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I am submitting herewith a thesis written by Hugh B. Britten entitled "Genetics of Insular Peromyscus leucopus Populations at Norris Lake, Tennessee." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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GENETICS OF INSULAR *PEROMYSCUS LEUCOPUS* POPULATIONS AT NORRIS LAKE, TENNESSEE

A Thesis

Presented for the

Master of Science

Degree

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ABSTRACT

A total of 138 Peromyscus leucopus were sampled from 9 island and 3 mainland sites at Norris Lake in eastern Tennessee. Liver and muscle extracts were used to identify 17 allozyme loci using starch gel electrophoresis, 9 of these loci were polymorphic. Using the 8 largest collection of insular mice and the two largest collections of mainland mice it was determined that the insular populations are no less genetically variable (estimated as P, proportion of polymorphic loci, and $\overline{H}_0$, mean individual heterozygosity) than the mainland populations. Genetic identities were not significantly correlated with geographical distances between island pairs. Gene flow is the probable mechanism that prevents these populations from diverging. Significant differences between island and mainland heterogeneity and among subpopulation genetic variance ($\overline{F}_{st}$) estimates could not be shown. Significant genetic heterogeneity was found among the insular populations at the 4 most robustly polymorphic loci (EST, αGPD, IPO, and 6-PGD). Social structuring of these populations may account for the significant genetic heterogeneity among them. A pattern of heterozygote deficiency was found at the 6-PGD and EST loci in both insular and mainland populations. There are 4 possible explanations for these results: 1) negative heterosis, 2) population structuring, 3) Wahlund effect, and 4) the presence of "null" alleles. It could not be shown that insular P. leucopus populations were any more subject to the stochastic processes usually attributed to island habitation than the mainland populations at Norris Lake. A large difference was

found between $\overline{F}_{st}$ estimates of males from 6 islands with the largest collections ($\overline{F}_{st}$ = .0399) and females from 4 islands with the largest collections ($\overline{F}_{st}$ = .1929). Sexual differences in dispersion probably account for these results. Males move further than females and are, therefore, probably less closely related to one another within a sample.

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CHAPTER 1

INTRODUCTION

Populations of animals and plants isolated on islands can be viewed as experiments in evolution. The isolated population may differ in allele frequencies from larger source populations for three reasons: (1) the founder effect where the founders of an isolated population hold only a small and perhaps biased sample of the genetic diversity of the source population in their genomes; (2) random processes (genetic drift) which affect smaller, isolated populations more than larger or continuously distributed populations; and (3) differential selection pressures may be acting on the isolated population since it is physically removed from the source population. In general, small isolated populations tend to be less genetically variable than large, panmictic populations due to the actions of the founder effect and genetic drift.

This study deals with populations of the white-footed mouse, Peromyscus leucopus, isolated on islands in a Tennessee Valley Authority (T.V.A.) impoundment, Norris Lake, north of Knoxville, Tennessee. The lake was formed in 1936 with the completion of a dam which resulted in flooding of the Clinch and Powell River valleys. The islands are former hilltops now surrounded by lake water. Mainland populations were also studied to provide a basis for comparison of genetic diversity.

This study is an attempt to measure the amount of genetic divergence among populations that have not been isolated very long and,

in some cases, not completely isolated from possible gene flow from other populations. Both of these factors, a short period of isolation and incomplete isolation, should, theoretically, lower the genetic similarity among islands and between islands and mainland. Differential selection would also be expected to have similar effects but is probably of less importance in this case because of the relatively short period of isolation and the physical proximity of the populations to one another. This is a unique set of circumstances for a study of this kind because the effects of the founder effect and genetic drift are examined on unusually small scales of time and distance.

Therefore, this study is an attempt to: (1) determine if P. leucopus populations on islands in Norris Lake are genetically less variable than nearby mainland populations; (2) determine if any genetic heterogeneity exists between island populations; (3) determine if any genetic heterogeneity exists between mainland sites; and (4) interpret the results obtained with consideration to the demography and history of the newly isolated insular mouse populations at Norris Lake.

CHAPTER 2

LITERATURE REVIEW

Electrophorosis has been used to investigate the population genetics of a number of species. It is a particularly useful tool in studying the genetic differentiation of geographically or socially isolated populations.

Allozyme studies of natural populations of many species have shown that there is a considerable amount of genetic variability within species (Ayala, 1976; King, 1968; Mayr, 1970; Nei and Koehn, 1983). In most species populations are polymorphic at 25 to 50 percent of their loci and individuals have an average heterozygosity of 5 to 15 percent (Ayala, 1976). The amount of detectable genetic variation in a population, however, may be less than 25 percent of the possible variation present (Shaw, 1965). This low figure results from the fact that most possible amino acid substitutions will not produce the change in net charge on a polypeptide necessary to distinguish one allozyme from another electrophoretically. Despite these limitations, electrophoresis is the most efficient method of screening large numbers of individuals for genetic study.

Populations of animals that colonize islands or other isolated habitats tend to be less genetically variable than larger, mainland populations (Ayala, 1976; Baker and Stebbins, 1965). Founder effect and genetic drift are presumably the main mechanisms by which island populations become less genetically variable than mainland populations (Ayala, 1976, and Kilpatrick, 1981).

The founder effect, as an agent of rapid evolution, has been studied in several rodent species (eg. Berry and Murphy, 1970; Berry, 1975; and Patton et al., 1975). Berry (1975) states that Apodemus sylvaticus populations living on the islands north and west of Britain have diverged genetically from one another. This is a classic case of the result of founder effect where two forces come into play: (1) the separation of a small group from a larger one, and (2) the subsequent adjustment of the founders' gene pool. Berry (1975) was unable to find evidence of clinal or other patterns in the genetic heterogeneity among those isolated populations which would indicate forces other than the founder effect in causing these populations to diverge genetically. Mus musculus populations that were introduced onto 6 of the Faroe Islands north of Britain also were found to be genetically and morphologically distinct (Berry et al., 1978). The populations are the result of human introductions, one as recently as 40 years ago. Berry et al. (1978) found that even the youngest population had diverged from the others as much as the older ones. This "instant subspeciation" (Berry et al., 1978) is probably a direct result of the small number of founders for each population.

