Evolutionary differentiation within the northern Great Basin pocket gopher, *Thomomys townsendii*. II. Genetic variation and biogeographic considerations

Mary Anne Rogers

*Field Museum of Natural History, Chicago, Illinois*

Follow this and additional works at: https://scholarsarchive.byu.edu/gbn

Recommended Citation


Available at: https://scholarsarchive.byu.edu/gbn/vol51/iss2/4

This Article is brought to you for free and open access by the Western North American Naturalist Publications at BYU ScholarsArchive. It has been accepted for inclusion in Great Basin Naturalist by an authorized editor of BYU ScholarsArchive. For more information, please contact scholarsarchive@byu.edu, ellen_amatangelo@byu.edu.
EVOLUTIONARY DIFFERENTIATION WITHIN THE NORTHERN GREAT BASIN POCKET Gopher, THOMOMYS TOWNSENDII.
II. GENETIC VARIATION AND BIOGEOGRAPHIC CONSIDERATIONS

Mary Anne Rogers

ABSTRACT.—Genetic variation across the known geographic range of Thomomys townsendii was examined by starch gel electrophoresis and nondifferentially stained karyotypes. All specimens examined had a diploid number of 76, but some populations possessed one pair of acrocentric chromosomes in an otherwise biarmed karyotype. Electrophoretic analyses of 16 populations revealed Thomomys townsendii to be among the least variable of pocket gopher species studied. Of 27 loci examined, 17 were monomorphic and heterozygosity values were low (H = .000-.028, H = .012). Genic differentiation between populations was also low (S = .896-.998, S = .956) and revealed little concordance with current subspecific units. The most marked differentiation is between the Honey Lake Valley/Humboldt River region and the Snake River drainage. Within each of these regions population variation is, in some cases, greater within than between currently defined subspecies. F-statistics show that the greatest genic differentiation is seen between populations, and a comparison of subspecies within a region shows the greatest homogeneity. The evolutionary history of Thomomys townsendii is discussed in the context of both the physiographic history of the region and the affinities of this species to Thomomys bottae. Results of this study and the patterns of differentiation found in the morphological analyses of the accompanying paper (Rogers 1991) indicate that the only consistent pattern to be discerned from the overall morphological and genetic homogeneity of Thomomys townsendii is that between populations of the Humboldt and Snake River drainage systems, which are here assigned to Thomomys townsendii nevadensis and Thomomys townsendii townsendii, respectively.

Key words: Thomomys townsendii, pocket gophers, genetic variation, evolutionary differentiation, geographic variation, electrophoresis, karyotype.

Since the revisions by Merriam (1895) and Bailey (1915), many studies have focused on defining and understanding morphological variation within the family Geomyidae. Aspects of fossoriality, such as specificity to soil type and low vagility, and environmental influences, such as climate, topography, and food resources, have long been considered in this context (Bailey 1915, Grinnell 1927, Davis 1937, 1940, Hall 1946, Ingles 1950). More recently, patterns of chromosomal and electrophoretic variation have been compared to and correlated with interrelationships among habitat preference, physiographic features, gene flow, and population size (Patton 1970, 1972, 1981, Nevo et al. 1974, Penney and Zimmerman 1976, Patton and Yang 1977, Honeycutt and Schmidly 1979, Tucker and Schmidly 1981, Sudman et al. 1987). To explain the patterns found, investigators have presented different arguments for a variety of evolutionary mechanisms. Patterns of genetic variation in pocket gophers have been attributed to the selective forces associated with the homogeneous fossorial environment (Nevo et al. 1974, Penney and Zimmerman 1976) or to a series of stochastic processes and physiographic changes (Patton 1972, 1981, Patton and Yang 1977).

The geographic distribution and phylogenetic affinities of Thomomys townsendii make this species an interesting subject for genetic analyses. The presence of T. townsendii in the northern Great Basin is influenced by the distribution of deep fluviatile and lacustrine soils and by the physical and biological barriers that interrupt and restrict these habitats. Patton and Smith (1981) examined allozymic and karyotypic relationships within the bottae group and determined T. townsendii to be derived from one of the geographic units of T. bottae. This genetic evidence and the morphological similarity found between these two species (Patton and Smith 1989) provide an evolutionary framework within which to interpret the patterns...
of allozymic and karyotypic variation of *T. townsendii*. Given the apparent phylogenetic affiliation, results of genetic analyses of *Thomomys bottae* synthesized by Patton (1981) are especially relevant to the present examination of genetic differentiation within *Thomomys townsendii*. In general, genic patterns in *T. bottae* do not reflect subspecific, topographic, or vegetational boundaries. Instead, broader geographic units are defined both karyotypically and genetically. This pattern suggests that environmental factors often do not explain patterns of genetic variation, but historical biogeography and features of gopher populations such as vagility and effective population size may be influential.

The results of the genetic analyses of this study and the patterns of morphological variation discussed in the accompanying paper (Roger 1991) will be considered in the context of the biogeographic history of the region and the phylogenetic affinities of this species. These components of the biology of *Thomomys townsendii* make it possible to assess its evolutionary differentiation and the validity of current taxonomic designations of this species.

**MATERIALS AND METHODS**

**Electrophoretic Procedures**

During the spring and summer of 1981 and the spring of 1982, 252 gophers were collected using Macabee gopher traps. Sixteen populations from areas representing all seven recognized subspecies and the entire geographic range of *Thomomys townsendii* were sampled. The localities (numbered as in the accompanying morphological study [Roger 1991]) and sample sizes are detailed in Figure 1 and in the Appendix. These animals were preserved as skin and skull, skeleton only, or skull only specimens and are deposited in the Museum of
Vertebrate Zoology, University of California, Berkeley. Kidney, liver, and hemolysate and plasma blood fraction samples were prepared and then frozen in liquid nitrogen. Samples were later stored under ultra-cold conditions (−76°C) in the laboratory. Kidney and liver samples were homogenized in grinding buffer and centrifuged to produce extracts. Extracts and plasma samples were then analyzed by horizontal starch gel electrophoresis following procedures similar to Selander et al. (1971).

The 27 loci scored and the tissue types used (K = kidney, L = liver, P = plasma) are as follows: enzymatic proteins: aconitase (E.C. 4.2.1.3, ACON; K), adenosine deaminase (E.C. 3.5.4.4, ADA; K), α-glycerophosphate dehydrogenase (E.C. 1.1.1.8, αGPD; K), alcohol dehydrogenase (E.C. 1.1.1.1, ADH-2; L), esterase (E.C. 3.1.1.1, EST-4; K), glucosephosphate isomerase (E.C. 5.3.1.9, GPI; K), glutamate-oxaloacetate transaminase (E.C. 2.6.1.1, GOT-1, GOT-2; K), glyceraldehyde phosphate dehydrogenase (E.C. 1.2.1.12, GAPDH; K), isocitrate dehydrogenase (E.C. 1.1.1.42, ICD-1, ICD-2; K), lactate dehydrogenase (E.C. 1.1.1.27, LDH-1, LDH-2; K), leucine aminopeptidase (E.C. 3.4.11 or 3.4.13, LAP; K), malate dehydrogenase (E.C. 1.1.1.37, MDH-1, MDH-2; K), mannose phosphate isomerase (E.C. 5.3.1.8, MPI; K), peptidase (leucyl-alanine substrate, E.C. 3.4.11 or 3.4.13, PEP-C; K), peptidase (leucyl-glycyl-glycine substrate, E.C. 3.4.11 or 3.4.13, PEP-B; K), phosphoglucomutase (E.C. 2.7.5.1, PGM-2; K), phosphogluconate dehydrogenase (E.C. 1.1.1.44, 6 PGD; K), purine nucleoside phosphorylase (E.C. 2.4.2.1, NP; K), sorbitol dehydrogenase (E.C. 1.1.1.14, SORDH; K), superoxide dismutase (E.C. 1.15.1.1, SOD; K); nonenzymatic proteins: albumin (ALB; K), prealbumin (FREALB; P), transferrin (TRF; P).

Karyotypic Procedures

Forty-one animals, representing all recognized subspecies of *Thomomys townsendii* (Appendix), were examined. Most were pretreated with yeast (Lee and Elder 1980, with modifications in dosage). Chromosome preparations were made from bone marrow cells as described by Patton (1967) except that KCl was used as the hypotonic solution. Air-dried slides were stained in Giemsa (10% stock stain solution in phosphate buffer) and air-dried before mounting with coverslips. Determination of diploid numbers and construction of karyotypes followed standard procedures (Bender and Chu 1963, Patton 1967). Bi-armed chromosomes were categorized into either a metacentric/submetacentric class or a subtelocentric class after Patton and Dingman (1970), utilizing the arm ratio criteria of Patton (1967).

