SYSTEMATIC IMPLICATIONS OF mtDNA SEQUENCE VARIATION IN A DEER MOUSE SPECIES ENDEMIC TO ISLANDS IN THE GULF OF CALIFORNIA

A Senior Honors Thesis

by

ASHLI FRANCILLE MOORE

Submitted to the Office of Honors Programs
& Academic Scholarships
Texas A&M University
in partial fulfillment of the requirements of the

UNIVERSITY UNDERGRADUATE
RESEARCH FELLOWS

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Group: Life Sciences

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ABSTRACT

Systematic Implications of mtDNA Sequence Variation in a Deer Mouse Species Endemic to Islands in the Gulf of California. (April 2003)

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The wide distribution and variety of species of deer mice, *Peromyscus,* provide a unique opportunity to examine the phylogenetic relationships of the mammals of western North America. Recent studies have raised questions concerning the specific validity, systematic relationships and geographic origin of *P. sejugis*, a species of deer mouse endemic to two islands in the Gulf of California. To determine genetic affinities, sequence variation was analyzed for a 1,439 base pair region (ND3/ND4L/ND4) of the mitochondrial DNA for *P. sejugis, P. maniculatus* (from Baja California and the central and northwestern United States) and *P. keeni* (from the Pacific Northwest). Phylogenetic and pairwise distance analyses of the sequence data closely associate *P. sejugis* with the *P. maniculatus* from Baja California and place them in a cluster that is genetically closer to *P. keeni* than it is to *P. maniculatus* from the central and northwestern United States. These data support the hypothesis that *P. sejugis* is conspecific with the deer mice currently recognized as *P. maniculatus* from Baja California. Additionally, the data support the geographically improbable sister-group

relationship between the deer mice from Baja California and *P. keeni* and suggest that the deer mice from Baja California are specifically distinct from the *P. maniculatus* from the central and northwestern United States.

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INTRODUCTION

Mice of the genus *Peromyscus* comprise the most successful small mammals native to North and Central America. The vast distribution and diversity of species and habitats in the genus have made it a favorite model organism for studies encompassing virtually all areas of organismal biology. In particular, mice of this genus have played a central role in the development of systematic mammalogy in North America with this impact being favorably compared to the importance of *Drosophila* in the growth of systematic biology and evolutionary genetics as a whole (Carleton 1989).

Of the more than 50 species of *Peromyscus*, none is more widely distributed nor intensively studied than is *P. maniculatus* and the closely related species in the *P. maniculatus* species group. The monophyly of the *P. maniculatus* group and the systematic relationships of its major taxa (*P. maniculatus*, *P. polionotus*, and *P. melanotis*) are well supported by morphologic, cytogenetic and molecular data (reviewed by Carleton 1989). Within this group, however, the phylogenetic relationships and evolutionary history of two peripherally distributed species, *P. sejugis* (endemic to Isla San Diego and Isla Santa Cruz in the Gulf of California) and *P. keeni* (coastal deciduous forests from northern Washington to southeastern Alaska and southwestern Yukon), remain problematic. Protein electrophoretic (Avise et al. 1979) and chromosomal data (Gunn and Greenbaum 1986, Smith et al. 2000) associate *P. keeni* and *P. sejugis* with *P. maniculatus*, but the divergence of these species was apparently too recent for the evolution of synapomorphies in these characters, yielding an unresolved trichotomy. Preliminary data comparing sequence variation at the ND3/ND4L/ND4 region of the

mitochondrial DNA (mtDNA) from *P. sejugis* and *P. keeni* (Hogan et al. 1997) suggest the geographically improbable sister-group relationship between these species. Distributional proximity and morphologic similarity (Hooper and Musser 1964) clearly support the alternative hypothesis that *P. sejugis* was derived by dispersal from a *P. maniculatus* ancestor native to Baja California. However, the critical data relative to testing these alternative hypotheses are lacking.

This study was designed to provide the data necessary to clarify the specific status of *P. sejugis* and to discriminate between the alternative hypotheses for its phylogenetic and geographic origin. To this purpose, sequence variation at the ND3/ND4L/ND4 region of the mtDNA was assessed for both island populations of *P. sejugis* and for a population of *P. maniculatus* from Baja California Norte. These results were compared to reference sequences for *P. keeni* from Washington and for *P. maniculatus* from Baja California Sur, Vancouver Island and Colorado. These analyses suggest previously unrecognized partitioning if the biodiversity of the deer mice in this region, yield an improved understanding of phylogenetic relationships of these mice, and offer new insights into the post-Pleistocene biogeographic history of Baja California and the southwestern most United States.