Factors other than geographical isolation may be responsible for genetic divergence among populations. The social interactions of Thomomys Bottae (Patton and Feder, 1981) and Cynomys ludovicianus (Chesser, 1983) account for genetic divergence within populations of this species. Fossorial habits, patchy distribution and male and female exclusive territories tend to subdivide populations of T. bottae (Patton and Feder, 1981). Populations of C. ludovicianus are

also subdivided by a complex social structure including single male harems (Chesser, 1983). In both these cases, stochastic processes may cause the genetic divergence among subdivided populations (Chesser, 1983 and Patton and Feder, 1981).

Several electrophoretic studies have been done on both continuous (egs. Avise et al., 1974a,b; Rasmussen, 1964, and Selander et al., 1971) and isolated (eg. Aquardo and Kilpatrick, 1981; Avise et al., 1974a,b; and Gill, 1976) populations of mice in the genus Peromyscus. Rasmussen (1964 and 1970) found that continuous populations of the deer mouse, Peromyscus maniculatus, may be subdivided genetically by social behavior such as territoriality. The genetically effective population size (Ne) may be so reduced to allow stochastic processes, such as genetic drift, to effect allele frequencies (Rasmussen, 1970). This genetic differentiation due to social behavior is effective over short geographical distances in continuous habitat. Continuously distributed populations of Peromyscus may also show genetic structuring for ecological reasons. Destruction of cotton fields resulted in relict populations of P. polionotus which diverged genetically after colonizing five year old uncultivated fields (Biggers and Dawson, 1971). Selander et al. (1971) found low levels of heterozygosity in populations of P. polionotus isolated on islands off the Florida coast. Other populations of this mouse living in beach habitat, an unusual habitat for P. polionotus, were also found to be less genetically variable than other populations.

Studies on the population genetics of insular Peromyscus populations have found the island populations to be significantly lower in genetic variability than mainland populations (Aquadro and Kilpatrick, 1981;

Avise et al., 1974a,b; Browne, 1977; Gill, 1976; and Selander et al., 1971). P. maniculatus populations on islands off the coast of Maine, on mainland Maine and mainland New York were compared electrophoretically and morphologically (Aquadro and Kilpatrick, 1981). Both measures showed reduced variability in island mice with the genetic variability of island mice being correlated with the square of the distance of an island to a colonizing source (Aquadro and Kilpatrick, 1981). Peromyscus of the subgenus Haplomyomys inhabiting islands in the Gulf of California also were found to have a very low degree of genetic variability, and it was hypothesized that founder effect and genetic drift contributed to among island population genetic differentiation (Avise et al., 1974b).

Three insular P. leucopus populations were compared genetically to two populations on the mainland in Lake Erie and northern Ohio (Browne, 1977). Island populations were found to be less genetically variable than the mainland populations at 9 polymorphic loci (Browne, 1977). Browne (1977) found a direct correlation between average individual heterozygosity and land mass area from which the mice were sampled. Founder effect probably accounted for the fixation of one allele at the α-G pdh locus on one of the islands (Browne, 1977). Browne (1977) states that more alleles may have reached fixation in the island populations if gene flow was reduced.

In general, comparative genetic studies of island and mainland rodent populations have found a reduction in average individual heterozygosity in island populations. This decrease in genetic variability in insular populations has been attributed to the founder

effect. That similar results are found over a wide number of rodent species with populations that have been semi-isolated or completely isolated for various lengths of time suggests that the founder effect can be evolutionarily quite powerful.

CHAPTER 3

STUDY AREA

The field work for this study was carried out at Norris Lake, a Tennessee Valley Authority (T.V.A.) impoundment approximately 48 kilometers north of Knoxville in Union County, Tennessee. Norris Dam was build to provide flood control and hydroelectric power to the area. The project began in 1933 and was completed in 1936. It was the first T.V.A. project.

The lake extends 116 kilometers up the Clinch River and 90 kilometers up the Powell River. There are 1287.5 kilometers of shore line. The islands are former hilltops protruding above the water.

The island and mainland sites are similar in topography and habitat. The elevation of both the mainland and island trapping sites ranges from 312.7 meters to 335.5 meters above sea level. The topography is generally sloping on both the islands and the mainland. Kuchler (1966) puts this area within the Appalachian oak forest oak-chestnut forest association. This forest type is prevalent in the southern Appalachian Mountains. The dominant tree species are oaks, Quercus spp. Beech, Facus grandifolia, maples, Acer spp., and hickories, Carya spp. are present (VanKat, 1979). The understory consists of dogwoods, Cornus spp., blackberry and/or raspberry, Rubus spp. and poison ivy, Rhus toxicdendron (VanKat, 1979). The ground is uniformly covered with several inches of leaf litter. Eastern cedar, Juniperus virginiana and willows, Salix spp. are present near the shore line. This forest type is extremely diverse but appears to be the same on the islands and the mainland.

Mice were trapped from 9 islands in Norris Lake. Island locations are shown in Figure 1. The islands are in two geographical groups, one consisting of Pilot, Woodduck, Bearhole, and "Peninsula" Islands, and the other containing Gourd, "Knob", "Sliver" and "Crow" Islands. Dollar Island is located between these two groups.

Island perimeters, areas and distances to the nearest mainland are given in Table 1. All the islands are small, ranging in area from 0.029 ha. for Woodduck and Bearhole Islands to 0.008 ha. for "Sliver" and "Crow" Islands. The islands farthest from the shore are "Crow" and "Knob" at 0.40 km. "Knob" Island is extremely close to Gourd Island and is connected to it when the lake water level is low. The distance between Woodduck and Bearhole Islands is 0.15 km. These islands are closer to each other than to the nearest mainland shore. "Sliver" and "Peninsula" Islands are very near the mainland and are connected to it by a weedy sandbar at low water levels.

The three mainland trap sites were located near the Loyston Point Public Use Area south of the Chuck Swan Management Area (Figure 1). The sites were spaced along the road to Loyston Point such that the distance between site 1 and site 2 was equal to the distance between "Peninsula" and Pilot Islands, 0.97 km . The 2.01 km between sites 2 and 3 equals the distance between Pilot and Woodduck Islands. Site 1 was located 0.5 km. after the entrance to the Loyston Point Public Use Area on the north side of the road. Sites 2 and 3 were also on the north side of the road at 0.97 and 2.98 km from site 1, respectively.

