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GENETIC VARIATION OF WOODRATS (NEOTOMA CINEREA) AND DEER MICE (PEROMYSCUS MANICULATUS) ON MONTANE HABITAT ISLANDS IN THE GREAT BASIN

William T. Mewaldt\textsuperscript{1,2} and Stephen H. Jenkins\textsuperscript{1}

Abstract.—Seventeen loci were examined for polymorphism in four populations of Neotoma cinerea and Peromyscus maniculatus on isolated mountain ranges in the Great Basin, one population of each in the Sierra Nevada, and one of each in the Rocky Mountains. All Peromyscus populations had higher levels of heterozygosity than syntopic Neotoma populations. Results indicate; interstriae 1 moderately elevated, very slightly higher than interstriae 3, with a median

deviation. Populations of species restricted to terrestrial habitat islands may be similar to those on oceanic islands in patterns of gene frequency change over time (Kilpatrick 1981). For example, Glover et al. (1977) studied pikas (Ochotona princeps), which are generally restricted to talus slopes and other rocky habitats at high elevations. Their findings of low heterozygosity within populations are consistent with patterns on oceanic islands reviewed by Soule (1976) and Kilpatrick (1981), who concluded that the stochastic processes of founder effect and genetic drift may cause unpredictable shifts in gene frequency and reduced heterozygosity. The distribution of montane habitats in the Great Basin of the western U.S. provides an opportunity for "island-mainland" comparisons of montane mammals. In the Great Basin, isolated patches of forested habitat act as refugia for many populations of mammals that apparently cannot live in or cross the intervening deserts (Brown 1971). As recently as 8,000 years ago, climatic conditions were such that forests (interspersed with pluvial lakes) existed continuously across the Great Basin from the Sierra Nevada to the Rocky Mountains. Since that time, the climate has become drier, resulting in isolation of montane habitat at higher elevations of the mountain ranges (Wells 1983). We analyzed allozymes in several populations of two cricetid rodent species, Neotoma cinerea acraia (Elliot) (bushy tailed woodrat) and Peromyscus maniculatus sonoriensis (Le Conte) (deer mouse), to test some genetic predictions of the hypothesis that stochastic effects should be more pronounced for isolated island populations than for "mainland" populations. Peromyscus maniculatus sonoriensis is distributed continuously across the Great Basin (Hall 1946), whereas Neotoma cinerea acraia is found in isolated populations on most of the Basin ranges (Brown 1971).

Biochemical variation within at least 20 species of Peromyscus has been reported (e.g., Selander et al. 1971, Kilpatrick and Zimmerman 1976, Zimmerman et al. 1978, Avise et al. 1979, Gill 1980). Of special interest here are the studies by Avise et al. (1979) and Gill (1980), both of which included P. m. sonoriensis. Avise et al. reported mean heterozygosity (H) values for populations of this subspecies ranging from 0.074 to 0.124, whereas Gill found an H of 0.118.

Electrophoretic studies of Neotoma are few. Mascarello (1975) studied three chromosomal races of Neotoma lepida in the southwest but did not report H values, whereas Zimmerman and Nejtek (1977) reported H values for three semispecies of Neotoma (N. albigula, N. micropus, and N. floridana) in southern North America ranging from 0.024 to 0.140, with an average of 0.078. Heterozygosity measures for populations of N. cinerea have not been reported.

Materials and Methods

Six mountain ranges with populations of N. c. acraia and P. m. sonoriensis were chosen

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Table 1. Allele frequencies for polymorphic loci of Neotoma cinerea and Peromyscus maniculatus, and mean heterozygosity per locus over all loci sampled (H).*