MATERIALS AND METHODS

Frozen tissues (stored at -80°C) of *P. sejugis* (Mexico: Baja California del Sur; Isla San Diego (n=13), Isla Santa Cruz (n=7)) and *P. maniculatus* (Mexico: Baja California del Nte; Vallecitos, Sierra de San Pedro Martir (n=20)) were available from collections made (under TAMU Animal Use Protocol #92-1054) in September 1993 in association with prior research conducted under NIH Grant GM27014-12/16, "Chromosomal rearrangement incorporation in mammals" to Ira F. Greenbaum, Department of Biology, Texas A&M University. The use of the tissues from these specimens was in accordance with the Guide for Care and Use of Laboratory Animals (U.S. Department of Health and Human Services as approved by the Texas A&M University Laboratory Animal Care Committee AUP #2000-275).

Isolation of mtDNA from liver or spleen samples was accomplished using the Qiagen purification kit and procedure. Amplification and sequencing of the 1,439 base-pair (bp) region of mtDNA (from the 3' end of the glycine tRNA through 672 bp of the 5' end of the ND4 gene) generally followed the techniques of Arevalo et al. (1994). The primers used in amplification of this region included: PI', Marg, MargRev, ND4L, and Nap2 (Arevalo et al. 1994). Amplification reactions (Perkin Elmer/Cetus DNA Thermal Cycler) were conducted with the following components and concentrations: 1 μL DNA (approximately 100 ng), 15 μL H_2O, 2.5 μL of 10X PCR Buffer II (PE Applied Biosystems), 2 μL of 25 mM $MgCl_2$, 0.5 μL BSA, 4 μL of 8 mM dNTPs (Amersham Pharmacia Biotech), 0.4 μL of forward and reverse primers, and 0.2 μL *Taq* (TaKaRa, Japan). Amplifications proceeded in three stages including an initial denaturation cycle

at 95°C for five min, followed by 35 cycles of 45 sec at 95°C, 30 sec at 50°C, and 90 sec at 72°C, and concluded with an extension cycle of 10 min at 72°C. Some minor modifications of technique were implemented as needed. Amplified products were purified using the QIAquick PCR purification protocol (Qiagen).

The sequencing reaction included 1 μL of amplified/purified DNA, 2 μL sequencing standard (DNA sequencing kit, PE Applied Biosystems), 6 μL H_20, and 1 μL of primer at a concentration of 3 nm. The sequencing reaction began with one denaturation cycle of 3 min at 95°C and continued with 30 cycles each including: 25 sec at 95°C, 25 sec at 47°C, and 4 min at 60°C (Perkin Elmer/Cetus DNA Thermal Cycler). Sequences were determined by electrophoresis in an Applied Biosystems model 377 automated DNA sequencer. Nucleotide sequences were aligned and the open reading frame was determined using the computer program Sequencher 3.1.1 (Genes Code Corporation). Unique sequences were interpreted as individual haplotypes. All novel sequences were deposited in GenBank.

The haplotype sequences for the samples of *P. sejugis* and *P. maniculatus* from Baja California were compared to previously obtained sequences (I. F. Greenbaum, unpublished data) for the same region of the mtDNA for reference samples of *P. keeni* and *P. maniculatus*. Included in this analysis were haplotypes of one specimen representing the most common haplotype from each of the following localities: *P. keeni*: U.S.A.; Washington, Okanogan Co, Lone Fir Campground and Gray's Harbor Co, 3.0 mi N, 1.0 mi E Grisdale, Satsop Workcamp; *P. m. austerus*: Canada, British Columbia; Vancouver Island, 35.7 km W Port Alberni, Sproat Lake; *P. m. coolidgei*: Mexico, Baja

California del Sur; 25 km SE Guerrero Negro; *P. m. rufinus*: U.S.A., Colorado; 7.2 km N, 8.8 km W Central City, Elk Park.

Phenetic and phylogenetic analyses followed those described by Chirhart et al. (2001) and included both neighbor-joining and maximum-parsimony approaches in PAUP* version 4.0b (Swofford 1999). Pairwise distances were computed using the two-parameter method of Kimura (1980). Maximum parsimony analyses of the sequence data consisted of exhaustive searches with equal weighting and with differential weightings for transitions and transversions (following Hogan et al. 1997). Comparable sequence data (Chirhart et al. 2001) for *P. melanotis* (Mexico: Hidalgo; *Peromyscus* Stock Center) were used as the designated outgroup for the phylogenetic analysis. Bootstrap estimates (Felsenstein 1985) based on 1000 replications were obtained for the maximum parsimony analyses.