TABLE 1

Island Perimeters, Areas, and Distances to Nearest Mainland

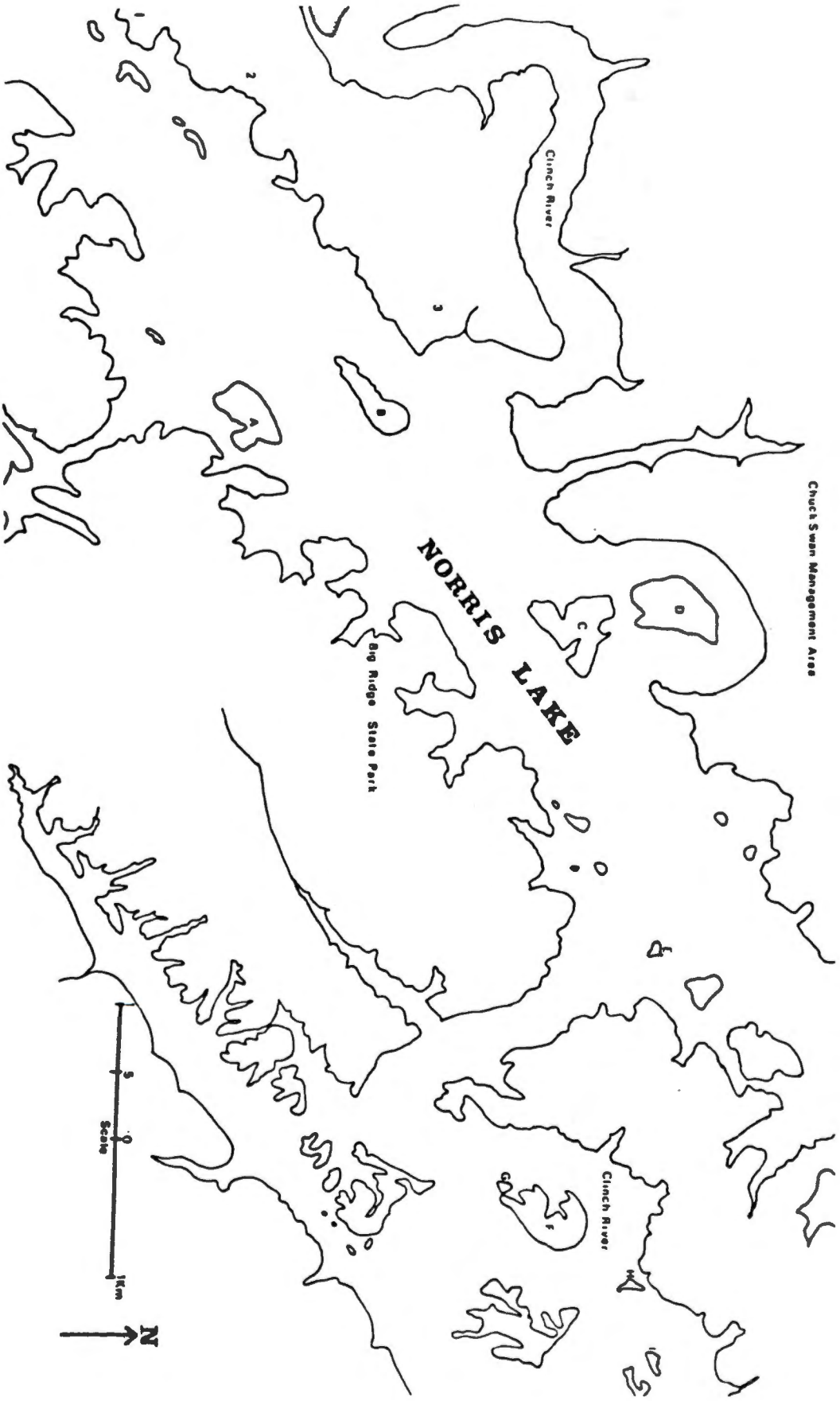
Island	Perimeter Km	Area ha	Distance to Mainland Km
Pilot	1.78	0.021	0.40
"Peninsula"	1.63	0.021	0.12
Woodduck	2.56	0.029	0.25*
Bear Hole	2.04	0.029	0.29
Dollar	0.23	0.010	0.30
Gourd	2.25	0.020	0.38**
"Knob"	0.92	0.010	0.40
"Sliver"	0.43	0.008	0.06
"Crow"	0.35	0.008	0.40

*0.15 km to Bear Hole Island

**0.03 Km to "Knob" Island

Figure 1. Map of study area with collection sites indicated as:

1 - Mainland 1 ; 2 - Mainland 2 ; 3 - Mainland 3 ; A - "Peninsula"; B - Pilot ; C - Woodduck ; D - Bearhole ; E - Dollar ; F - Gourd ; G - "Knob" ; H - "Sliver" ; I - "Crow"


Clinch River
Chuck Swan Management Area
NORRIS LAKE
Big Ridge State Park
Clinch River
Scale
1Km
N

Since Norris Lake is a manmade reservoir, the water level fluctuates on a yearly basis for flood control. Table 2 gives the 15 year median water levels for each month in meters above sea level. The high water mark is reached in May and the low in October and November. There is an average difference between maximum and minimum water levels of 10.2 meters. All the islands used in this study are above flood levels.

Island names in quotation marks above are names assigned by the author to those islands that are unnamed on T.V.A. maps.

TABLE 2

Monthly 15 Year Median Water Levels in Meters
Above Sea Level as Measured at Norris Dam

Month	Water Level Meters Above Sea Level
January	301.1
February	303.3
March	306.0
April	308.5
May	309.1
June	308.2
July	305.7
August	302.4
September	300.2
October	299.3
November	299.3
December	299.9

CHAPTER 4

MATERIALS AND METHODS

Collection

Museum Special small mammal traps were placed in 20-meter by 20-meter grids at each site (Figure 1). Each grid contained 25 traps at 5-meter intervals (Southwood, 1971). The traps were baited with a rolled oats and peanut butter mixture. Four grids were set at each site for a total of 100 traps. Exceptions were "Knob" and Dollar Islands which could accomodate only 2 trap grids at one time, "Sliver" Island, which was trapped using 2 rows of 6 traps each at 5-meter intervals due to its size and shape, and "Crow" Island which was trapped with one 20-meter by 20-meter grid. Trap grids were set in the afternoon and left in place either 3, 5, or 7 consecutive days, depending on the success at a given site.

Island trapping was carried out in June, October, and November of 1982, January and February of 1983, and through the spring to the first of July, 1983. The mainland was trapped during the summer and fall of 1983 and for one week in January and February, 1984. A total of 6,200 island trap nights and 4,200 mainland trap nights were accrued.