Statistical Analyses: Electrophoretic Data

Alleles were designated alphabetically in order of increasing mobility, and genotype frequencies were analyzed using the BIOSYS-1 computer program (Swofford and Selander 1981). Analyses of geographic differentiation utilized Wright's (1978) $F$-statistics, and trees were constructed from coefficients of genetic similarity and genetic distance (Rogers' $S$, $D$ [1972] and modified $D$ [Wright 1978]) using UPGMA clustering and the distance Wagner method (Farris 1972).

RESULTS

Intrapopulation Variation

Seventeen of the 27 loci examined were monomorphic. All polymorphic loci are represented by dominant alleles with frequencies of 0.95 or less with the exception of GOT-1 (Table 1). This locus is fixed for alternate alleles in the populations of Honey Lake Valley and the Humboldt River drainage system versus those of the Snake River system. Using the 0.95 criterion of polymorphism, only EST-4 is polymorphic in more than 3 of the 16 populations studied.

Intrapopulation variation is also low across loci. Population averages for $H$ (mean proportion of loci heterozygous per individual, direct count estimate), $P$ (proportion of loci polymorphic, 0.95 criterion), and $A$ (mean number of alleles per locus) are presented in Table 1. The mean number of alleles per locus per population ranges from 1.0 to 1.11, with a mean across populations of 1.07. The proportion of the loci that is polymorphic per population ranges from .000 to .111. Mean polymorphism, $P$, calculated across the *T. townsendii* populations studied, is .053. Heterozygosity values range from .000 in Murphy ($n = 4$) and .002 in Pocatello ($n = 19$) to .028 in Grandview-$t$. ($n = 8$). The average
<table>
<thead>
<tr>
<th>Locus/Allele</th>
<th>Population No.</th>
<th>Lovelock</th>
<th>Valmy</th>
<th>Quinn River Crossing</th>
<th>Narrows</th>
<th>Ryncl</th>
<th>Palisade</th>
<th>Austin</th>
<th>Hi-Lon</th>
<th>Standish</th>
<th>American Falls</th>
<th>Pocatello</th>
<th>Grandview-o.</th>
<th>Murphy</th>
<th>Grandview-t.</th>
<th>Payette</th>
<th>Ontario</th>
</tr>
</thead>
<tbody>
<tr>
<td>GOT-1</td>
<td>a</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PGM</td>
<td>a</td>
<td>.625</td>
<td></td>
<td>.625</td>
<td>.375</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>.375</td>
<td></td>
<td>.375</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>.375</td>
<td></td>
<td>.375</td>
<td>.375</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>.375</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>c</td>
<td>.375</td>
<td></td>
<td>.111</td>
<td>.111</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>.111</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ADH</td>
<td>a</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>.250</td>
<td>1.000</td>
<td>.370</td>
<td>.111</td>
<td>.750</td>
<td>.750</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>c</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EST-4</td>
<td>a</td>
<td>1.000</td>
<td>.929</td>
<td>1.000</td>
<td>.929</td>
<td>1.000</td>
<td>.929</td>
<td>.929</td>
<td>.929</td>
<td>.929</td>
<td>1.000</td>
<td>.929</td>
<td>1.000</td>
<td>.929</td>
<td>.929</td>
<td>.929</td>
<td>.929</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>c</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GAPDH</td>
<td>a</td>
<td>.048</td>
<td></td>
<td>.048</td>
<td>.048</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>.048</td>
<td></td>
<td>.048</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>b</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>c</td>
<td>.904</td>
<td></td>
<td>.904</td>
<td>.904</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>.904</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PREALB</td>
<td>a</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>.800</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 1. Allele frequencies for polymorphic loci, and values for $H$, $P$, and $A$. 

M.A. Rogers (Volume 51)
### Table 1 continued.

<table>
<thead>
<tr>
<th></th>
<th>TRF</th>
<th>ADA</th>
<th>MPI</th>
<th>PEP-B</th>
<th>H</th>
<th>P</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>1.000</td>
<td>0.275</td>
<td>0.167</td>
<td>0.000</td>
<td>0.014</td>
<td>0.037</td>
<td>1.04</td>
</tr>
<tr>
<td>b</td>
<td>1.000</td>
<td>0.050</td>
<td>0.833</td>
<td>0.833</td>
<td>0.009</td>
<td>0.074</td>
<td>1.11</td>
</tr>
<tr>
<td>c</td>
<td>1.000</td>
<td>0.053</td>
<td>0.053</td>
<td>0.053</td>
<td>0.012</td>
<td>0.037</td>
<td>1.04</td>
</tr>
<tr>
<td></td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>0.019</td>
<td>0.037</td>
<td>1.04</td>
</tr>
<tr>
<td></td>
<td>1.000</td>
<td>0.053</td>
<td>0.053</td>
<td>0.053</td>
<td>0.031</td>
<td>0.074</td>
<td>1.11</td>
</tr>
<tr>
<td></td>
<td>1.000</td>
<td>0.053</td>
<td>0.053</td>
<td>0.053</td>
<td>0.016</td>
<td>0.111</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>1.000</td>
<td>0.053</td>
<td>0.053</td>
<td>0.053</td>
<td>0.031</td>
<td>0.074</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>1.000</td>
<td>0.053</td>
<td>0.053</td>
<td>0.053</td>
<td>0.016</td>
<td>0.111</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>1.000</td>
<td>0.053</td>
<td>0.053</td>
<td>0.053</td>
<td>0.031</td>
<td>0.074</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>1.000</td>
<td>0.053</td>
<td>0.053</td>
<td>0.053</td>
<td>0.016</td>
<td>0.111</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>1.000</td>
<td>0.053</td>
<td>0.053</td>
<td>0.053</td>
<td>0.031</td>
<td>0.074</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>1.000</td>
<td>0.053</td>
<td>0.053</td>
<td>0.053</td>
<td>0.016</td>
<td>0.111</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>1.000</td>
<td>0.053</td>
<td>0.053</td>
<td>0.053</td>
<td>0.031</td>
<td>0.074</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>1.000</td>
<td>0.053</td>
<td>0.053</td>
<td>0.053</td>
<td>0.016</td>
<td>0.111</td>
<td>1.07</td>
</tr>
</tbody>
</table>

**Notes:**
- TRF, ADA, MPI, and PEP-B are enzyme activities.
- H and P are other variables measured.
- A is the average activity.

**Source:** GENETIC VARIATION IN THOMOMYS TOWNSENDII.
heterozygosity was calculated across the 12 populations of $n \geq 10$. The value for $H$ was not altered ($\bar{H} = .012$).

**Interpopulation Differentiation: Electrophoretic Analysis**

The populations of *T. townsendii* examined were arranged within four hierarchical levels: local population, subspecies, region, and species. The geographic regions (and corresponding subspecies) included the following: the Humboldt River drainage system (*T. t. bachmani*, *T. t. elkoensis*, *T. t. nevadensis*), Honey Lake Valley (*T. t. relictus*), and the Snake River drainage system (*T. t. owyhensis*, *T. t. similis*, *T. t. townsendii*). Tables 2 and 3 represent the matrices of genetic similarity based on Rogers’ $S$ (1972) for the 16 populations, 7 subspecies, and 3 regions examined.

The range in similarity values for the populations of *T. townsendii* is .896 to .998, with $S = .956$. Examination of the subspecific and regional treatments of these data reveals some discordance between subspecific or regional affinity and degree of genetic similarity. For example, in Tables 2 and 3 some populations of *T. t. bachmani* exhibit, on average, more genetic similarity to *T. t. elkoensis* and *T. t. relictus* than to other members of their own subspecies. These results are similarly displayed in the regional comparison where some populations of the Humboldt River region show a higher average similarity to Honey Lake than to some of the other populations within the Humboldt River system.
The Snake River subspecies are, however, on average most similar to the other subspecies of that region.

The unweighted pair group method of analysis was employed to cluster these data and illustrate these same trends in interpopulation similarities. Figure 2 presents the results of this analysis in the form of a contour diagram. Beyond general homogeneity among the *T. townsendii* populations (*S* = .939), the most obvious feature of the contour diagram is the separation of the Honey Lake Valley and Humboldt River populations from the Snake River populations, forming two major clusters (*S* > .95). This dichotomy is concordant with subspecific designations and hydrographic relationships. Within each cluster, however, similarity values do not correspond to current taxonomy or geographic affinities. For instance, within the Humboldt River/Honey Lake cluster, the populations of geographically peripheral *T. t. relictus* (Standish and Herlong) show affinities to some of the populations of the Humboldt River subspecies. The Standish population from Honey Lake Valley and the Valmy population from north central Nevada are the most similar pair of that major cluster and are therefore more similar to each other than either is to any other representative of its own subspecies. The *T. t. nevadensis* sample from Austin is the most divergent population from the Humboldt River region. Within the Snake River cluster, the greatest genic similarity values are also found between geographically well-separated populations. Grandview-t., a *T. t. townsendii* population situated centrally in the Snake River distribution, is the most differentiated population of that cluster.
Figure 3 provides a phylogenetic tree produced by the distance Wagner procedure of Farris (1972) based on Wright's (1978) modification of Rogers' D. Additional trees, constructed with and without the use of Swofford's (1981) optimization algorithm and using Rogers' D (1972), give the same general topology. The most notable difference among these trees is in the position of the divergent populations within the Humboldt River cluster. Trees generated using Rogers' D (1972) show these populations arising from different small clusters (all separated from adjacent clusters by branch lengths less than .01), in contrast to their peripheral position in trees generated with the modified Rogers' D (Wright 1978). Of the four trees generated, the one presented in Figure 3 was chosen for its high correlation coefficient (range in cophenetic correlation coefficients = .986-.995).