<table>
<thead>
<tr>
<th>Population</th>
<th>Sample size</th>
<th>ES-B</th>
<th>ES-C</th>
<th>AAT-1</th>
<th>GDH</th>
<th>PGD</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neotoma cinerea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sierra Nevada (Carson Range)</td>
<td>16</td>
<td>100</td>
<td>100</td>
<td>100 (.93)</td>
<td>84 (.04)</td>
<td>100</td>
<td>0.013</td>
</tr>
<tr>
<td>Shoshone</td>
<td>17</td>
<td>82 (.925)</td>
<td>100</td>
<td>100 (.50)</td>
<td>84 (.05)</td>
<td>92 (.925)</td>
<td>0.034</td>
</tr>
<tr>
<td>Toiyabe</td>
<td>14</td>
<td>100</td>
<td>94 (.18)</td>
<td>100 (.93)</td>
<td>84 (.21)</td>
<td>100</td>
<td>0.046</td>
</tr>
<tr>
<td>Toquima</td>
<td>15</td>
<td>100</td>
<td>94 (.07)</td>
<td>100 (.87)</td>
<td>84 (.10)</td>
<td>100</td>
<td>0.033</td>
</tr>
<tr>
<td>Snake</td>
<td>14</td>
<td>100</td>
<td>100 (.93)</td>
<td>100 (.77)</td>
<td>100 (.97)</td>
<td>92 (.03)</td>
<td>0.037</td>
</tr>
<tr>
<td>Rocky Mountains (Tushar Range)</td>
<td>15</td>
<td>100</td>
<td>94 (.31)</td>
<td>100 (.97)</td>
<td>100</td>
<td>100</td>
<td>0.030</td>
</tr>
<tr>
<td>Population</td>
<td>Sample size</td>
<td>ES-A</td>
<td>ES-C</td>
<td>AAT-1</td>
<td>GDH</td>
<td>LDH-2</td>
<td>PGD</td>
</tr>
<tr>
<td>Peromyscus maniculatus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sierra Nevada (Carson Range)</td>
<td>18</td>
<td>100 (.91)</td>
<td>100 (.74)</td>
<td>100 (.76)</td>
<td>89 (.15)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Shoshone</td>
<td>15</td>
<td>100 (.97)</td>
<td>100 (.63)</td>
<td>100 (.77)</td>
<td>100 (.97)</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Toiyabe</td>
<td>15</td>
<td>100 (.97)</td>
<td>100 (.73)</td>
<td>100 (.67)</td>
<td>89 (.13)</td>
<td>100</td>
<td>83 (.13)</td>
</tr>
<tr>
<td>Toquima</td>
<td>18</td>
<td>100 (.94)</td>
<td>100 (.58)</td>
<td>100 (.53)</td>
<td>89 (.14)</td>
<td>100</td>
<td>83 (.14)</td>
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<tr>
<td>Snake</td>
<td>21</td>
<td>100</td>
<td>100 (.64)</td>
<td>100 (.57)</td>
<td>89 (.045)</td>
<td>91 (.02)</td>
<td>83 (.02)</td>
</tr>
<tr>
<td>Rocky Mountains (Tushar Range)</td>
<td>13</td>
<td>100 (.96)</td>
<td>100 (.81)</td>
<td>100 (.65)</td>
<td>89 (.08)</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>

*Alleles designated according to proportional electrophoretic mobility relative to the most common allele (100). Frequencies given in parentheses. H calculated according to formula (5) in Nei (1978), for 17 scorable loci for Neotoma and 16 scorable loci for Peromyscus.

for analysis (Table 1). All mountain ranges are over 80 km long and have peaks of over 3,000 m. Animals were collected in the summers of 1978 and 1979. Total sample sizes were 91 for N. c. acraia and 100 for P. m. sonoriensis (Table 1).

Techniques of tissue (liver and kidney) preparation and enzyme staining for all loci except esterases were modified from Selander et al. (1971) and Gabriel (1971). Esterase analysis using naphthol-AS-D-acetate as a substrate followed Van Deusen and Kaufman (1978). All electrophoresis was done in polyacrylamide slab gels, with both homogeneous and gradient type gels run in a water-cooled Pharmacia electrophoresis tank. Use of polyacrylamide rather than starch gels permitted better resolution of separate bands for some loci, such as the esterases.

In all, seventeen presumed loci were analyzed for each species. These included carboxylesterase (ES-A, ES-B, and ES-C; E.C. 3.1.1.1.), phosphoglucomutase (PGM; E.C. 5.4.2.2), malate dehydrogenase (MDH-1 and MDH-2; E.C. 1.1.1.37), malate dehydrogenase (oxaloacetate-decarboxylating) (NADP+)
Table 2. Genetic distances* between pairs of Neotoma cinerea populations (above diagonal) and pairs of Peromyscus maniculatus populations (below diagonal) on mountain ranges in the Great Basin.

<table>
<thead>
<tr>
<th></th>
<th>Sierra Nevada</th>
<th>Shoshone</th>
<th>Toiyabe</th>
<th>Toquima</th>
<th>Snake</th>
<th>Rocky Mountains</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sierra Nevada</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shoshone</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Toiyabe</td>
<td>0.0003</td>
<td>0.0028</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Toquima</td>
<td>0.0040</td>
<td>0.0047</td>
<td>0.0024</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Snake</td>
<td>0.00217</td>
<td>0.00093</td>
<td>0.00331</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rocky Mountains</td>
<td>0.00258</td>
<td>0.00236</td>
<td>0.00371</td>
<td>0.00793</td>
<td></td>
<td>0.00477</td>
</tr>
</tbody>
</table>

*Formula for genetic distance (D) from Nei (1978).

