encroach, such that there are now many more trees on the Ross than in the 1950's. Currently one third of the Ross is burned each year on a rotating basis to reduce woody vegetation and enhance the grassland habitat (E. J. Finck, pers. comm.).

During the 1950's, there was a severe decline in woodrat populations in Douglas County, Kansas (Rainey, 1956) which is north of my study area, but still in eastern Kansas. The factors affecting those populations, such as weather conditions and loss of good habitat (Rainey, 1956),

likely have affected the woodrats in Lyon and Chase counties. The relatively low reproductive rate of woodrats may have retarded their recovery (Rainey, 1956). Due to the patchiness of available habitat in my study area, migrants from large populations of woodrats were likely unavailable to help repopulate the declining populations in eastern Kansas (Rainey, 1956). According to Rainey (1956), during periods of low numbers woodrats move around more frequently and so are more vulnerable to predators, thus further delaying the population's regrowth.

The lack of genetic diversity in the woodrat of eastern Kansas is probably due to the combination of a number of factors. For example, the probability of a substantial bottleneck during the last glaciation would have yielded an overall low genetic variability in the western lineage of N. floridana. Thus, the gene pool available for the woodrats in my study would have contained little variability. The possibility of more recent, localized bottlenecks with few founders as a result of: 1) the patchiness of the woodrat's distribution, 2) the danger of dispersal across grasslands, and 3) the serious population decline in the mid 1950's, may have produced the current population structure. The recent availability of quality woodrat habitat in my study area may not have allowed sufficient time for differentiation to occur.

The low genetic diversity of the eastern woodrat in

this portion of its range should be strongly considered in any conservation or management plan that would affect this species. This lack of diversity may hamper its ability to adapt to changes in its environment. It is possible that occasionally individuals from distant populations, or even from other subspecies, would need to be brought into this population to introduce new alleles. Further work needs to be done, however, to determine how widespread the low genetic variation is in this species.

LITERATURE CITED

ad hoc Committee on Acceptable Field Methods in Mammalogy. 1987. Acceptable field methods in mammalogy: preliminary guidelines approved by the American Society of Mammalogists. J. Mamm. 68, suppl.:1-18.

Andreas, A. T. 1883. The history of Kansas. Chicago, IL.

Birney, E. C. 1976. An assessment of relationships and effects of interbreeding among woodrats of the Neotoma floridana species-group. J. Mamm., 57:103-132.

Bonnell, M. L., and R. K. Selander. 1974. Elephant seals: genetic variation and near extinction. Science, 184:908-909.

Chepko-Sade, B. D., W. M. Shields, J. Berger, Z. T. Halpin, W. T. Jones, L. L. Rogers, J. P. Rood, and A. T. Smith. 1987. The effects of dispersal and social structure on effective population size. Pp. 287-321, in Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics (B. D. Chepko-Sade and Z. T. Halpin, eds.). The Univ. of Chicago Press, Chicago.

Chesser, R. K. 1983. Isolation by distance: relationship to the management of genetic resources. Pp. 66-77, in Genetics and conservation: a reference for managing wild animal and plant populations (C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, eds.). The Benjamin/Cummings Publishing Co., Inc., Menlo Park, California.

Dubach, J. 1986. Pinna tissue, a source of allozymic information. Southwestern Nat., 31:419-420.

Fitch, H. S. 1958. Home ranges, territories, and seasonal movements of vertebrates of the Natural History Reservation. Univ. Kansas Publ., Mus. Nat. Hist., 11:63-326.

Fitch, H. S., and D. G. Rainey. 1956. Ecological observations on the woodrat, Neotoma floridana. Univ. Kansas Publ., Mus. Nat. Hist., 8:499-533.

French, L. M. 1929. History of Emporia and Lyon County.

Hafner, M. S. 1991. Evolutionary genetics and zoogeography of Middle American pocket gophers, genus Orthogeomys. J. Mamm., 72:1-9.

Harris, H., and D. A. Hopkinson. 1976. Handbook of enzyme electrophoresis in human genetics. American Elsevier Publishing Co., Inc., New York.

Hayes, J. P., and R. G. Harrison. 1992. Variation in mitochondrial DNA and the biogeographic history of woodrats (Neotoma) of the eastern United States. Syst. Biol., 41:331-334.