Specimens were collected as early as possible each morning. All traps were rebaited and reset when necessary. The specimens were given a number, sealed in a plastic bag, and transported to the laboratory on ice. Upon arrival at the laboratory the animals were sexed, weighed and measured for total length, tail length, hand foot length, and ear

length. The specimens were then placed in an ultra-cold freezer at -85° C for storage until tissue processing.

Electrophoresis

The method of tissue preparation used follows Selander et. al. (1971). The specimen was thawed enough to allow dissection out of the entire liver and as much skeletal muscle as possible. Each tissue sample was weighed, and the muscle tissue was minced in a spot plate on ice with sharp scissors. Each muscle sample was then placed in a centrifuge tube. A volume, of pH 6.8 grinding buffer, equal in millileters to the weight in grams of the muscle sample was added to the tube. The muscle-grinding buffer mixture was placed in a refrigerator for one half hour. Liver extracts were prepared in a similar manner except that each liver sample was pulverized in a centrifuge tube with a glass stirring rod after the appropriate volume of grinding buffer had been added. The tissue extracts were then spun in a refrigerated centrifuge at 2°C to 5°C and 13,000 r.p.m. for 40 minutes. The supernatant liquid was then removed with a pipette and put into labelled test tubes for storage in the ultra-cold freezer until needed.

Standard methods of horizontal starch gel electrophoresis (Harris and Hopkins, 1978 and Selander et al., 1971) were used to identify 17 protein loci of which 9 were polymorphic [esterase (EST); general protein 2 and 4 (GP-2 and GP-4); glucose-6-phosphate dehydrogenase (G-6-PD); α glucerophosphate dehydrogenase (αGPD); indophenol oxidase 1 (IPO-1); levcere aminopeptidase (LAP); phosphoglucomutase (PGM) and 6-phosphogluconate dehydrogenase (6-PGD)]. Letters were assigned

to each alternate allele at the polymorphic loci. Table 3 provides a summary of the tissues and electrophoretic conditions used for each protein locus.

Statistical Methods

Expected genotype frequencies predicted by Hardy-Weinberg equilibrium theory were calculated using Levene's (1949) formulae for small sample sizes. Correspondence between observed and expected genotype frequencies was tested with a chi-square test. Heterozygote deviation (D) from Hardy-Weinberg expectations was calculated for each population at each locus. This test indicates whether the observed number of heterozygotes at each locus were in excess, deficient or identical to the expected under Hardy-Weinberg conditions. A binomial test (Siegel, 1956) was used to test the significance of the heterozygote deviations. A G-test was used to test for possible differences in observed allele frequencies between males and females at all polymorphic loci for each population.

Mean observed heterozygosity per individual ($\overline{H}_0$) and proportion of polymorphic loci (P) were calculated for each population (Browne, 1977). A locus was considered polymorphic if any variation was found.

F-statistics (Wright, 1965) were calculated for each population at each polymorphic locus. Of particular interest is F_{ST}, the amount of subpopulation variance in allele frequency (Hartl, 1980). The genetic variance within subdivisions, F_{IS}, and between subdivision, F_{ST}, are partitions of the genetic variance in the total population F_{IT} (Hartl, 1980).

TABLE 3

Protein loci, tissues and electrophoretic conditions used to measure variation in Peromyscus leucopus (Selander et al., 1971)

Protein locus	Tissue Extract	Electrophoretic Conditions[a]
*Esterase (EST-1)	liver	A
Fumerase (Fum)	muscle	D
*General Protein 1 (GP-1)	muscle	A
General Protein 2 (GP-2)	muscle	A
General Protein 3 (GP-3)	muscle	A
*General Protein 4 (GP-4)	muscle	A
*Glucose-6-Phosphate dehydrogenase (G-6-PD)	muscle	C
Glutamate oxalate transaminase 1 (GOT-1)	muscle	C
Glutamate oxalate transaminase 2 (GOT-2)	muscle	C
α *Glycerophosphate dehydrogenase (α GPD)	muscle	D
*Indophenol oxidase 1 (IPO-1)	muscle	D
Indophenol oxidase 2 (IPO-2)	muscle	D
*Leucine aminopeptidase (LAP)	muscle	A
Malate dehydrogenase 1 (MDH-1)	liver	B
Malate dehydrogenase 2 (MDH-2)	liver	B
*Phosphoglucomutase (PGM)	liver	B
*6-Phosphatoglucenate Dehydrogenase (6-PGD)	muscle	C

TABLE 3 (continued)

[a]A = Lithium hydroxide; B = Phosphate pH 7.0, electrode buffer phosphoglucose isomerase; C = Tris-maleate; D = Tris-versene borate (Selander et al., 1971)

*Polymorphic locus

A G-test for heterogeneity (Sokal and Rohlf, 1981) was used to test genetic heterogeneity at each locus. This test, like F_{ST}, gives an indication of the among subpopulation variance in allele frequency at each locus. The least common alleles at each loci were pooled.

The normalized genetic identity (I) (Nei, 1972) was calculated for each population. This is a pairwise test in which the probability that identical alleles at identical frequencies will occur in two populations is estimated. The genetic distance (D), given as $D = -\ln I$, was also calculated for each pair of populations compared (Hartl, 1980).

The product-moment correlation coefficient (Sokal and Rohlf, 1981) was calculated between the genetic identity of a pair of populations and the linear distance in kilometers between the two sites. This correlation coefficient was calculated for all possible combinations of islands.

Table 4. Numbers of Peromyscus leucopus and other species captured at 9 island and 3 mainland sites at Norris Lake, 1982-1984.

Site	Males	Females	Total	Other Species
"Sliver"	5	2	7	0
"Crow"	2	1	3	2[a], 1[b]
"Knob"	7	0	7	0
Gourd	9	3	12	1[a]
Dollar	9	0	9	0
Pilot	16	8	24	0
"Peninsula"	10	12	22	0
Bearhole	9	9	18	0
Woodduck	11	9	20	0
Mainland 1	5	2	7	0
Mainland 2	2	0	0	1[b]
Mainland 3	4	3	7	0
Total	89	49	138	5

[a] Blarina brevicauda

[b] Sorex cinereus

CHAPTER 5

RESULTS

Genetic information was obtained from 138 P. leucopus. These mice were captured at 12 sites as summarized in Table 4. The smallest collection, 2 mice, came from mainland 2. The largest number of mice, 24, was captured on Pilot Island. Sex ratios summed over all collections favor males (89 males vs. 49 females; Table 4; $p < .005$; X^2 test). This is probably because males have higher trap exposures due to larger home ranges than females (Terman, 1968). Two species of shrew, Blarina brevicauda and Sorex cinereus, were represented by five specimens, 3 of these from "Crow" Island and 1 each from Gourd Island and Mainland 2. Because these other species were captured so rarely they are not considered further. Also, because of small sample sizes, P. leucopus from mainland 2 and "Crow" Island (2 and 3 mice respectively) were not considered in the statistical analyses.