Several features are shared by the contour diagram derived from the UPGMA phenogram and all four Wagner trees. The most notable is the existence of two major clusters that separate the populations into the two river drainage systems. Divergent populations within each of these clusters are consistently well differentiated in all the algorithm/coeficient combinations utilized. These populations are Austin, Narrows, Lovelock, and Grandview-t. Each main cluster consists of a group of populations that cluster at a relatively high level of similarity and whose identity as a group is maintained in all analyses. Beyond the basic dichotomy between the two major river systems, there is no apparent concordance between geographic distance or hydrographic relationship and genic similarity.

The F-statistics of Wright (1978) were calculated to assess how genetic differentiation is partitioned within and between the hierarchical levels established in this study. As mentioned above, the 16 populations sampled correspond to the lowest level of the hierarchy, with subspecies, regions, and the total as higher levels. The variance components and $F_{ST}$ values estimating the amount of variation accounted for by each of the subdivisions relative to another are given in Table 4. These were calculated for the polymorphic loci only. The greatest amount of differentiation is seen in comparing all the populations sampled ($F_{ST} = .672$). Of the comparisons made, subspecies compared within a region are the least differentiated ($F_{ST} = .151$). Within the total, interpopulation comparisons show greater differentiation than those between subspecies; these in turn show greater genic divergence than do comparisons between regions. 

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Variance component</th>
<th>$F_{ST}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population-subspecies</td>
<td>.252</td>
<td>.392</td>
</tr>
<tr>
<td>Population-region</td>
<td>.366</td>
<td>.484</td>
</tr>
<tr>
<td>Population-total</td>
<td>.798</td>
<td>.672</td>
</tr>
<tr>
<td>Subspecies-region</td>
<td>.114</td>
<td>.151</td>
</tr>
<tr>
<td>Subspecies-total</td>
<td>.547</td>
<td>.460</td>
</tr>
<tr>
<td>Region-total</td>
<td>.433</td>
<td>.364</td>
</tr>
</tbody>
</table>

Similarly, within a region, interpopulation differentiation is greater than that measured between subspecies. Averaged across all loci, the $F_{ST}$ calculated for all populations is .130.

The same statistics were calculated for a classification scheme with two regions, Honey Lake Valley populations being included with those of the Humboldt River drainage (Table 4). This set of $F$-statistics shows decreased differentiation between the populational and subspecific units within a region and greater differentiation between regions compared to the results of the three-region scheme. Honey Lake Valley populations fit relatively homogeneously into the Humboldt River region. The overall pattern still suggests that the greatest extent of differentiation is between the smallest subdivisions and that there is relative homogeneity between the subspecies of a region.

The total limiting variance or total gene diversity ($HT$ of Nei 1973, 1977) per locus was calculated for each of the 10 polymorphic loci. GOT-1 exhibits the highest level of diversity, reflecting the fixed difference between the Humboldt/Honey Lake region and the Snake River region ($HT = .492$). This locus is probably responsible for most of the homogeneity (low $F_{ST}$) found among subspecies within a region. Four polymorphic loci have moderate $HT$ values (.120-.147) while the five remaining polymorphic loci are low (.012-.049). Locus-by-locus chi square tests for heterogeneity between populations were also calculated. Those loci that exhibit the most significant levels of heterogeneity (GOT-1, PGM-1, ADH-2, and PREALB) are, for the most part, the same loci that create the greatest differentiation between the various hierarchical levels in the $F$-statistic analysis. These loci also contribute to the level of differentiation seen in the four divergent populations, Austin, Narrows, Lovelock, and Grandview-t.

Interpopulation Variation:

Karyotypic Analysis

All individuals karyotyped showed a diploid number of 76. Five of the seven subspecies (T. t. elkoensis, T. t. nevadensis, T. t. owyhen-sis, T. t. similis, and T. t. townsendii) are represented by 16 pairs of meta-or submetacentric chromosomes ranging in size from large to small, and 21 pairs of large to small subtelocentric chromosomes (fundamental number [FN] = 148). In contrast, T. t. bachmanii and T. t. relictus are characterized by 16 pairs of meta- or submetacentrics, 20 pairs of subtelocentrics, and a single medium-sized acrocentric pair (FN = 146). All seven subspecies have a large submetacentric X chromosome and a minute acrocentric (dot) Y chromosome.

Physiographic History of the Northern Great Basin

The Great Basin extends from the Sierra Nevada and Cascade Range in the west to the Wasatch Range and Colorado Plateau in the east. The northern and southern limits are defined by the Columbia and Colorado plateaus and the Mojave and Sonoran deserts. The Great Basin has internal drainage and is made up of over 150 smaller basins, separated by more than 160 north-south-oriented mountain ranges (Morrison 1965). Many of the rivers, lakes, and playas of these basins are remnants of the Pleistocene lakes Bonneville and Lahontan.

The climate of the Great Basin is semiarid to arid. Mean annual precipitation varies from year to year and increases with elevation. Precipitation may range from 10 cm in the basins...
Fig. 4. Map of late Pliocene and Pleistocene lakes of the northern Great Basin (after Morrison 1965 and Wheeler and Cook 1954). The limits of Idaho Lake, Lake Lahontan, and Lake Bonneville are indicated by diagonal shading. Idaho Lake is of late Pliocene/early Pleistocene age. Lakes Lahontan and Bonneville and smaller lakes (stippled) are of Pleistocene age. Present-day lakes are represented by solid black areas. Point of overflow of Lake Bonneville at Red Rock Pass is indicated by arrow.

to over 76 cm in some of the higher mountains. Average January temperatures range from 25°F (-4°C) at Burns, Oregon, to 44.5°F (7°C) at Las Vegas, Nevada. Average July temperatures range from 67°F (19°C) at Burns to 86°F (30°C) at Las Vegas (Morrison 1965). As there are no drainages from the basin, precipitation is lost only to evaporation and transpiration. Evaporation increases and precipitation decreases in a southward trend. This latitudinal trend, coupled with the effect of elevation on temperature and evaporation, influences hydrographic features of the present-day Great Basin, as well as the existence and size of Pleistocene lakes (Meinzer 1922, Mifflin and Wheat 1979).

Pleistocene Lake Lahontan

The Great Basin of the Quarternary was divided, as today, into many hydrographic basins, the two largest of which were Lake Lahontan and Lake Bonneville (Fig. 4). Only the features of Lake Lahontan will be emphasized here, as the area covered by this drainage is closely reflected by the range of Thomomys townsendii in the northern Great Basin. Details of the features of Lakes Lahontan and Bonneville can be found in the monographs of Russell (1885) and Gilbert (1890). Broecker and Kaufman (1965), Morrison (1965), and Benson (1978) provide more recent discussions of the history of these basins.

The present-day Lahontan drainage includes parts of eastern California, southeastern Oregon, and much of northern Nevada. To the west and south it includes the Eagle Lake, Honey Lake, Lake Tahoe, and Walker Lake systems. The Reese and Humboldt rivers drain into Lahontan Basin from the east and south while the Quinn River makes
up the northern component. The boundaries of the lake, at its highest level during the Wisconsin, encompassed the following drainage basins: Honey Lake, Pyramid Lake, Winnemucca Lake, Carson Lake, Walker Lake, Smoke Creek Desert, Black Rock Desert, part of the Truckee River, Humboldt River (eastward to a point near Golconda), and Quinn River (Russell 1885, Benson 1978).

The climate of the Wisconsin was characterized by great fluctuations in temperature and precipitation. Cool, wet times (pluvials), synchronous with the glacial intervals, resulted in high water levels in the Great Basin lakes. Each lacustral maximum was followed by warmer, drier periods during which the lakes subsided. A variety of interpretations exists for the extent and timing of the fluctuation of the level of Lake Lahontan (Broecker and Kaufman 1965, Morrison 1965, Benson 1978). Benson (1978) suggests that besides the most recent pluvial episode (spanning roughly 25,000 to 9,000 years before present [YBP]) Lake Lahontan reached at least one other high stage before 40,000 YBP. He found no evidence for high lake levels between 40,000 and 25,000 YBP but recognized two subsequent to that time: 25,000–21,500 YBP and 13,600–11,000 YBP. The intervening period represented lower lake levels, but most basins remained connected during this time.

