ALLOZYMIC AND MORPHOLOGIC VARIATION AMONG *DIPODOMYS INSULARIS, DIPODOMYS NITRATOIDES,* AND TWO POPULATIONS OF *DIPODOMYS MERRIAMI* (RODENTIA: HETEROMYIDAE)

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ABSTRACT—Electrophoretic and morphologic variation was examined among two populations of *Dipodomys merriami* from Baja California, one population of *Dipodomys nitratoides* from southern California, and *Dipodomys insularis* from San José Island, Baja California. Analysis of allozyme variation resulted in a mean genetic distance of 0.07 among the two populations of *D. merriami* and *D. insularis.* Analyses of morphologic variation among these populations indicated that *D. insularis* is distinct from populations of *D. merriami* and *D. nitratoides* using bacular, cranial, and external characters. Although *D. insularis* is geographically isolated and is statistically significantly different in several morphologic characters from *D. merriami,* we recommend placement of *D. insularis* as a subspecies of *D. merriami* based upon their allozymic similarities and because other species of *Dipodomys* exhibit similar degrees of intraspecific geographic variation in morphologic characters.

Of the 21 species of kangaroo rats (*Dipodomys*), two are endemic to oceanic islands near the coast of southern Baja California Sur, Mexico; *Dipodomys insularis* occurs on San José Island, and *Dipodomys margaritae* occurs on Santa Margarita Island (Hall, 1981). Although currently considered to be a distinct species, *D. insularis* is similar morphologically to *Dipodomys merriami* and *Dipodomys nitratoides* (Grinnell, 1921; Setzer, 1949; Lidicker, 1960; Hall, 1981; Best and Thomas, 1991). *Dipodomys merriami* is widely distributed in desert habitats in the southwestern United States and northwestern Mexico, including the mainland adjacent to the islands where *D. insularis* and *D. margaritae* occur. *Dipodomys nitratoides* is confined to the southern San Joaquin Valley of California (Hall, 1981). Whether *D. insularis* and *D. margaritae* are species distinct from *D. merriami* is not clear (Lidicker, 1960; Honacki et al., 1982; Hall, 1981).

Limited data on cranial and post-cranial morphology have been available for comparisons of *D. insularis* with other *Dipodomys* (Lidicker, 1960; Schnell et al., 1978; Best, in press). However, studies that have examined relationships among *Dipodomys* using internal morphology (Setzer, 1949), karyotypes (Stock, 1974), bacula (Best and Schnell, 1974), and allozymes (Johnson and Selander, 1971) have not included *D. insularis.* The primary objective of the present study was to compare variation in allozymes, bacula, and external and cranial characters among two populations of *D. merriami* from the mainland of Baja California, *D. nitratroides* from California, and *D. insularis* from San José Island, Baja California. These comparisons were designed to provide insight into the taxonomic position of *D. insularis.*

MATERIALS AND METHODS—Twenty-four individuals were used to assess allozyme variation among four populations of kangaroo rats: *D. merriami*—40 km N San Felipe, Baja California (two males, two females); *D. merriami*—13 km SW Santa Rita, Baja California Sur (four males, five females); *D. insularis*—San José Island, Baja California Sur (two males, two females); *D. nitratoides*—6 miles [9.6 km] W Buttonwillow, Kern Co., California (three males, four females). Live-trapped