RESULTS

Analysis of the ND3/ND4L/ND4 region of the mtDNA for the population of mice from Baja California revealed the presence of three haplotypes (A, B and C) characterizing *P. m. gambelii* with an overall sequence divergence of 0.3%. Haplotype A characterized 10 of the 20 individuals, while the other two haplotypes (B and C) occurred in somewhat smaller proportions of the population sample (6 and 4, respectively). Two haplotypes (D and E) with an overall sequence divergence of 0.7% were found for the individuals of *P. sejugis*. Haplotype D characterized all 13 of the individuals from Isla San Diego, and haplotype E occurred in all seven of the individuals from Isla Santa Cruz.

Genetic distances within and between populations of the mice from Baja California and representative samples of *P. maniculatus* and *P. keeni* were obtained using a pairwise distance matrix in PAUP* and are summarized in Table 1. Percent sequence divergence between *P. sejugis* and *P. m. gambelii* (2.2%) was significantly lower (t-test, $p < 0.05$) than the distances between all of the other interspecific comparisons and than the distance between *P. m. gambelii* from Baja California and the *P. maniculatus* from central and northern populations (4.5%).

The maximum parsimony analysis with equal weighting of substitutions yielded one most parsimonious tree (Figure 1) with a total length of 233, a consistency index of 0.833, and a retention index of 0.791. Maximum parsimony analyses using differential weighting schemes for transitions and transversions and the neighbor-joining analysis of Kimura two-parameter distances produced optimal trees all of which had topologies

Table 1. Total percent sequence divergence between the sequences for the ND3/ND4L/ND4 region of the mtDNA for the deer mice (*Peromyscus*) from Baja California (*P. m. gambelii* and *P. sejugis*) and for each of the reference samples examined.

Taxon	1	2	3	4	5	6	7	8	9	10	11
1. *P. m. gambelii* A	-										
2. *P. m. gambelii* B	0.49	-									
3. *P. m. gambelii* C	0.28	0.21	-								
4. *P. sejugis* D (Isla San Diego)	1.67	2.09	1.88	-							
5. *P. sejugis* E (Isla Santa Cruz)	2.37	2.78	2.58	0.70	-						
6. *P. keeni* (Satsop)	3.13	3.62	3.41	3.41	3.83	-					
7. *P. keeni* (Lone Fir)	3.48	3.97	3.76	3.62	4.04	0.77	-				
8. *P. m. coolidgei*	1.25	1.74	1.53	2.30	2.51	4.11	4.32	-			
9. *P. m. austerus* (BC)	4.38	4.66	4.52	4.66	5.22	4.32	4.67	4.74	-		
10. *P. m. rufinus* (CO)	4.32	4.59	4.46	4.32	4.73	4.11	4.46	4.46	1.46	-	
11. *P. melanotis*	6.89	7.31	7.10	6.96	7.45	7.31	7.80	7.38	7.66	7.10	-

identical to that obtained from maximum parsimony with equal weighting. All analyses of the sequence data grouped the three haplotypes of *P. m. gambelii* and placed them in a cluster that otherwise comprised the two populations of *P. sejugis*. The samples of *P. sejugis* and *P. m. gambelii* from Baja California clustered to the reference samples of *P. keeni* before clustering to the reference sample of *P. maniculatus* from the central and northern United States.

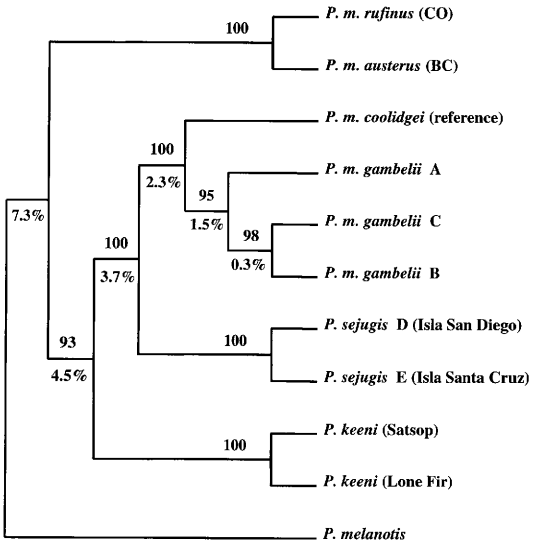

Figure 1. The single most parsimonious tree produced by both neighbor-joining and maximum-parsimony (exhaustive search) analyses of the ND3/ND4L/ND4 sequence data of the mtDNA among the samples included in this study. Bootstrap values (above line) are those obtained from the analysis with characters equally weighted for the maximum-parsimony analysis. Percentages below the line indicate the percent sequence divergence obtained from pairwise distance comparisons.