Subsequent to the second deep-lake period, the climate of the Great Basin began a warming and drying trend (Antevs 1948). From 9000 to 5000 YBP the Lahontan Basin was warm and arid, with all lakes except Pyramid Lake desiccated. In the last 5000 years water levels rose in Pyramid and Walker lakes until they were tapped for agricultural use during the past 100 years (Benson 1978).

The pre-Wisconsin history of the Great Basin is not as well documented as that of Lake Lahontan time. Since lakes of the early and mid-Quaternary probably occupied regions that lakes Lahontan and Bonneville occupied subsequently, the majority of these deposits have been buried by younger ones. Exposed deposits, however, suggest two pre-Wisconsin lacustrine intervals correlated with the Kansan and Illinoian glaciations. Early deposits from outside the areas inundated by Lake Lahontan have been found in the following regions: along the middle Reese River, Pine Valley, Smith Valley, and Carson Valley (Morrison 1965).

Snake River Plain

While the Snake River Plain is hydrographically not part of the Great Basin, it is a natural component in terms of fauna, flora, and climate (Davis 1939, Cronquist et al. 1972). As much of the northern part of the distribution of T. townsendii lies within this area, the physiographic history of the Snake River is pertinent to this study.

The Snake River Plain has been shaped by a long history of lava flows. The geography of the eastern plain is more dominated by remnants of volcanic activity than the west. These eastern lavas are, in general, younger (late Pleistocene to Recent) than those of the western basin. Kuntz et al. (1986) suggest a minimum age range of 15,000–2,000 YBP for some of these formations. Pleistocene lavas forced the Snake River into its present course along the east plain and formed the surface of the plain there (Malde 1965).

The topographically diverse western plain is cut by more tributaries and canyons of the Snake River and is covered with lacustrine and fluvialite deposits. Some of the western lacustrine deposits can perhaps be explained by the former route of the Snake River and the establishment of Idaho Lake (Fig. 4). Wheeler and Cook (1954) suggest a possible late Pliocene route to the Pacific, running from western Idaho to southern Oregon via the Owyhee River. The route continues southward along the Steens, Pueblo, and Pine Forest mountains, across Black Rock and Smoke Creek deserts of Nevada to Honey Lake Valley. From here it moves to Chiloost Pass and westward to the Feather River. In the late Pliocene/early Pleistocene the waters of the Snake were impounded and Idaho Lake formed in western Idaho and eastern Oregon. In early Pleistocene times Idaho Lake found an outlet, and the Snake River began its northward course into the Columbia drainage. Alternatively, Taylor (1960) suggests that the early route of the Snake River may have emptied into the Pacific via the Klamath River rather than the Feather River.

Another hydrographic link within the northern Great Basin is seen in the incidence of overflow of Lake Bonneville into the Snake River Plain. The Bonneville basin experienced a Wisconsin pluvial history similar to that described for Lake Lahontan. During one of the deep-lake periods, Lake Bonneville
overflowed at Red Rock Pass (SE of Pocatello, Idaho; Fig. 4) into a tributary of the Snake River (Morrison 1965). Malde’ (1968) discusses the details of the catastrophic flood and the confusion over the age of the event. It is here regarded as late Wisconsin, about 12,000 YBP (Broecker and Kaufman 1965, Morrison 1965). The flood path extended across the Snake River Plain and parts of the bed of ancient Idaho Lake to a point only several miles from the Oregon border. The duration of major flood effects is estimated at a few days, although discharge continued for at least a year.

**HISTORICAL BIOGEOGRAPHY OF *THOMOMYS TOWNSENDII***

Today *Thomomys townsendii* is found in fluviatile and lacustrine soils of southern Oregon and Idaho, northern Nevada, and northeastern California (Rogers 1991: Fig. 1). At the western edge of its distribution, *townsendii* is found in the Honey Lake Valley. To the northeast the species inhabits the Quinn River drainage system, Black Rock Desert, Alvord Desert, and the basin of Harney and Malheur lakes. Gophers follow the Humboldt River from Lovelock to the vicinity of Wells, Nevada. They are distributed along the Little Humboldt River and other tributaries to the north of the Humboldt. To the south they are found along the Reese River, in Pine and Huntington Creek valleys, Independence Valley, and Diamond Valley. Along the Snake River Plain they inhabit the vicinity of American Falls Reservoir and, to the west, the stretch of the Snake River and its tributaries from Hammett, Idaho, to the vicinity of Vale, Oregon.

The physiographic history of the northern Great Basin explains many aspects of the current distribution of *Thomomys townsendii*. The Great Basin in the Miocene and Pliocene was characterized by moderate topographic relief and a trend toward warming climates. By the end of the Pliocene there were widespread grasslands and well-developed lacustrine and riparian environments (Axelrod 1950). As discussed previously, southern Oregon and Idaho had a history of lava flows. The Pleistocene topography of the Great Basin was in part characterized by lakes and rivers that formed a network of interconnected drainage basins as their water levels rose and fell with climatic fluctuations. Remnants of these Pliocene and Pleistocene hydrographic features are the deep and moist lacustrine and fluviatile soils of the type that *Thomomys townsendii* inhabits today. It was not until post-Wisconsin times that desert conditions prevailed in the Great Basin to the extent that some of these soils became uninhabitable.

The disjunct nature of the current distribution of *Thomomys townsendii* reflects the boundaries of these historical drainage basins and gaps in the distribution of the preferred soil type of the species (Rogers 1991: Fig. 1). A major division in the current distribution of *townsendii*, and one that is reflected in both genetic and morphological analyses of this and the companion study (Rogers 1991), lies between populations of the Snake River and Humboldt River drainages. These two regions of the *townsendii* distribution persist primarily on the remnants of historical Lake Idaho and Lake Lahontan drainage basins (Fig. 4). Today they are well isolated from each other by mountain ranges and scrub desert. Suitable habitat for *townsendii* was clearly once more abundant and continuous than it is today.

It is useful here to discuss historical events and hydrographic features relevant to establishing where suitable habitat once existed for *Thomomys townsendii*, including where the populations of the Snake River and Humboldt River may have once been connected. A historical network of drainage basins extended from Malheur Lake and the Owyhee River, south through Honey Lake Valley and Lake Lahontan, and east to the limits of the Bonneville basin. Remnants of Idaho Lake (late Pliocene/early Pleistocene) can also be included here as a potential continuation of lacustrine deposits extending from southwestern Oregon into southern Idaho (Fig. 4). Davis (1937) discusses the possibility of an eastern hydrographic link leading from the Humboldt River and Pleistocene Lake Lahontan into the Snake River drainage via the historical overflow at Red Rock Pass mentioned earlier. While this information will be useful in interpreting the general history of this species, both chronologically and geographically, the geological data for the area under consideration are sufficiently limited.
that the correlation of specific historical events with specific patterns found in *Thomomys townsendii* cannot be undertaken. A review of the distributions of other Great Basin organisms will be used to help reconstruct the historically suitable habitats and dispersal routes for *Thomomys townsendii*.

Evidence from fossil and Recent freshwater fish and invertebrate distributions not only substantiates the existence of hydrographically related connections through the Great Basin, but also suggests possible corridors through which *T. townsendii* could have colonized the northern part of its present range. In his study of the fish of the Lahontan basin, Snyder (1918) found that some fish species are most closely allied to the fauna of the southeastern Oregon lakes. He found potential affinities with the Bonneville basin also. Miller (1958) similarly discusses affinities between the Lahontan and Bonneville basins based on their respective fish faunas and notes that there may have been a historical connection between the basins in the Pliocene or early Pleistocene. Miller found the fauna of the upper Snake River to be sufficiently similar to the Bonneville basin to be included in the Bonneville system.

Taylor (1960) presented distributional information for fossil and Recent freshwater clams and snails that suggests a historical network of lakes and streams leading from the Snake River through southern Oregon and northeastern California into the western Great Basin. His evidence does not suggest a Lahontan-Bonneville link. The investigation by Bisson and Bond (1971) into the origin of the fish of Harney Basin in southeastern Oregon and northeastern California, as suggested by Taylor's (1960) data, remains unclear. However, such a western hydrographic network appears to be a more viable corridor for pocket gopher dispersal than does the eastern Lahontan-Bonneville-Snake connection described for Great Basin fishes by Miller (1958). In fact, *Thomomys townsendii* is not known from the Lake Bonneville region, and, as outlined in the companion paper (Rogers 1991), there is no fossil evidence to suggest that this was ever part of the species range.