specimens were processed in the field; heart, kidneys, and liver taken from each animal immediately after death were frozen in liquid nitrogen. Tissues were maintained at −80°C until processed. Heart and kidney extracts were combined. Techniques of tissue preparation, horizontal starch-gel electrophoresis, and biochemical staining were described by Harris and Hopkinson (1976) and Selander et al. (1971). In multiple-locus systems, the isozyme migrating most anodally was designated as "1." Peptidase loci were designated for their substrate specificity. The most common allele at a locus was designated as 100; additional alleles at each locus were numbered according to the mobility of their products relative to that of the common allele. Twenty-four enzymatic and nonenzymatic proteins encoded by 33 loci were examined including (with Enzyme Commission abbreviations and numbers) malate dehydrogenase (Mdh-1, Mdh-2; 1.1.1.37), malic enzyme (Me; 1.1.1.40), lactate dehydrogenase (Ldh-1, Ldh-2; 1.1.1.27), isocitrate dehydrogenase (Idh-1, Idh-2; 1.1.1.42), purine nucleoside phosphorylase (Np; 2.4.2.1), 6-phosphogluconic acid dehydrogenase (6Pgd; 1.1.1.44), glucose phosphate isomerase (Gpi; 5.3.1.9), phosphoglucomutase (Pgm-1, Pgm-2, Pgm-3; 2.7.5.1), adenylate kinase (Ak-1, Ak-2; 2.7.4.3), creatine kinase (Ck-1, Ck-2; 2.7.3.2), hexokinase (Hk; 2.7.1.1), glucose-6-phosphate dehydrogenase (G6pdh; 1.1.1.49), superoxide dismutase (Sod; 1.15.1.1), sorbitol dehydrogenase (Sdh; 1.1.1.14), alcohol dehydrogenase (Adh; 1.1.1.1), aspartate aminotransferase (Aat-1, Aat-2; 2.6.1.1), glycerol-3-phosphate dehydrogenase (Gpd; 1.1.1.8), general protein (Gp-1, Gp-2), esterase (Es-1; 3.1.1.1), diaphorase (Dia), glycyl-leucine peptidase (P-gl; 3.4.11), leucyl-glycyl-glycine peptidase (P-lgg; 3.4.11), phenyl-alanyl-proline peptidase (P-pap; 3.4.11), and leucyl-leucyl-leucine peptidase (P-lll; 3.4.11).

Coefficients of Rogers' (1972) genetic distance (D) were computed for all possible paired combinations from the allelic frequency data for each population. Phenetic relationships among the four populations were determined by cluster analysis of the matrix of coefficients of D employing the unweighted pair-group method using arithmetic averages (UPGMA) option of the BIOSYS-1 package of Swofford and Selander (1981). Phenetic relationships among populations were further summarized in the form of an unrooted tree produced by a Fitch and Margoliash (1967) analysis of the Rogers' distance matrix using the PHYLIP package of Felsenstein (1989).

Morphologic variation was assessed by examination of five post-cranial and 14 cranial characters for adult specimens from four populations: *D. merriami*—5 miles [8 km] N San Felipe, Baja California (San Diego Natural History Museum, 19 males, 20 females) and San Felipe, Baja California (University of California Museum of Vertebrate Zoology, four males, three females; referred to herein as the population from San Felipe); *D. merriami*—4.5 miles [7.2 km] N El Refugio, Baja California Sur (University of New Mexico Museum of Southwestern Biology, 31 males, 31 females; referred to herein as the population from Santa Rita); *D. insularis*—San José Island, Baja California Sur (United States National Museum of Natural History, one male, three females; MSB one female; MVZ six males, six females; University of California at Los Angeles, two females); *D. nitratoides* (all from Kern Co., California)—3.4 miles [5.5 km] N McKittrick on Hwy. 33 (MVZ one male, four females); McKittrick, 1,111 feet [333 m] (MVZ three males, four females); 2 miles [3.2 km] E McKittrick, 1,000 feet [300 m] (MVZ five males, five females); 2 miles [3.2 km] N McKittrick, 700 feet [210 m] (MVZ six males, four females); 3 miles [4.8 km] NW McKittrick (SDNHM two males, one female). Characters used, methods of measuring, and aging techniques follow Best (1978, in press). Because *D. merriami, D. insularis,* and *D. nitratoides* exhibit statistically significant sexual dimorphism in size (Best, in press), sexes were analyzed separately. Character heterogeneity among the four populations was tested using a single-classification analysis of variance for each character. Student-Newman-Keuls multiple range tests were used to determine maximally nonsignificant subsets. Mean measurements of each character for each population were used in the multivariate procedures. Characters were standardized (mean of 0, standard deviation of 1) across populations, and distance matrices were calculated (Sneath and Sokal, 1973). Clusters of populations were obtained employing the UPGMA. Principal components were calculated from a correlation matrix among characters, and projections of the populations were plotted on the first two components. Bacula were measured as described in Best and Schnell (1974).

Specimens used in the genic studies are deposited in The Auburn University Museum, Auburn, Alabama, The University of New Mexico Museum of Southwestern Biology, Albuquerque, and the Universidad Autónoma Nacional de México, Mexico City. Statistical analyses were performed using BIOSTAT I (Pimentel and Smith, 1986) and NTSYS-pc (Rohlf, 1988).