DISCUSSION

The fixation of alternate but extremely similar haplotypes (D and E, p = 0.7%) at the ND3/ND4L/ND4 region of the mtDNA in the two island populations of *P. sejugis* indicates both the close genetic association of these populations and the lack of recent gene flow between them. These observations are entirely consistent with those from chromosomal studies of these populations (Smith et al., 2000) that reported only a minor, but fixed, difference in the presence of a small distal heterochromatic segment on the short arm of chromosome 13 of the *P. sejugis* from Isla Santa Cruz. Considering the level of haplotype variation observed for the population of *P. m. gambelii* from mainland Baja California (three haplotypes with a mean sequence divergence of 0.3%), the lack of observed haplotype variation in the island populations of *P. sejugis* is probably the result of founder effects and subsequent genetic drift.

The mtDNA sequence similarities (Table 1) and genealogical analyses (Fig. 1) clearly associate the populations of *P. sejugis* with those of the deer mice from mainland Baja California. The sequence divergence among the haplotypes of the *P. maniculatus* from mainland Baja California (including the population of *P. m. gambelii* and the reference haplotype of *P. m. coolidgei*) averaged 0.9%, and that between these and the haplotypes of *P. sejugis* averaged 2.3%. These differences are far more consistent with those obtained for geographic conspecific populations than with sequence divergences characteristic of even closely related species; the sequence divergence between the central and northern populations of *P. maniculatus* was 1.46%, whereas that between *P. maniculatus* and the biologically distinct species *P. keeni* was 4.4%. The intermediate

divergence of the haplotypes of *P. sejugis* as compared to the *P. maniculatus* from mainland Baja California is consistent with the aforementioned evidence of the effects of geographic isolation on the populations of *P. sejugis*. The systematic association of *P. sejugis* and the deer mice from mainland Baja California is further supported by the consistent phenetic and cladistic clustering of the these samples (Fig. 1). Although the specific distinction of allopatric populations is problematic, these data are consistent with the hypothesis that the populations of "*sejugis*" are conspecific with, and insular isolates of, the *P. maniculatus* from mainland Baja California.

Considering the alternate fixation of haplotypes in the two island populations of "*sejugis*" and the genealogical association of "*sejugis*" with the deer mice from mainland Baja California, three hypotheses can be erected concerning the details of the founding of the populations of "*sejugis*." An unlikely scenario hypothesizes that Isla San Diego and Isla Santa Cruz were originally one island that experienced a single founding event. Subsequent geologic separation of Isla San Diego and Isla Santa Cruz and independent evolution between the two geographically separated populations could account for the fixed (but genetically similar) haplotypes within each of the current island populations of "*sejugis*." There is, however, no geologic evidence for the origin of Isla San Diego and Isla Cruz from an initial single island. A second and more likely hypothesis proposes the sequential founding of the two islands. According to this hypothesis, one island population of "*sejugis*" was derived from the mainland stock, and the second island was subsequently founded by dispersal from the first. In this case, the genetic similarity of the haplotypes of "*sejugis*" reflects true genealogical propinquity of the island

populations. As the two haplotypes of "*sejugis*" (D and E) are genetically closer to each other than either haplotype is to the *P. maniculatus* from the mainland, the sequence divergence data are consistent with both the single and sequential founding hypotheses. However, the greater sequence similarity between the haplotype in the "*sejugis*" from Isla San Diego and those of the deer mice from mainland Baja California (mean = 2.0%) than between the haplotype of "*sejugis*" from Isla San Cruz and the deer mice from mainland Baja California (mean = 2.6%) is more consistent with the sequential founding hypothesis. A third possibility is that the island populations of "*sejugis*" were independently founded by dispersal from the mainland. According to this hypothesis, the haplotype similarity between the two populations of "*sejugis*" would be the result of coincidental founder effects (and subsequent genetic drift), and the apparent sister-group relationship of the two populations reflects lineage sorting (Avise 2000) rather than a true phylogenetic relationship. This independent founder event hypothesis is supported by the relationship of sequence divergence between the "*sejugis*" haplotypes and the frequency distribution of haplotype variation in the mainland population of *P. m. gambelii*. Consistent with the genetic expectations for founder effects, both haplotypes of "*sejugis*" are most similar to the most common haplotype (A) of *P. m. gambelii* (Table 1). An ultimate resolution of these alternative hypotheses will require a thorough assessment of the sequence variation for the extent of the range of deer mice from mainland Baja California and comparable data for additional populations of deer mice from islands in the Gulf of California.