Morphological evidence presented by Davis (1937) suggests affinities between Pocatello (*T. t. similis*) and northeastern Nevada (*T. t. elkoensis*) animals and therefore an eastern link between northern and southern populations. To explain the apparent similarity, he proposed that the gophers followed the northern Bonneville shores into Idaho during the flood at Red Rock Pass (late Wisconsin). This study gives no clear indication of which route may have been taken. Only the color analysis shows any obvious similarity between
populations of the two river systems, again between *T. t. elkoensis* and *T. t. similis* populations (Rogers 1991). However, it has been demonstrated that pelage data should be treated carefully in interpreting the historical patterns of pocket gophers. Studies of *T. bottae* (Patton et al. 1979, Smith and Patton 1980, Smith et al. 1983) have clearly shown the environmental influence on variation in pocket gopher coloration. In fact, the correspondence between pelage color and vegetation zone suggests that dark soils may be a factor these two subspecies have in common (Rogers 1991).

A further suggestion that Red Rock Pass did not serve as a dispersal corridor for *T. townsendii* is presented by Wells’s (1983) discussion of montane conifer dispersal in the Great Basin. Red Rock Pass is one of the two topographically high connections between the high central plateau of the Great Basin and the western Rocky Mountains. The 1820-meter contour that Wells uses to outline these high mountain connections is graphically complementary to the distribution of *T. townsendii* and delineates historical and present-day boundaries to eastward dispersal.

**DISCUSSION**

Causes of genic homogeneity in fossorial rodents have been of particular interest to some authors. Nevo and Shaw (1972) and Nevo et al. (1974) have applied a model for selection for homozygosity in uniform subterranean environments to data for *Spalax ehrenbergi* and *Thomomys talpoides*, which both show very low levels of genic variation within and among populations. Other authors have found this selection model inappropriate for explaining the genetic patterns seen in *Thomomys*, arguing that features of pocket gopher population biology and stochastic factors explain their genetic divergence (Patton and Yang 1977, Patton 1981, Patton and Feder 1981). In contrast to the pattern of genic homogeneity seen in *talpoides*, variation within and among populations of *bottae* is high. Small, effective population size, nonrandom breeding, and migration rate in conjunction with historical changes in habitat, distribution, and population connectedness are cited as variables that have affected the genetic patterns of *T. bottae* and its relatives (Patton 1981). Results of this study are also consistent with the expected effects of these kinds of historical and population factors.

**Patterns of Genetic Variation in *Thomomys townsendii***

The results of genic and karyotypic analyses of *Thomomys townsendii* reveal a pattern of extreme genetic homogeneity across a very broad and disjunct geographic range. The parameters of intrapopulation variation presented in this study categorize *townsendii* as being one of the least variable of the pocket gopher species studied. This species shows less variability (63% monomorphic) than other members of the *bottae*-group or *Thomomys* in general (*T. bottae*: 9% monomorphic, Patton and Yang 1977; *T. umbrinus*: 17%, Hafner et al. 1987; *T. talpoides*: 29%, Nevo et al. 1974).

*Thomomys townsendii* is also low in heterozygosity values and in average proportion of polymorphic loci relative to other rodents and to mammals in general (mean *H* = .039 for 50 mammals species examined, Avise and Aquadro 1982; also, see reviews by Selander et al. 1974, Powell 1975, Nevo 1978, Kilpatrick 1981). While the ranges in population values for *P* and *H* in *T. townsendii* overlap with those values in other gopher species, the means across populations in this species are among the lowest known in pocket gophers (*P* = .053 and *H* = .012). The means and ranges of values for closely related species are *P* = .334 (.130-.565) and *H* = .093 (.030-.169) for *Thomomys bottae* (Patton and Yang 1977) and *P* = .183 (.043-.391) and *H* = .051 (.008-.100) for *Thomomys umbrinus* (Hafner et al. 1987). Of the pocket gopher species exhibiting lower levels of within-population variability (Selander et al. 1974, Honeycutt and Williams 1982, Hafner and Barkley 1984), none maintains these low levels so uniformly over such a broad geographic range as does *Thomomys townsendii*.

Analyses of genic variation have also shown a high level of similarity (*S* = .956) among the populations of *townsendii*. While these values are not unique among rodent studies (Avise 1974), they are extreme among *Thomomys* species (*T. bottae*: *S* = .81, Patton and Yang 1977; *T. umbrinus*: *S* = .80, Patton and Feder 1978, and Hafner et al. 1987; *T. talpoides*: *S* = .84, Nevo et al. 1974). Whereas values in *townsendii* are high in comparison to *bottae*
as a whole, comparable levels of similarity are seen among the Great Basin populations of *bottae* (Patton and Yang 1977).

The nature of allozymic variation between populations in this species reflects the effects of rare variants at a small number of those loci examined. Wright's $F$-statistics show that populations are the units of greatest differentiation (highest $F_{ST}$) of any of the hierarchical levels compared. Within a geographic region, populations are more differentiated than are the subspecies of that region. However, all populations are united at a high level of genic similarity, $S = .939$. $F_{ST}$ values for *Thomomys bottae* (Patton and Yang 1977) similarly show interpopulation differentiation representing a large component of the variation. This was true throughout the populations sampled in this study and within each of the geographic areas. Variation within this group of pocket gophers is generally greatest between the local units of any given area. The subspecific or regional categories within these species are thus internally quite heterogeneous.

The distinction between the two geographic regions is the only clear division at any level in *T. townsendii* and is due mostly to the effect of the single locus GOT-1, which is fixed for alternate alleles in populations of the Humboldt River/Honey Lake Valley versus the Snake River. The divergent populations within each of the regions are differentiated slightly from the remainder of their respective clusters by shifts in allele frequencies or by possession of an allele not found elsewhere. These few variants are of little absolute significance in distinguishing these populations from the remainder of their cluster, however.

Patton and Feder (1981) showed in studies of *Thomomys bottae* at Hastings Reservation that genic differentiation between fields can be as high as the differentiation found between subspecies of a region in *T. townsendii* ($F_{ST} = .142, T. townsendii F_{ST} = .151$ and .124). Considered in this context, the genic differentiation represented among the populations and subspecies within the two geographic units is remarkably low.

Results of the karyotypic analysis corroborate the findings of Wentworth and Sutton (1969) and Thaeler (1973) that the diploid number is 76 in all *Thomomys townsendii* subspecies. The only differentiation found within the otherwise totally biarmed karyotype is the presence of a single acrocentric pair of chromosomes in samples of *T. t. bachmani* and *T. t. relictus*. This pattern differs from the karyotypes reported by Wentworth and Sutton (1969) and Thaeler (1973), who group the chromosomes of all seven subspecies in the following way: 12 pairs of metacentrics, 22 pairs of submetacentrics, and 3 pairs of acrocentrics ($FN = 142$); the X chromosome is a large submetacentric, and the Y is a small acro- or subtelocentric. The lack of agreement with the published results can be explained, in part, by the lack of resolution in standard karyotypes. Without the aid of banded material, one is forced to use an arbitrary morphological classification. This may explain the disagreement in the numbers of chromosome pairs in each of the biarmed categories.

Although the distinction between uniarmed and biarmed chromosomes is more easily made, Wentworth and Sutton (1969) and Thaeler (1973) assigned three pairs of chromosomes to the uniarmed group, while one or none was so assigned in this study. Therefore, the single uniarmed pair in *T. t. bachmani* and *T. t. relictus* remains somewhat ambiguous. However, the existence of such a variant in an otherwise karyotypically homogeneous species is almost to be expected. Variation seen in related species is often of this nature; arm number may be polymorphic or polytypic, while the diploid number remains constant within a given taxon (Patton 1972, Patton and Feder 1978, Patton and Sherwood 1982, Hafner et al. 1987). In addition, it is significant that the alternative karyotype is found in the Honey Lake Valley and in the neighboring *T. t. bachmani* populations which together form the western component of the Humboldt River region. Since southeastern Oregon samples of *T. t. bachmani* were not karyotyped in this study, it cannot be determined whether this pattern extends to those populations as well.

The discrepancy found in the morphology of the Y chromosome is less easily explained as preparation artifact. The Y chromosomes presented by Wentworth and Sutton (1969) are substantially larger than the dot chromosomes found in this study. As all other *bottae*-group karyotypes exhibit the minute acrocentric morphology in the Y chromosome (Patton and Dingman 1970, Patton 1972, Patton and Feder 1978, Hafner et al. 1987), it is probable...
that *Thomomys townsendii* also shows this pattern.