Allele frequencies for the 9 polymorphic loci identified are given in Table 5 for each population. The EST and α GPD loci are the most variable with at least 2 alleles in each population. The G-6-PD, PGM, GP-2 and GP-4 loci are the least variable with alternate alleles in only two populations each. Alternate alleles at these loci all occur at frequencies of 8 percent or less. The observed genotype frequencies were not found to be statistically different from Hardy-Weinberg expectations in any populations at any locus. The overall pattern of observed heterozygote deviation from Hardy-Weinberg expectations (Levene, 1949) are given in Table 5. For the 9 polymorphic loci identified in the 10 largest populations there were 13 heterozygote

Table 5. Polymorphic loci, allele frequencies and heterozygote deviations of 8 island and 2 mainland populations of Peromyscus leucopus.

Locus	Allele	Populations "Sliver"	"Knob"	Gourd	Dollar	Pilot	"Peninsula"	Bearhole	Woodduck	Mainland 1	Mainland 2
EST	A	.36	.25	.25	.10	0	.06	.31	.11	0	.08
	B	.57	.75	.44	.80	.92	.69	.61	.89	.83	.71
	C	0	0	.06	.10	0	0	.08	0	0	0
	D	.07	0	.25	0	.08	.25	0	0	.17	.21
*D		-	-	-	-	-	-	-	+	-	-
aGPD	A	.07	.14	.46	.17	.23	.14	.14	.10	.14	.29
	B	.93	.86	.54	.83	.63	.84	.37	.50	.86	.50
	C	0	0	0	0	.14	.02	.47	.40	0	.21
D		0	+	+	+	-	-	+	+	-	-
IPO	A	.29	0	0	.33	.27	.16	.28	.20	.07	.07
	B	.71	1.0	1.0	.67	.73	.84	.72	.80	.93	.93
D		+			-	+	+	+	-	0	0
6-PGD	A	0	.14	0	0	.08	0	.11	.05	.28	.14
	B	1.0	.86	1.0	1.0	.92	1.0	.89	.95	.72	.86
D			-			-		-	-	-	-
LAP	A	.07	0	0	.50	0	.02	0	0	0	0
	B	.93	1.0	1.0	.50	1.0	.98	1.0	1.0	1.0	1.0
D		0			+						
G-6-PD	A	1.0	1.0	1.0	1.0	1.0	1.0	.92	.97	1.0	1.0
	B							.08	.03	0	0
D		0	0	0	0	0	0	-	0		
PGM	A	0	0	.05	0	0	.05	0	0	0	0
	B	1.0	1.0	.95	1.0	1.0	.95	1.0	1.0	1.0	1.0
D				0			+				
GP-2	A	0	0	0	0	0	.02	0	0	0	0
	B	1.0	1.0	1.0	1.0	1.0	.98	.94	1.0	1.0	1.0
	C	0	0	0	0	0	0	.06	0	0	0
D							0	+			
GP-4	A	1.0	1.0	1.0	1.0	.96	.93	1.0	1.0	1.0	1.0
	B	0	0	0	0	.04	.07	0	0	0	0
D							-				

*Calculated as $H_0 - H_e/H_e$, where H_0 = observed # heterozygotes ahd H_e = # expected heterozygotes from Hardy-Weinberg equilibrium.

Genotypic proportions did not differ significantly from Hardy-Weinberg expectations (Levene, 1949)
Summary: "+" = 13 ; "-" = 24 ; P = .035

excesses and 24 heterozygote deficiencies identified (Table 5). There are heterozygote deficiencies in 9 of the 10 populations at the EST locus and in all 6 populations that were polymorphic for the 6-PGD locus (Table 5).

Allele frequencies of males and females from the four largest populations (Pilot, "Peninsula", Woodduck and Bearhole) are given in Table 6 for the four most robustly polymorphic loci (EST, αGPD, IPO and 6-PGD). Only the four largest populations were considered for the allele frequency comparison of males and females because if differences in allele frequencies exist between sexes the largest samples provide the best opportunity of detecting them. Likewise, the most robustly polymorphic loci provide the best opportunity of detecting any existing differences in allele frequencies between sexes because these contain more information than less polymorphic loci. Significant sexual differences in allele frequencies were detected in the Woodduck population at the EST and IPO loci ($p < .05$; G-test for both loci), and in the Pilot population at the αGPD locus ($p < .05$; G-test).

Males from the 6 islands that contain the largest samples of males ("Knob", Dollar, Pilot, "Peninsula", Bearhold and Woodduck; all with samples of 7 or more males) were used to estimate genetic heterogeneity among populations of males and to calculate F-statistics for the 4 most robustly polymorphic loci (Table 7). The males from these populations have significant genetic heterogeneity at 2 loci (αGPD; $p < .025$ and IPO $p < .05$; G-test). Mean F_{st} among these 6 populations of males was estimated to be $\overline{F}_{st} = .0399$.

Genetic heterogeneity and F-statistics at the 4 most polymorphic loci also were estimated for the 4 largest collections of females

Table 6. Polymorphic loci and allele frequencies in females and males from 4 island populations of Peromyscus leucopus

Locus	Allele	Pilot		"Peninsula"		Woodduck		Bearhole	
		♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
EST	A	0	0	.12	0	0	.22*	.22	.39
	B	.81	.69	.56	.80	1.0	.78	.67	.55
	C	0	0	0	0	0	0	.11	.06
	D	.19	.31	.31	.20	0	0	0	0
αGPD	A	.25	.23*	.08	.20	.17	.04	.11	.17
	B	.75	.56	.92	.75	.33	.64	.39	.39
	C	0	.23	0	.05	.50	.32	.50	.44
IPO	A	.31	.25	.20	.10	.06	.32*	.33	.22
	B	.69	.75	.80	.90	.94	.68	.67	.78
6-PGD	A	.12	.06	0	0	0	.09	.11	.11
	B	.88	.94	1.0	1.0	1.0	.91	.89	.89
nos.		8	16	12	10	11	9	9	9

*Indicates a significant difference ($p < .05$; G-test) in allele frequencies of ♀♀ vs ♂♂ . All other differences within populations are nonsignificant.