The ND3/ND4L/ND4 sequence data were also used to assess the genealogical relationships of "*sejugis*" and the *P. maniculatus* from mainland Baja California relative to central and northwestern populations of *P. maniculatus* and to the northwestern peripheral species *P. keeni* (Fig. 1). The mean sequence divergence between the deer mice from Baja California (including "*sejugis*" and *P. maniculatus* from mainland Baja California) and *P. keeni* was 3.7% whereas that compared to the central and northwestern populations of *P. maniculatus* was 4.6%. Neighbor-joining analyses of genetic distances (with high bootstrap values) and maximum parsimony analyses produced topologically identical trees (Fig. 1). As has been previously suggested from preliminary analyses (Hogan et al. 1997), the current data support the geographically improbable sister-group relationship between the deer mice from Baja California and *P. keeni*. Although on a much larger geographic and temporal scale relative to the origin of "*sejugis*," the apparent sister-group relationship between the deer mice from Baja California and *P. keeni* may be alternatively explained by either true phylogenetic association or lineage sorting. An historical ancestral continuity hypothesis posits that *P. keeni* and the deer mice from Baja California are true sister taxa and shared a common ancestor after divergence from the lineage that gave rise to *P. maniculatus*. This ancestor would have occupied a coastal range isolated west of the Cascade and Sierra Nevada Mountains. The current distributions of *P. keeni* and the deer mice from Baja California would have resulted from the extinction of the hypothetically intervening populations. Alternatively, the genetic similarity between *P. keeni* and the deer mice from Baja California may be an artifact of independent founder effects yielding the

coincidental retention of common (primitive) haplotypes that were present in the common ancestor of these mice and the stock that gave rise to central and northern populations of *P. maniculatus*. According to this lineage sorting hypothesis, *P. keeni* and the deer mice from Baja California would be independently-derived peripheral isolates from the *P. maniculatus* central stock and not actual sister groups. Distinguishing between these hypotheses will require extensive analyses of the distribution of genetic variation in deer mice from Baja California, the far southwestern United States and the Pacific coastal region of North America.

Regardless of the particular evolutionary histories of *P. keeni* and the deer mice from Baja California, the data presented here support the hypothesis that *P. maniculatus*, as currently recognized, is polyphyletic. Studies of chromosomal, morphologic, allozymic and molecular variation (Gunn and Greenbaum 1986, Allard et al. 1987, Allard and Greenbaum 1988, Gunn 1988, Hogan et al. 1993) are uniform in indicating that *P. keeni* is reproductively isolated from sympatric populations of *P. maniculatus*. Although caution must be applied in making species-level decisions from mtDNA sequence data, it is reasonable to assume that the greater mean sequence divergence between the deer mice from Baja California and those from Colorado and Vancouver Island (4.6%) than between the latter samples and *P. keeni* (4.4%) is indicative of the specific distinction between the deer mice from Baja California and *P. maniculatus* from the more northern portions of its currently recognized distribution. Resolution of the specific status of the deer mice from Baja California will require intensive sampling and genetic analyses to determine the extent of its geographic range and the presence or

absence of gene flow between these mice and populations representing the more northern genetic stock of *P. maniculatus*.

CONCLUSION

The two island populations of *P. sejugis* show an extremely high level of genetic similarity; haplotype fixation within the island populations is attributed to founder effect and subsequent genetic drift. The high level of genetic similarity between *P. sejugis* and the deer mice from Baja California is consistent with the hypothesis that "*sejugis*" represent insular isolate populations of the *P. maniculatus* from mainland Baja California. The current data suggest a geographically unlikely sister-group relationship between the mice from Baja California (including "*sejugis*," *P. m. gambelii* and *P. m. coolidgei*) and *P. keeni* from the Pacific Northwest. This apparent association may be due to either coincidental founder effects or true propinquity of descent. The mice from Baja California do not appear to be conspecific with populations of deer mice from more central and northwestern portions of the range of *P. maniculatus*.

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