The amount of genic variation found in geomyids is often accompanied by greater karyotypic differentiation than that seen in *Thomomys townsendii* as well. Average similarity values within *Geomys bursarius* and *G. personatus* (data of Y. J. Kim presented by Nevo et al. 1974 and Selander et al. 1974) are .76 and .86, respectively, and both species are karyotypically polymorphic. Of the specimens analyzed allozymically by Kim (Selander et al. 1974), *G. bursarius* was represented by seven chromosomal forms (2n = 70, 72, 74 and FN = 68–74), and *G. personatus* was represented by five (2n = 68, 70 and FN = 68–74). Chromosomal variation in these species is due to Robertsonian changes (centric fusions and fissions), inversions, and translocations. Examination of contact zones in other studies of *G. bursarius* has shown that barriers to genetic exchange exist between some chromosomal forms (Honeycutt and Schmidly 1979, Tucker and Schmidly 1981, Bohlin and Zimmerman 1982). Within the *Thomomys talpoides* complex (Nevo et al. 1974), average genetic similarity for the six karyotypic variants examined is .874. Thaeler believes that these morphs represent at least five separate species (Nevo et al. 1974). Within this complex diploid numbers range from 40 to 60, and chromosomal changes are typically due to Robertsonian changes and pericentric inversions.

Patton and Yang (1977) discussed differences in genetic variability of *T. bottae* and members of the *T. talpoides* complex. The pattern seen in *talpoides* is one of genic homogeneity and chromosomal differentiation to the point of reproductive isolation. Historical fragmentation and isolation of populations, bottlenecks, and founder effects may have resulted in the fixation of chromosomal rearrangements and fixation for alternate alleles where loci were once polymorphic. It is suggested that if reproductive isolation were attained, genic homogeneity would be maintained in these isolates. In contrast, chromosomal variability of *T. bottae* does not seem to affect reproductive isolation and interpopulation genic variability and within-population heterozygosities are high. Extensive range fragmentation is not suggested for *bottae*, gene flow is believed to have been less interrupted, and therefore genetic variability has been maintained. Historically, isolated populations of *bottae* were not chromosomally differentiated to the point of being reproductively isolated from other populations. Therefore, recontact with populations could have meant interbreeding, and bottlenecks that occurred due to isolation could have been overcome.

**Evolutionary and Biogeographic History of *Thomomys townsendii***

While *Thomomys townsendii* does not share the genetic diversity characteristic of the *bottae*-group, its distributional history is more similar to that of *bottae*, undisturbed by glaciation, than to *talpoides*, whose boreal distribution was sculpted by glacial influences. Furthermore, the genic pattern in *townsendii* is remarkably similar to the kind of variation seen in the Great Basin populations of *bottae* (Patton and Yang 1977). The concordance between genic patterns of these two species in the same geographic area suggests that a similar history of biogeographic and stochastic events may have influenced their evolution in the Great Basin.

Given that historical biogeography may have affected the genetic patterns of *bottae* and *talpoides*, it is useful to understand the evolutionary history and affinities of *T. townsendii* before trying to interpret the patterns seen in this species. Studies by Bailey (1915), Thaeler (1980), and Patton and Smith (1981) support a dichotomy within *Thomomys*. Morphological, electromorphic, and karyological analyses place *Thomomys townsendii* in the *bottae*-group, which also contains *T. bottae*, *T. umbrinus*, and *T. bulbivorus*. This group, characterized as the “heavy-rostrum” group by Bailey (1915), can be distinguished karyotypically as having diploid numbers ranging from 74 to 86 (Thaeler 1980, Patton and Seward 1982). These characters distinguish the *bottae*-group from *T. talpoides* and other members of Bailey’s (1915) “slender-rostrum” group (with diploid numbers ranging from 40 to 60 [Thaeler 1980]), including *T. clusius*, *T. idahoensis*, *T. maxima*, and *T. monticola*. Thaeler (1980) formalized this dichotomy by recognizing the slender- and heavy-rostrum groups as separate subgenera, *Thomomys* and *Megascapheus*, respectively. Patton and Smith (1981) did an electrophoretic analysis of
six *Thomomys* species (*talpoides* and *monticolus* in addition to the *bottae*-group species) and treated *T. townsendii* as part of the *bottae* unit; all alleles found in *townsendii* were also found in *bottae*. The same study determined that *bottae* and *townsendii* were a sister-group relative to *umbrinus*, that *townsendii* stemmed from within one of the major geographic units of *T. bottae*, and therefore that *bottae* was paraphyletic relative to *townsendii*. An analysis of cranial shape also supports this relationship (Patton and Smith 1989).

The evolutionary relationships of *bottae*, *townsendii*, and *umbrinus* are manifested in comparisons of karyotypic morphology and cellular DNA content, and in hybrid zone studies. The whole-arm heterochromatin found in *townsendii* resembles the pattern seen in *bottae* and is distinct from the interstitial heterochromatin characteristic of *umbrinus* (Patton and Sherwood 1982). Similarly, the amount of cellular DNA (C-value) found in *townsendii* is within the range found in *bottae* populations, whereas *umbrinus* has a higher C-value than would be expected for *T. bottae* with a similar karyotype (Sherwood and Patton 1982).

The karyotypic similarity between *bottae* and *townsendii* can be contrasted to the meiotically problematic structural rearrangements found between *bottae* and *umbrinus* (Patton 1973, Patton 1981), although studies of hybrid zones indicate that genetic introgression does not occur in either case. Both *townsendii* and *umbrinus* are known to hybridize minimally with *bottae* (12% and 11–15% hybrids, respectively). In *bottae-* *umbrinus* hybrids, F1 males are sterile, female fertility is reduced, and there is no genetic introgression (Patton 1973). While some F1 individuals from crosses of *bottae* and *townsendii* show normal reproductive characteristics, there is again no evidence for genetic or morphological introgression into the parental populations (Patton et al. 1984). Both pairs of hybridizing species remain genetically isolated species, but only the *bottae-* *umbrinus* case is likely to be chromosomally mediated. The lack of genetic introgression in the presence of karyotypic similarity between *bottae* and *townsendii* suggests other influences. The significance of behavior in this case has been suggested (Patton et al. 1984).

The evolutionary affinities between *townsendii* and *bottae* are further reflected in information from studies of the distribution of gopher lice. Pocket gopher species often serve as hosts to more than one species of louse, and a single louse species may be found on more than one species of pocket gopher (Emerson and Price 1981). *T. townsendii* is known to be the host of one louse species, *Geomydooecus idahoensis*, except in two zones of hybridization with *bottae* (Patton et al. 1984). In Honey Lake Valley *T. townsendii relictus* hybridizes with *T. bottae saxatilis* and *T. bottae canus*. In these hybrid zones the *bottae* louse is found on some of the "pure" *townsendii* as well as on some of the hybrids. *G. idahoensis* belongs to the *oregonus* species group. Another member of this group, *Geomydooecus shastensis*, is morphologically very similar to *idahoensis* and, interestingly, is the louse found on *T. bottae saxatilis* (Price and Hellenthal 1980).

The level of chromosomal and genic similarity of *townsendii* and *bottae* and the evidence for paraphyly (Patton and Smith 1981, 1989) suggest that *Thomomys townsendii* was derived from *Thomomys bottae*. In addition, Bailey (1915) and Davis (1937) recognized the morphological affinities between the two species. Further examination of the nature of this morphological similarity demonstrates that there is basically no difference in cranial shape between the two species. It has been suggested that the difference in body size between the two species may have resulted in differences in demographic features that eventually created genetic isolation (Patton and Smith 1989).

What can be determined from the results of this study regarding the nature of the distribution of this species from the time of its founding population to the present? Was the range of *townsendii* once continuous over the northern Great Basin and subsequently fragmented by unsuitable habitats? Or is the distribution of *townsendii* the result of relatively recent dispersal from one segment of the species range?

The concordance of genetic data with historical and biogeographic patterns has been emphasized in other pocket gopher studies. Patton (1981) discusses the influences of history and features of pocket gopher population biology in the context of the agreement of karyotypic and genic data for *Thomomys*.
bottae. Morphological patterns of differentiation, however, are often best explained by environmental factors such as quality and color of the soil and nutritional value of available food and probably do not provide much information regarding the evolutionary history of T. bottae (Smith and Patton 1980). Further studies (Patton and Bryliski 1987, Smith and Patton 1988) have demonstrated that while pelage coloration and body size are strongly influenced by environmental factors, cranial shape variation is more likely to represent genetically based changes. In the absence of an analysis focusing on cranial shape in Thomomys townsendii, the results of the genetic analyses will be emphasized in developing a historical scenario for this species.