Hays, J. P., and M. E. Richmond. 1993. Clinal variation and morphology of woodrats (Neotoma) of the eastern United States. J. Mamm., 74:204-216.

Highton, R., and T. P. Webster. 1976. Genetic variation and divergence in populations of the salamander Plethodon cinereus. Evolution, 30:33-45.

Hillis, D. M., M. T. Dixon, and A. L. Jones. 1991. Minimal genetic variation in a morphologically diverse species (Florida tree snail, Liguus fasciatus). J. Heredity, 82:282-286.

Jones, J. K., D. M. Armstrong, and J. R. Choate. 1985. Guide to mammals of the plains states. Univ. Nebraska Press, Lincoln and London.

Jones, Jr, J. K., D. M. Armstrong, R. S. Hoffmann, and C. Jones. 1983. Mammals of the northern great plains. Univ. Nebraska Press, Lincoln and London.

Leberg, P. L. 1992. Effects of population bottlenecks on genetic diversity as measured by allozyme electrophoresis. Evolution, 46:477-494.

Lidicker, W. Z., Jr., and J. L. Patton. 1987. Patterns of dispersal and genetic structure in populations of small rodents. Pp. 144-161, in Mammalian dispersal patterns: The effects of social structure on population genetics (B. D. Chepko-Sade and Z. T. Halpin, eds.). Univ. Chicago Press, Chicago.

Mathews, N. E., and W. F. Porter. 1993. Effect of social structure on genetic structure of free-ranging white-tailed deer in the Adirondack Mountains. J. Mamm., 74:33-43.

Mayden, R. L., and R. H. Matson. 1992. Systematics and biogeography of the Tennessee Shiner, Notropis leuciodus (Cope) (Teleostei: Cyprinidae). Copeia, 1994:954-968.

McClenaghan, L. R., Jr., J. Berger, and H. D. Truesdale. 1990. Founding lineages and genic variability in plains bison (Bison bison) from Badlands National Park, South Dakota. Conservation Biol., 4:285-290.

Menotti-Raymond, M., and S. J. O'Brien. 1993. Dating the genetic bottleneck of the African cheetah. Proc. Nat. Acad. Sci., USA, 90:3172-3176.

Moritz, C., T. E. Dowling, and W. M. Brown. 1987. Evolution of animal mitochondrial DNA: Relevance for population biology and systematics. Ann. Rev. Ecol. Syst., 18:264-292.

Nei, M. 1972. Genetic distance between populations. Amer. Nat., 106:282-292.

Nei, M. 1977. F-statistics and the analysis of gene diversity in subdivided populations. Ann. Human Genetics, 41:225-233.

O'Brien, S. J., D. E. Wildt, M. Bush, T. M. Caro, C. FitzGibbon, I. Aggundey, and R. E. Leakey. 1987. East African cheetahs: Evidence for two population bottlenecks? Proc. Nat. Acad. Sci., USA, 84:508-511.

Post, D. M. 1992. Change in nutrient content of foods stored by eastern woodrats (Neotoma floridana). J. Mamm., 73:835-839.

Rainey, D. G. 1956. Eastern woodrat, Neotoma floridana: Life history and ecology. Univ. Kansas Publ., Mus. Nat. Hist., 8:535-646.

Richmond, R. W. 1974. Kansas, a land of contrasts. Forum Press, Inc., Arlington Heights, IL.

Rogers, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in Genetics. VII. Univ. Texas Publ., 7213:145-153.

Shields, W. M. 1987. Dispersal and mating systems: investigating their causal connections. Pp. 3-24, in Mammalian dispersal patterns: The effects of social structure on population genetics (B. D. Chepko-Sade and Z. T. Halpin, eds.). Univ. Chicago Press, Chicago.

Smith, M. H., H. O. Hillestad, M. N. Manlove, and R. L. Marchinton. 1976. Use of population genetics data for the management of fish and wildlife populations. Trans. North Amer. Wldlf. and Nat. Res. Conf., 41:119-133.

Spencer, D. 1979. Ross Natural History Reservation: The first twenty years, 1959 to 1979. unpublished report, Division of Biological Sciences, Emporia State Univ., Emporia, KS.

Swofford, D. L., and R. B. Selander. 1981. BIOSYS-1, a computer program for the analysis of allelic variation in genetics. Department of Genetics and Development, Univ. Illinois, Urbana.