TABLE 7. Genetic Heterogeneity and F-statistics among males in 6 island populations of *Peromyscus leucopus*

Locus	G-Het*	df	P	F_{st}
EST	4.635	5	< .50	.0157
αGPD	13.111	5	< .025	.0506
IPO	11.462	5	< .05	.004
6-PGD	6.918	5	< .50	.0894

*rare alleles were pooled

$\overline{F}_{st}$ = .0399

(Pilot, "Peninsula", Woodduck and Bearhole all with samples of 8 or more females; Table 8). All other populations had 3 or fewer females each. Significant heterogeneity among these collections of females was detected at 2 loci (EST; $p < .01$ and αGPD ; $p < .01$; G-test). Mean female F_{st} was estimated as $\overline{F}_{st} = .1929$ for those 4 populations.

The proportion of polymorphic loci (P) for the 17 loci examined and the estimated mean heterozygosity per individual ($\overline{H}_0$) for males from the 6 largest male collections, for females from the 4 largest female collections and for sexes combined (all 10 populations) are given in Table 9. Among males P ranges from 12 percent on "Knob" to 35 percent on "Peninsula". Mean P among males from these 6 populations is 26 percent. Among females P ranges from 18 percent on Pilot and Woodduck to 29 percent on Bearhold. Mean P among females for these 4 populations is 22 percent. Mean heterozygosity per individual ($\overline{H}_0$) among males ranges from $\overline{H}_0 = .017$ on "Knob" to $\overline{H}_0 = .118$ on Bearhole. Mean $\overline{H}_0$ among males for the 6 populations considered is $\overline{H}_0 = .078$. $\overline{H}_0$ among females ranges from $\overline{H}_0 = .039$ on "Peninsula" to $\overline{H}_0 = .078$ on Bearhole with a mean of $\overline{H}_0 = .060$ among females for the 4 populations considered. With sexes pooled P ranges from 12 percent on "Knob" and Gourd to 41 percent on "Peninsula". Mean P with sexes pooled is 25 percent for islands and 23 percent for mainland populations. The range of $\overline{H}_0$ when sexes are pooled is from $\overline{H}_0 = .008$ from mainland 1 to $\overline{H}_0 = .104$ for Dollar Island. The mean $\overline{H}_0$ for the 8 island populations when sexes are pooled is $\overline{H}_0 = .067$. The mean $\overline{H}_0$ for the 2 mainland populations when sexes are pooled is $\overline{H}_0 = .029$.

TABLE 8. Genetic Heterogeneity and F-statistics among females among 4 island populations of Peromyscus leucopus

Locus	G-Het*	df	P	F_{st}
EST	14.969	3	< .01	.1476
GPD	22.320	3	< .01	.2886
IPO	5.716	3	< .20	.1173
6-PGD	6.727	3	< .10	.2182

*rare alleles were pooled $\overline{F}_{st} = .1929$

TABLE 9. Proportion of polymorphic loci* (P) and estimated mean heterozygosity per individual ($\bar{H}_0$) among male, female, and sexes pooled of *Peromyscus leucopus* from 8 island and 2 mainland sites

Population	♂♂		♀♀		Sexes Pooled	
	P	$\bar{H}_0$	P	$\bar{H}_0$	P	$\bar{H}_0$
"Sliver"	-	-	-	-	.23	.067
"Knob"	.12	.017	-	-	.12	.017
Gourd	-	-	-	-	.12	.049
Dollar	.23	.104	-	-	.23	.104
Pilot	.29	.074	.18	.059	.29	.066
"Peninsula"	.35	.076	.24	.039	.41	.059
Bearhole	.29	.118	.29	.078	.35	.098
Woodduck	.25	.080	.18	.065	.29	.073
Mainland 1	-	-	-	-	.23	.008
Mainland 3	-	-	-	-	.23	.059
Island Mean	.26	.078	.22	.060	.25	.067
Mainland Mean	-	-	-	-	.23	.029

*Total # of loci examined = 17

Genetic heterogeneity and F-statistics for islands with sexes pooled are given in Table 10. Genetic heterogeneity among insular populations is significant at 5 (EST, αGPD, IPO, 6-PGD and LAP) of the 9 polymorphic loci identified. These are also the most polymorphic loci and, as a result, they provide more information than less variable loci. This increases the probability of detecting heterogeneity among populations if it is present. The island F_{st} values range between $F_{st} = .033$ at the PGM locus and .389 at the LAP locus. Mean F_{st} was estimated to be $\overline{F}_{st} = .101$ for insular populations.

Genetic heterogeneity estimates for the two mainland collections with seven individuals (mainland 2 with $N = 2$ is not considered) are given in Table 11 for the 4 polymorphic loci identified. Genetic heterogeneity is significant at one locus (αGPD). No mainland F_{st} estimates are possible since there are only 2 populations of adequate size from the mainland. F_{st} is a variance estimate (in among subpopulation allele frequencies) and, therefore, requires at least 3 populations for its calculation.

Genetic identities and distances (Nei, 1978) between all pairs of populations are given in Table 12. The highest genetic identity ($I = .996$) is between Woodduck and Pilot Islands. Thirteen of the total of 45 pairwise comparisons have genetic identities above $I = .990$. The least similar populations are mainland 3 and Bearhole Island ($I = .960$). There are 10 population pairs that have genetic identities less than $I = .980$. The means for all island comparisons are $\overline{I} = .984 \pm .007$ and $\overline{D} = .016 \pm .007$. The genetic identity between the two mainland populations is $I = .992$ with genetic distance being $D = .008$.

TABLE 10. Genetic heterogeneity and F-statistics in 8 island populations of Peromyscus leucopus

Locus	G-Het*	df	P	F_{st}
EST	35.39	7	< .005	.103
αGPD	35.39	7	< .005	.150
IPO	22.47	7	< .005	.065
6-PGD	15.07	7	< .05	.049
LAP	47.42	7	< .005	.389
G-6-PD	10.62	7	< .50	.053
PGM	7.69	7	< .50	.033
GP-2	11.03	14	< .50	.035
GP-4	9.91	7	< .50	.037

*rare alleles were pooled. $\overline{F}_{st} = .101$

TABLE 11. Genetic heterogeneity in 2 mainland populations of *Peromyscus leucopus*

Locus	G-Het*	df	P
EST	.5256	1	< .50
αGPD	4.27	1	< .05
IPO	0	1	< .975
6-PGD	.8617	1	< .50

*rare alleles were pooled

TABLE 12. Genetic Identity (Nei, 1978), above diagonal, and genetic distance, below diagonal, between all pairs of 8 island and 2 mainland populations of P. leucopus based on 17 loci.