While the nature of the historical distribution of Thomomys townsendii is not easily determined by the results of this study and its companion paper (Rogers 1991), evidence does exist that eliminates some possibilities and suggests others. A description of the historical biogeography of the northern Great Basin that focuses on the changes in and the availability of suitable habitat for Thomomys townsendii has been presented. It indicates that the wetter climates of the Pleistocene of the northern Great Basin produced a network of lacustrine and fluviatile soils that were occasionally continuous until desert conditions prevailed, rendering some of these soils uninhabitable. The continuity of these habitats could have provided historical corridors for dispersal.

However, while these historical connections can be reconstructed, it is unlikely that the species could have maintained a continuous range over most of the northern Great Basin at one time. Rather, it seems feasible that after the origin from T. bottae, segments of the range of T. townsendii were connected to various degrees at different points in its distributional history. Barriers to the continuity of the range probably arose at different times in different places. As climates increased in aridity and lakes receded, some areas became unable to support gopher populations, and townsendii remained along rivers and receding lake shores. Further fragmentation and isolation of some sections of the range of T. townsendii probably occurred with the intrusion of lava flows. Information from this study supports the idea that a fragmented distribution has always been characteristic of this species and also suggests in which areas a more continuous distribution may have existed historically.

For instance, analyses of the genetic data indicate that populations of the Snake River belong to a very cohesive cluster (S = .984) despite the geographical separation of the T. t. similis populations by more than 100 miles. Fossil evidence from Wilson Butte Cave (Gruhn 1961, Rogers 1991) suggests that continuity between the western (T. t. owyhenensis and T. t. townsendii) and eastern (T. t. similis) parts of the Snake River distribution may have existed fairly recently. Only the eastern T. t. townsendii population (22) is clearly differentiated from the other Snake River populations. Most of the samples from this region differ from each other in allele frequencies and, in one case, in the presence of a rare ADA allele in low frequency. The magnitude of the differentiation of the Grandview T. t. townsendii population (22) is primarily due to the appearance of the PGM c allele in relatively high frequency (.625). This allele was not encountered in other populations. The reason for the divergence of this population is not clear, but geologic evidence suggests that historically this area may have been isolated by lava flows (Malde and Powers 1962, Malde 1965).

While variation in the Humboldt River region is very limited, more genetic differentiation is seen among these populations than among those of the Snake River region. The only karyotypic differentiation documented in this study is seen in representatives of two of the Humboldt River subspecies. Analyses of the populations of this region resulted in a cluster of six genetically very similar (S > .97) populations and three more differentiated populations: Lovelock, Narrows, and Austin. The members of the more cohesive cluster include T. t. elkoensis, two of the four T. t. bachmani populations, and the Honey Lake Valley (T. t. reliictus) populations. These samples are differentiated from one another by the presence of one to four alleles in low frequency that are not found in other populations of that cluster.

Despite their peripheral location, Honey Lake Valley populations display affinities to the Humboldt River populations as they did in the morphological analyses of the
Genetic Variation in Thomomys townsendii

The genic divergence of two of the T. t. bachmani populations (Lovelock and Narrows) is due to the prevalence of a single allele not found elsewhere. The T. t. nevadensis sample from Austin is the most differentiated population of the Humboldt River region. The magnitude of this divergence is attributable almost entirely to a fixed difference for a PREALB allele. This allele is otherwise only present, in moderately low frequency (.200), in a single T. t. elkoensis population. Austin and Narrows animals are consistently differentiated from the other populations in both genetic and morphological analyses (Rogers 1991). This may reflect their peripheral position relative to the Lahontan drainage system. Although located in a Pleistocene lake basin, Narrows is actually outside the Lahontan hydrographic basin, but it was probably once connected to the main basin. The divergence of this population from other units of this region probably reflects its isolation due to a combination of encroaching desert regions and the influence of the drainage divide.

Austin is located in the Reese River valley, south of the Humboldt River. The Reese River was a tributary of the Humboldt River during Lahontan times but was not represented by a pluvial lake (Morrison 1965), suggesting relative aridity in this basin even during pluvial times. Today the Reese River reaches the Humboldt only intermittently so that habitable areas for T. townsendii may be restricted to the southern portions of this valley. Isolation by inadequate habitat may have contributed to separation and divergence of this population. Furthermore, T. talpoides is currently found in this valley only 24 miles north of Austin. The presence of this species may have subsequently enforced existing physical barriers.

Another possible explanation for the differentiation exists if this area was one of the earliest colonized subsequent to the derivation of townsendii from bottae. Davis (1937) remarked that, of the townsendii subspecies, T. t. nevadensis is structurally most similar to bottae. If the Reese River valley were colonized from the south rather than from the Humboldt River to the north, it is possible that distribution through this area was never continuous with the remainder of the Humboldt River distribution, or that this area was isolated relatively early.

Much of the information presented above regarding genic differentiation among T. townsendii populations has a morphological counterpart from the analyses of cranial and pelage differentiation (Rogers 1991). However, relative to the genic data, morphological characters reflect a general pattern of more overlap with fewer strongly differentiated populations. As one would expect, some aspects of the biogeographic history of T. townsendii populations seem to be more closely reflected in the genic data. For instance, the four most divergent populations (Austin, Narrows, Grandview-t., and Lovelock) all have an alternative allele as the predominant one at some locus. This kind of pattern is sometimes associated with isolation, whether it be a result of a founder event or range fragmentation. For some of these populations the features maintaining biogeographic isolation are obvious, although the mechanism by which isolation began is difficult to determine. The factors that might have contributed to the isolation of the Austin, Narrows, and Grandview-t. populations have already been discussed. Explaining the extent of differentiation seen in the T. t. bachmani population at Lovelock is more problematic. Since this area is part of the large and continuous Pleistocene Lake Lahontan, reasons for isolation and differentiation are not clear. However, it is peripherally located in the species range, and the nearest neighboring specimens examined in this study are from about 75 miles up the Humboldt River.
Thomomys townsendii is characterized not only by genetic homogeneity within populations, but by shifts in allele frequencies and appearance of rare alleles in high frequencies among populations. In addition, patterns of genic similarity between populations do not correspond to geographic distance, and populations of different subspecies or geographic subunits are often more similar than are other members of the same subspecies. These features do not suggest a broadly continuous species distribution historically. It is not surprising that this pattern instead suggests the effects of drift and independent evolution on population isolates that arose from the colonization of new areas or by the fragmentation of once more continuous habitat. Pocket gophers are strongly susceptible to drift due to small, effective population size and their inability to cross various environmental barriers, which may include other gopher species.

A reasonable explanation of the events in the origin and distribution of Thomomys townsendii begins with a relatively recent derivation from Thomomys bottae. In their analysis of T. bottae genic evolution, Patton and Smith (1981) discuss what appears to be a decreased rate of allozymic change in T. townsendii. However, they suggest that their results probably do not represent actual rate changes, but reflect low levels of within-population variation in T. townsendii. They hypothesize that this homogeneity is the result of a founder event and subsequent isolation, and later morphological studies suggest that the derivation from bottae was a relatively recent event (Patton and Smith 1989). While sufficient information is not available to pinpoint when and where townsendii arose from bottae, an origin from the southern part of the current townsendii distribution has been suggested. Davis (1937) noted the similarity between bottae and the most southern subspecies, T. t. nevadensis, and later stated that townsendii had probably moved into Idaho from the south (Davis 1939). In addition, in comparing T. townsendii to T. bottae populations, Patton and Smith (1989) show that townsendii is genetically most similar to bottae populations from central and southern California.

The low level of variation seen throughout T. townsendii suggests that stages of isolation and subsequent genetic drift followed the divergence from T. bottae. Derivation from a single highly homozygous founding population would provide the genetic background necessary for dominant alleles to be maintained across the distribution despite discontinuities that inevitably arose after T. townsendii colonized the area. High interpopulation similarity suggests that low levels of genic variability were maintained as the founding population eventually dispersed through the Great Basin. The remnants of Pleistocene lakes served as a corridor for the dispersal of the species through northern Nevada, northeastern California, and southeastern Oregon and possibly into lake beds to the west of the present Oregon distribution, judging from fossil evidence (Allison 1966). Colonization of this area probably proceeded as a series of founder events with portions of the distribution becoming fragmented. The background of genetic homogeneity was maintained with diversification in the form of allelic variants. The fixed difference at the GOT-1 locus and the homogeneity seen among the Snake River populations suggest that this region was probably colonized by a single founding population from the Humboldt River region. Subsequent to dispersal of the species across the Snake River plain, discontinuities to the range arose and populations became slightly differentiated.