Warner, R. G. 1986. Reproduction, movement and survival of the eastern woodrat. Unpubl. M.S. thesis, Emporia State Univ., Emporia, KS.

Wiley, R. W. 1980. Neotoma floridana. Mammalian Species, no. 139:1-7.

Wright, H. E., Jr. 1970. Vegetational history of the central plains. Pp. 157-172, in Pleistocene and recent environments of the central great plains (W. Dort, Jr. and J. K. Jones, Jr., eds.). Univ. Press of Kansas.

Wright, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution, 19:395-420.

Wright, S. 1978. Evolution and the genetics of populations, vol. 4, Variability within and among natural populations. Univ. Chicago Press, Chicago.

Zimmerman, E. G., and M. E. Nejtek. 1977. Genetics and speciation of three semispecies of Neotoma. J. Mamm., 58:391-402.

APPENDIX I

Appendix I. Sex, size and identification number of all woodrats (Neotoma floridana) captured from each subpopulation. M = male, F = female, A = adult, S = subadult, J = juvenile.

Site	Sex	Age class	Lengths in mm.			Toe #
			Total	Tail	Hindfoot	
Ross		A	290	85	36	001*
	M	A	280	105	34	002
	F	A	240	143	35	003
	F	A				004
	F	J	250	100		005
	F	J				006
	F	J				007
	F	A	320	140		008
	M	A	350	145		010
	M	A	330	140		011
	F	J				012
	F	J				013
	F	A	330	130		014
	M	J	255	110		015
	F	J	250	80		023
	M	A				024
	M	A				025
Leffler,	F	J	277	112		030
Lyon	F	J	260	108	32	031
	M	J	290			027
	M	J	335	110	38	028
Leffler,		A	308	135	37	016
Chase	F	A	310	134	35	017
	M	S	315	135		018
	M	S	310	120		040
	F	S	315	133		041
	F	A	356	138	40	022
	F	A	320	135	38	032
	M	S	320	131	36	033
	F	A	341	140		034
	F	J	274	105	34	035
	F	S	320	142		036
	M	J	220	91	25	037
	M	S	272	120	34	038
	M	S	323	130	28	040
	M	S				041

Appendix I. (cont.)

	F	A	344	142	37	042
	F	S	267	105	30	043
	M	A	354	145	38	044
Lind 1	F	S	315	133	37	045
	M	S	285	122	31	046
	F	A	323	140	38	047
	M	S	305	132	30	048
Rice	F	A	330	140	34	050
	M	S	240		32	051
	F	S	310	143	33	052
	M	A	280	100	30	053
	M	S	290	125	33	054
	M	A	350	160	30	055
	M	J	256	113	34	056
	M	S	315	136	37	057
	M	A	315	136	37	058*
	M	A	325	134	35	060
Lind 2	M	A	347	147	36	061
	M	A	323	142	38	062
	M	A	342	150	37	063
	M	A	332	152	39	064
	M	A	305	130	34	065
	M	A	305	140	34	066
Hutchison	M	A	305	113	32	067
	M	A	353	152	38	068
	M	A	325	131	36	070

* no tissue taken

APPENDIX II

Appendix II. F-statistics across all populations for each polymorphic loci and mean F-statistics across all loci.

Locus	F_{IS}	F_{IT}	F_{ST}
MDH-1	1.000	1.000	0.070
NP-1	0.063	0.121	0.062
PEPgl	-0.029	-0.004	0.024
PGM-2	1.000	1.000	0.051
Mean	0.351	0.391	0.062

L. Page Fredericks
Signature of Graduate Student

Signature of Major Advisor

I, L. Page Fredericks, hereby submit this thesis to Emporia State University as partial fulfillment of the requirements of an advanced degree. I agree that the Library of the University may make it available for use in accordance with its regulations governing materials of this type. I further agree that quoting, photocopying, or other reproduction of this document is allowed for private study, scholarship (including teaching), and research purposes of a nonprofit nature. No copying which involves potential financial gain will be allowed without written permission of the author.

L. Page Fredericks
Signature of Author

August 18, 1994
Date

Genetic variation in insular populations of the eastern woodrat (Neotoma floridana) in a forest-prairie mosaic
Title of Thesis Report

Signature of Graduate Office Staff Member

December 6, 1994
Date Received