	"Sliver"	"Knob"	Gourd	Dollar	Pilot	Penninsula	Bearhole	Woodduck	Mainland 1	Mainland 3
"Sliver"		.983	.982	.983	.987	.994	.981	.983	.985	.983
"Knob"	.017		.987	.975	.989	.993	.979	.988	.993	.991
Gourd	.018	.013		.994	.982	.986	.981	.979	.981	.993
Dollar	.017	.025	.006		.980	.981	.965	.973	.973	.971
Pilot	.013	.011	.018	.020		.983	.987	.996	.992	.994
"Peninsula"	.006	.007	.014	.019	.017		.980	.987	.993	.961
Bearhole	.019	.021	.019	.035	.013	.020		.994	.974	.960
Woodduck	.017	.012	.021	.027	.004	.013	.006		.985	.993
Mainland 1	.015	.007	.019	.027	.008	.007	.026	.015		.992
Mainland 3	.017	.009	.007	.029	.006	.039	.041	.007	.008	

Island $\overline{I}$ = .984 ± .007

Island $\overline{D}$ = .016 ± .007

Mainland I = .992

Mainland D = .008

CHAPTER 6

DISCUSSION

Data from studies invoking the founder effect and genetic drift as possible mechanisms for genetic divergence of insular populations have shown three trends: 1) a decrease in genetic variability among insular populations, 2) lower genetic identities between insular populations than mainland populations, and 3) higher degrees of genetic heterogeneity and among subpopulation genetic variance in insular as compared to mainland populations (summarized in Kilpatrick, 1981).

Genetic Variability of Insular and Mainland Populations

In several other studies on the genus Peromyscus the proportions of polymorphic loci (P) and mean individual heterozygosity estimates ($\overline{H}_0$) have been found to be lower in insular than in mainland populations (Aquadro and Kilpatrick, 1981; Avise et al., 1974a,b and Browne, 1977). This has been attributed to the founder effect and genetic drift. Sexes were not considered separately in these studies. In the present study, there is no significant difference between male and female polymorphism estimates (Table 9, $p < 1$; G-test) or mean individual heterozygosity estimates (Table 9, $p < 1$; G-test) for the 4 populations with the largest collections of each sex. When sexes are pooled, a comparison of the mean proportion of polymorphic loci estimated for mainland ($\overline{P}$ = .23) and insular ($\overline{P}$ = .25) Peromyscus populations (Table 9) reveals a difference of 2 percent, with the island mean larger than the mainland mean. With males and females pooled, the range of mean individual

heterozygosity estimates (.008 - .104, Table 9) found in this study falls within the range of $\overline{H}_O$ reported for the genus Peromyscus in other studies (Aquadro and Kilpatrick, 1981; Avise et al., 1974a,b). Considering all populations with sexes pooled, there is no significant difference between the mean heterozygosity levels of the insular and mainland populations ($p < .50$; G-test) in the present study with sexes pooled. The insular mouse populations do not have lower polymorphism levels and mean individual heterozygosity estimates than the mainland populations as would be expected if founder effect and/or genetic drift were acting on them to a greater extent than on the mainland populations.

Genetic Similarity and the Geographical Distribution of Islands

All genetic identity values (Table 12) are within the range given by Zimmerman et al. (1978) for local populations of 2 other species belonging to the genus Peromyscus. In the present study, the 2 mainland sites have a higher ($I = .992$) genetic identity than the mean genetic identity of all possible island pairs ($\overline{I} = .984$). However, many pairs of island populations (18%) have identity values as large or larger than exist between the mainland pair (Table 12). There appears to be no geographical pattern associated with the genetic identity values observed in the present study. The two pairs of least similar populations are mainland 3 and Bearhole Island ($I = .960$) and mainland 3 and "Peninsula" Island ($I = .961$). These islands are 2.62 and 1.36 kilometers from mainland 3, respectively. In contrast, Gourd Island is 6.57 kilometers from mainland 3 and is more similar to it genetically ($I = .993$). "Knob" and Gourd Islands are

connected at low water levels and have a genetic identity of I = .987. "Knob" and "Peninsula" Islands are separated by 5.59 kilometers of water and are even more similar genetically (I = .993). There is non-significant, but positive, correlation (r = .1103; df = 26) between genetic identities and geographical distances between all possible pairs of island populations. This shows that the geographical distance between island populations was not significantly correlated with genetic similarities.

Heterogeneity and Genetic Variance Among Populations

Substantial differences were found between the estimates of mean among subpopulation genetic variance for males ($\overline{F}_{st}$ = .0399) and females ($\overline{F}_{st}$ = .1929; Tables 7 and 8). This may reflect differences in social behavior between sexes. Metzgar (1979) has shown that males have considerably larger home ranges than females with the result that a single female home range may be overlapped by several male home ranges, and a single male home range can include parts of the home ranges of several females. Furthermore, male home ranges are largest, relative to female home ranges, in the spring and summer, the time when most of the trapping in this study was done. Aggregation of both sexes occurs in winter (Metzgar, 1979). In a given area, such as a trap grid, it seems probable that females are more related to each other than males because they disperse less and males captured in the same area were probably from a much larger area than were females. Sexual differences in F_{st} values warrants further study because this finding indicates that sexual differences in dispersion patterns may affect the overall genetics of

Peromyscus populations more than previously suspected. In many similar studies (eg. Avise et al., 1979a,b ; Browne, 1977, and Selander et al., 1971), sexes were pooled and potentially important differences in genetic structure between sexes were observed. In the present study, sexes were also pooled for two reasons: 1) to maximize sample sizes from each collection site, and 2) to allow comparison with similar studies in the current literature. With sexes pooled, genetic heterogeneity estimates among islands are significant for all robustly polymorphic loci (Table 10). The mainland populations are significantly different from one another at only one of these loci (Table 11). However, the conclusion that insular populations are more heterogeneous than mainland populations cannot be drawn from these results because the comparatively small number of mainland mice (n = 14) raises the probability of type 2 error (Sokal and Rohlf, 1978). In this case, small sample size may lead to the conclusion that there is no heterogeneity between mainland populations when, in fact, there is but it was not detected. F_{st} values among insular populations ($\overline{F}_{st}$ = .101) are in rough accordance with those reported for other animals of low vagility (eg. snails and house mice, $\overline{F}_{st}$ = .174, Selander and Kaufman, 1975; pocket gophers, $\overline{F}_{st}$ = .068; Patton and Feder, 1981). These animals do not move great distances and, as a result, are likely to be more inbred (resulting in higher F_{st} values) than species with greater vagility. From the data available in the present study, insular Peromyscus populations cannot be shown to possess genetic heterogeneity and genetic variance values that differ from mainland populations.