The relative homogeneity of the Snake River populations also suggests this region has had less time to differentiate than has the Humboldt River region. To demonstrate the relative difference in age among and between the Snake River and Humboldt River areas, estimated divergence times between populations were calculated and averaged for these two major geographic regions. Values generated for Nei's genetic distance and the methods of Nei (1971) as described by Patton and Yang (1977) were used for these estimates. An average divergence time between populations of these two geographic units is 255,400 years before present (maximum, 475,000 YBP; minimum, 190,000 YBP). The same value, calculated for populations of the Humboldt River region, is 92,083 years (maximum, 300,000 YBP; minimum, 5,000 YBP), while that for the Snake River populations is 27,143 years (maximum, 95,000 YBP; minimum, 0 YBP). As additional reference points, these divergence times were adjusted.
using the albumin immunological distance method (Sarich and Cronin 1976, Sarich 1977), again following Patton and Yang (1977). These estimates show average divergence time between populations of the two river systems to be 1,072,680 YBP; among Humboldt River populations the average divergence time is 386,749 YBP, and within the Snake River system it is 114,001 YBP. While these values present very different approximations of divergence times within *Thomomys townsendii*, they do indicate a general time frame and what the sequence of events might have been. These estimates suggest that divergence among the Snake River populations occurred subsequent to the isolation time between populations of the two river regions. The intermediate level of differentiation seen in the Austin sample is noteworthy in the context of understanding evolution within this species but does not warrant the level of distinction given to the two major geographic regions.

The absence of genetic variation in *Thomomys townsendii* is most remarkable considering the phylogenetic affinities between *townsendii* and *T. bottae*. The patterns of genetic variability found in *T. townsendii* and *T. bottae* are strikingly dissimilar. *Thomomys bottae* is characterized by extreme interpopulation differentiation in allozymes (Patton and Yang 1977), with an average Rogers’ $S$ between populations of .81. Similarly, karyotypic variability is great, consisting primarily of variation in arm number. These variants are the result of additions and/or deletions of heterochromatic arms (Patton and Sherwood 1982). Allozymic patterns of differentiation are concordant with geographic patterns of change in karyotype (Patton and Yang 1977, Patton and Smith 1981). Karyotypic and allozymic patterns are also concordant in *T. townsendii* in that they show homogeneity across geography. The type of chromosomal polymorphism found in *T. townsendii* is characteristic of species in the *bottae* group and apparently does not act as a fertility barrier (Patton and Sherwood 1982). It is therefore unlikely that such variants are of much consequence in the evolutionary differentiation within *townsendii*.

In summary, *Thomomys townsendii* can be characterized as having undergone little intraspecific morphological and genetic differentiation since its origin from an ancestral stock, probably *Thomomys bottae*. Based on cranial, external, and pelage measurements, the species is quite homogeneous (Rogers 1991). The only chromosomal differences in *T. townsendii* involve a single uniarm pair
in an otherwise completely biarmed complement. The variation found in the genic data is primarily based on shifts in allele frequencies in some populations and the presence of rare alleles in others. F-statistics indicate that genic differentiation is greatest between populations and slightest between the subspecies within each geographic region. Subspecific integrity is not maintained by any units within the two regions. Given this high level of homogeneity, a conservative interpretation of the details of differentiation is necessary in assessing meaningful taxonomic categories within *Thomomys townsendii*.

The only pattern that is concordant among the data sets presented here and in the accompanying paper (Rogers 1991) is the break between the Snake River populations and those of Honey Lake Valley and the Humboldt River. Discriminant function analyses based on cranial characters show some differentiation between these two groups, although overlap exists (Rogers 1991). A fixed difference at the GOT-1 locus provides a clear split between these two regions despite their generally high genic similarity ($S = .94$).

The evidence from this study suggests that only two geographical units can appropriately be given subspecific distinction. The ranges of these units correspond to (1) the Snake River Plain of Idaho and southeastern Oregon and (2) the Humboldt and Quinn River drainage systems in Nevada, southeastern Oregon (vicinity of Malheur Lake and Lake Alvord), and Honey Lake Valley, California. Within each of these regions there is local differentiation in some characters, but particular populations or subregions are not consistently delineated across many characters and modes of analysis (Rogers 1991). The currently recognized subspecies *T. t. bachmani*, *T. t. elkoensis*, *T. t. nevadensis*, and *T. t. relictus* are herein regarded as synonyms of *Thomomys townsendii nevadensis* Merriam, 1897, which has priority. The Snake River populations, representing *T. t. owyhensis*, *T. t. similis*, and *T. t. townsendii*, are treated as synonyms of *Thomomys townsendii townsendii* (Bachman 1839).

*Thomomys townsendii nevadensis* Merriam


*Thomomys relictus* Grinnell, 1926, University of California Publications in Zoology 30(1):2. Type from valley of Susan River two miles south of Susanville, Lassen County, California; Museum of Vertebrate Zoology no. 33771.

*Thomomys townsendii relictus* Grinnell, 1933, University of California Publications in Zoology 40(2): 137.


*Thomomys townsendii townsendii* (Bachman)

*Geomys townsendii* Bachman, 1839, (from Richardson's manuscripts) Journal of the Academy of Natural Sciences, Philadelphia 8(1):105. Type locality “Columbia River” is incorrect according to Bailey (1915:42), who feels the locality is near Nampa, Idaho; Academy of Natural Sciences Philadelphia no. 147.


**Acknowledgments**

I give special thanks to J. L. Patton for his support, guidance, and encouragement.
through all phases of this project and for the important contributions he made to the various drafts of this paper. D. B. Wake, W. Clemens, W. E. Bemis, B. D. Patterson, and W. T. Stanley read this and earlier drafts of the manuscript and provided useful criticism. R. D. Sage, M. F. Smith, M. Frelow, and E. Tang provided advice and assistance during the electrophoretic analyses. I thank D. S. Rogers for his guidance through my chromosome work and for his valuable support. N. Jo, M. A. Barros, and S. W. Sherwood also gave helpful suggestions on chromosome preparations. Many ranchers and landowners of the northern Great Basin were helpful and cooperative in my collecting efforts. For their support and confidence I thank my parents, Owen and Hally Rogers. I extend deep appreciation to W. E. Bemis for providing invaluable assistance in the field and consistent support throughout this project. This study and its companion paper are based on a thesis completed in partial fulfillment of requirements for the M.A. degree in the Department of Zoology, University of California, Berkeley. Financial support for this research was provided by the Department of Zoology, Museum of Vertebrate Zoology (two Louise M. Kellogg Grants-in-Aid), and National Science Foundation grant DEB 81-09677 to J. L. Patton. The Department of Anatomy, University of Chicago, and Field Museum of Natural History generously provided use of their facilities.

LITERATURE CITED


Benson, L. V. 1978. Fluctuations in the level of pluvial Lake Lahontan during the last 40,000 years. Quaternary Research 9: 300–318.


GENETIC VARIATION IN THOMOMYS TOWNSENDII


Received 16 January 1990
Revised 15 January 1991
Accepted 20 February 1991

APPENDIX
Specimens Examined

Listed below are specimens used in electrophoretic and karyotypic analyses. Boldface numbers preceding localities represent corresponding composite locality numbers. Sample sizes in parentheses represent the number used for electrophoretic analysis and the number karyotyped, respectively.

**Thomomys townsendii nevadensis**

**CALIFORNIA:** Lassen Co., [30], Bird Flat Ranch, 3 mi. S, 2.7 mi. W Herlong, 4080 ft. (n = 27,5); [31], 4 mi. W Standish, 4110 ft. (n = 18,2).

**NEVADA:** Elko Co., [10], 0.5 mi. SW Ryndon, 5100 ft. (n = 20,4); Eureka Co., [11], Hay Ranch, 17 mi. SE Fallon, 5160 ft. (n = 19,3); Humboldt Co., [5], Quinn River Crossing, 4100 ft. (n = 9,3); Lander Co., [15], 5.5 mi. W Austin, 5700 ft. (n = 22,5); Pershing Co., [3], Big Meadow Ranch, Lovelock, 4000 ft. (n = 16,3); [1], 2 mi. NW Valmy, 4450 ft. (n = 21,5).

**OREGON:** Harney Co., [4], 4 mi. SW Narrows, 4200 ft. (n = 6,0).

**Thomomys townsendii townsendii**

**IDAHO:** Bannock Co., [20], Floyd Johnson Ranch, 4 mi. NW Pocatello, 4500 ft. (n = 19,3); Elmore Co., [22], 3 mi. E Grandview, 2800 ft. (n = 8,0); Owyhee Co., [16], 7.5 mi. SE Grandview, 8600 ft. (n = 21,3); [17], 6 mi. SE Murphy, 3000 ft. (n = 4,1); Payette Co., [23], 1.5 mi. NE Payette, 2200 ft. (n = 9,1); Power Co., [19], 2.5 mi. NW American Falls, 4500 ft. (n = 10,2); Washington Co., [23], 2.9 mi. SE Weiser, 2100 ft. (n = 1,0).

**OREGON:** Malheur Co., [24], 2.5 mi. N Ontario, 2100 ft. (n = 20,1).