(MDH-3; E.C. 1.1.1.40), cytosol aminopeptidase (CAP; E.C. 3.4.11.1), L-lactate dehydrogenase (LDH-1 and LDH-2; E.C. 1.1.1.27), glucose dehydrogenase (GDH; E.C. 1.1.1.47), isocitrate dehydrogenase (NADP⁺) (IDH; E.C. 1.1.1.42), aspartate aminotransferase (AAT-1 and AAT-2; E.C. 2.6.1.1), xanthine dehydrogenase (XDH; E.C. 1.1.1.204), phosphogluconate dehydrogenase (PGD; E.C. 1.1.1.43), and superoxide dismutase (Sod; E.C. 1.15.1.1). Choice of enzymes for analysis was based on our ability to obtain reproducible and unambiguous results from among those enzymes listed and studied by Selander et al. (1971). Enzyme nomenclature and E.C. numbers are from Moss (1982) and International Union of Biochemistry (1984).

RESULTS AND DISCUSSION

Twelve of the loci analyzed were monomorphic in Neotoma and 10 were monomorphic in Peromyscus. For both species, the same allele was fixed in all 6 populations at each of the monomorphic loci. Five loci were polymorphic in one or more populations of Neotoma; 7 were polymorphic in one or more populations of Peromyscus (Table 1). Esterase-B was so variable in Peromyscus that it could not be scored accurately; this locus is omitted from Table 1. Extremely low interpopulation genetic distances, D (Nei 1978), and proportionately large standard errors showed no clear patterns in either species (Table 2). The mean D was 0.0028 for all pairs of P. maniculatus populations and 0.0025 for all pairs of N. cinerea populations. There was no significant correlation between genetic distance and geographic distance for either species (r = 0.48 for N. cinerea, 0.05 < P < 0.10; r = 0.12 for P. maniculatus; P > 0.50).

Heterozygosity (H) was significantly greater for P. maniculatus (mean for the 6 populations = 0.084) than for N. cinerea (mean = 0.032; P = 0.03 by randomization test for matched pairs). The difference between species would be even greater if we had not excluded the highly variable ES-B locus from calculations for Peromyscus. Heterozygosity values were greater for all the central Great Basin populations of N. cinerea than for either the Sierra or Rocky Mountain population. The same was true for all but one of the P. maniculatus Great Basin populations (Table 1).

Our results in general are not consistent with the expectation that gene flow should be less and genetic drift greater for Neotoma cinerea populations than for Peromyscus maniculatus populations on isolated mountain ranges in the Great Basin. One or both of two factors could account for this inconsistency. First, N. cinerea populations might not be as isolated in montane habitats on Great Basin ranges as we initially assumed. Indeed, N. cinerea are occasionally captured below the lower tree line in some parts of Nevada (Hall 1946, personal observations). Sufficient interpopulation gene flow could forestall genetic divergence. Second, the populations studied may have been too large or the time since isolation of their forested habitats too short for measurable genetic drift to have occurred.

Our finding of significantly greater heterozygosity for populations of P. maniculatus than for the syntopic populations of N. cinerea is consistent with a general pattern of greater genetic variability of P. maniculatus than is found in most other rodent species that have been examined (Smith et al. 1978, Avise et al. 1979, Smith 1981). The niche-width variation hypothesis (Nevo 1978) might account for this pattern, since P. maniculatus is more generalized in both diet and habitat than N. cinerea.
and many other rodents. The high reproductive rate of *P. maniculatus* may also contribute to its ability to maintain relatively high levels of heterozygosity (Smith 1981).

Populations of *N. cinerea* and *P. maniculatus* on isolated mountain ranges in the Great Basin were generally more heterozygous than populations in Sierra Nevada or Rocky Mountain sites. The latter sites were near the range limits for both *N. cinerea acraia* and *P. maniculatus sonoriensis*, the subspecies which were used in our study (Hall 1981). McClenaghan and Gaines (1981) documented greater genetic variability for central than for marginal populations of *Sigmodon hispidus*; our results exhibit a similar pattern at the sub-specific level.

Although our initial predictions were not verified for the particular populations we studied, the Great Basin system of terrestrial habitat islands seems to be well suited for testing a variety of hypotheses about mammalian populations genetics. The paleoecology of this area is well understood (Wells 1983), which provides a good foundation for such studies.

**ACKNOWLEDGMENTS**

We thank the University of Nevada Research Advisory Board for financial support, W. Welch for assistance with electrophoresis, and A. Gill, D. Hafner, and W. Welch for comments on the manuscript.

**LITERATURE CITED**