Population bottlenecks, the lowering of effective population size, may increase among island population genetic heterogeneity estimates

(Hartl, 1980). Predation may play a role in lowering effective population sizes and mainland and island sites. The effects of predation on mouse population size was not within the scope of this study. The inundation of islands at high water levels is another potential source of population bottlenecks. Complete flooding of the islands used in this study has not occured since Norris Lake has been in existence (T.V.A. Information, pers. comm.).

Genotype Frequencies within Populations

Although observed genotype frequencies did not deviate significantly from Hardy-Weinberg expectations, this test may not reveal individually nonsignificant but nonetheless biologically important patterns of heterozygote deficiency or excess. Such patterns may be apparent when all populations are considered. Of the 4 robustly polymorphic loci examined in both insular and mainland populations 2 were consistently deficient in heterozygotes (6-PGD, 0 "+" and 6"-", $p = .032$ and EST, 1 "+" and 9 "-", $p = .022$; Sign test). There are 4 possible explanations for these results: 1) negative heterosis or selection against individuals that are heterozygous at these loci, 2) population structuring, in which semi-isolated demes are low in heterozygosity because of inbreeding, 3) the sampling of individuals from 2 or more semi-isolated demes with slightly different allele frequencies resulting in apparent heterozygote deficiency within a sample (Wahlund effect ; Hartl , 1980), and 4) undetected "null" alleles may be segregating in some populations for one or both of these

loci. The presence of heterozygote deficiency in both insular and mainland populations implies that it is not due to some unique aspect of insular habitat. Population structuring resulting from social behavior has been found sufficient to produce genetic differences between populations of Peromyscus, even in continuous habitat (Rasmussen, 1970). "Family" units consisting of one adult female, several adult males and juveniles have been reported for Peromyscus leucopus (Myton, 1974). Territoriality, especially on the part of female Peromyscus leucopus, also contributes to the demic structure of these mice (Burt, 1943). Each collection was treated statistically as a deme. If this is not the case, Wahlund effect is probably contributing to the observed heterozygote deficiency since it would be highly probable that individuals from several breeding units were collected at each site. Negative heterosis may also be a factor, but there is no evidence for or against it in this study. The possibility that undetectable or "null" alleles exist at low frequencies at the EST or 6-PGD loci also cannot be discounted. Null alleles are fairly common at esterase loci (G.F. McCracken, pers. comm.). If this were the case, there would be more individuals heterozygous at this locus (EST) than were actually considered in the estimate of heterozygote deviation estimate. There were no individuals homozygous for the null allele detected in the Peromyscus sampled in this study; however, to expect to detect homozygotes for an allele that occurs at very low frequencies, a large number of individuals must be sampled. Null alleles at the EST locus may have occurred in a few individuals in this study but, their presence cannot be confirmed in any individual because they do not occur in the homozygous state.

Given the low vagility and social structuring of these mice, stochastic processes, such as founder effect and genetic drift, may be important factors in the population genetics of these populations. Under the conditions of the present study, stochastic processes could, theoretically, result in the fixation of alleles in genetically isolated populations at loci that are polymorphic in other populations (Browne, 1977). There are no populations in this study that are fixed for alleles that are rare in other populations. There is evidence, however, of substantial genetic differentiation at the LAP locus in the Dollar Island population. The rare allele occurs in only 2 other populations, "Sliver" and "Peninsula" Islands, at low frequencies of 7 and 2 percent, respectively; however, this same allele occurs at a frequency of 50 percent in the Dollar Island population (Table 5).

Summary and Conclusions

This study revealed significant genetic heterogeneity among insular populations at all robustly polymorphic loci examined. However, there was no apparent reduction in heterozygosity or polymorphism in insular populations relative to mainland populations, and there is no conclusive evidence that the insular populations are more heterogeneous than are the mainland populations connected by continuous habitat. Given theoretical considerations of the expected effects of small population size, the isolation of populations, and the results of previous studies of genetic structuring on islands (eg. Avis et al., 1974a,b; Browne, 1977; Chesser, 1983; Gill, 1976; Patton and Feder, 1981) these results are somewhat surprising. The most likely explanation is that these island populations are not, in fact,

genetically isolated. The proximity of the islands to one another and to the mainland (Table 1) appears to be a factor in the lack of evidence for founder effect and genetic drift in these populations. The geographical distances in this study also are much smaller than in previous studies finding significant reductions in heterozygosity and polymorphism among insular populations in comparison to mainland populations (eg., Avise et al., 1974a,b; Berry et al., 1978, and Browne, 1977). The greater isolation of populations in these studies may have resulted in restrictions in gene flow that do not occur the lake water level (Table 2) forms land bridges between some islands, greatly enhancing the probability of gene flow. Peromyscus has been found to be capable of swimming distances comparable to some of those in this study (7.6m - 233.2m, $\overline{X}$ = 38.4m; Sheppe, 1965a). Peromyscus has also been shown to move between nearby islands and mainland on a frequent basis (Sheppe, 1965b). Sheppe (1965b) recorded the movement of several Peromyscus from an island to the mainland and back across 7.6m of marshy sand bar. A single male made at least six crossings from another island to the mainland over the course of 2 months, each trip involved movement of at least 48.8m across a marshy connection (Sheppe, 1965b). Gene flow resulting from movement between insular populations would limit the degree to which populations can diverge (Hartl, 1980).

The apparent heterogeneity among populations does not appear to be the result of island habitation since mainland populations are as heterogeneous as insular ones. Rasmussen (1970) suggests that Peromyscus populations can be behaviorly structured to such an extent that gene

flow may be restricted between subpopulations in continuous habitat. Behavioral restrictions to gene flow may result in genetical differences over very short geographical distances (Rasmussen, 1970). This type of population structuring is probably occurring at both the island and mainland sites such that any possible effects of insularity, with respect to genetic heterogeneity, are not apparent.

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VITA

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