RESULTS AND DISCUSSION—*Genic Data*—Fourteen loci were polymorphic for the four populations of *Dipodomys* (Table 1). Nineteen loci were monomorphic across all populations and are not included in Table 1, but were used in calculating coefficients of genetic distance. *Dipodomys nitratoides* differed from the three other populations by a fixed allelic difference at Ldh-2. Also, *D. nitratoides* shared an allele at P-lll with the San Felipe population of *D. merriami* that was not present in the two other populations. Although *D. merriami* from Santa Rita had unique

TABLE 1—Allelic frequencies of 14 variable loci for four populations of *Dipodomys*. The common allele is designated as "100" and additional alleles at a locus are numbered according to the mobility of their product relative to that of the most common allele (positive values = allelic products migrating anodally from origin, negative values = allelic products migrating cathodally from origin). Loci abbreviations are defined in the text.

		D. merriami			
Locus	Allele	San Felipe $n = 4$	Santa Rita $n = 9$	*D. insularis* $n = 4$	*D. nitratoides* $n = 7$
Ldh-1	106	0.37	0.28		1.00
	100	0.50	0.44	0.75	
	88	0.13	0.28	0.25	
Ldh-2	−38				0.29
	−63				0.71
	−100	1.00	1.00	1.00	
Idh-2	185		0.06		
	100	1.00	0.94	1.00	1.00
6Pgd	139	0.13			0.93
	100	0.87	1.00	1.00	0.07
Pgm-3	100	1.00	1.00	1.00	0.93
	67				0.07
Ak-1	100	1.00	1.00	1.00	0.93
	75				0.07
Sod-1	193		0.44		
	100	1.00	0.56	1.00	1.00
Sdh	−85			0.13	
	−100	1.00	1.00	0.87	1.00
Adh	−87		0.11		
	−100	1.00	0.78	1.00	0.43
	−115		0.11		0.57
Agpd	260				0.29
	100	1.00	1.00	1.00	0.71
Gp-1	100	0.33	1.00	1.00	0.93
	93	0.67			0.07
Gp-2	−100	1.00	1.00	1.00	0.14
	−108				0.86
P-pap	106	0.75	0.11		0.86
	100	0.25	0.89	1.00	0.14
P-lll	100		0.56	1.00	
	85		0.44		
	63	1.00			1.00
A[1]		1.15	1.24	1.06	1.27
H[2]		0.023	0.020	0.008	0.017
P[3]		12.1	18.2	6.1	27.3

[1] Mean number of alleles per locus.
[2] Mean proportion of 33 loci heterozygous per individual.
[3] Proportion of 33 loci polymorphic per population.

alleles at three loci (Idh-2, Sod, Adh), and *D. insularis* had a unique allele at Sdh, these electromorphs were not fixed.

Estimates of genetic variability for each population included determinations of the mean number of alleles segregating per locus (A), mean proportion of loci heterozygous per individual based upon direct counts (H), and proportion of loci polymorphic per population (P; Table 1). Although small samples were used in our allo-

TABLE 2—Coefficients of Rogers' (1972) genetic distance for all paired combinations of four populations of *Dipodomys*.

	Population			
	D. merriami			
Population	San Felipe	Santa Rita	*D. insularis*	*D. nitratoides*
D. merriami				
San Felipe				
Santa Rita	0.095			
D. insularis	0.091	0.050		
D. nitratoides	0.146	0.192	0.201	

zyme study, our estimates of these statistics for *D. nitratoides* and the two populations of *D. merriami* were comparable to those reported by Johnson and Selander (1971), who examined samples of *D. merriami* from across its range. Estimates of genetic variability for *D. insularis* indicated low levels of heterozygosity and polymorphism (Table 1). These results probably are due to the isolated island distribution of *D. insularis* rather than to the small sample (Selander et al., 1971).

Coefficients of Rogers' (1972) genetic distance (D) were calculated for the four populations of *Dipodomys* (Table 2). Mean genetic distance (D) between the two populations of *D. merriami* was 0.095. This D-value was comparable to the findings of Johnson and Selander (1971), who recorded a mean value of genetic similarity (Rogers, 1972) of 0.956 (range of 0.92 to 0.99; D = 0.044, range of 0.01 to 0.08) among 11 populations of *D. merriami*. Phenetic relationships based on D-values among the four populations were examined using cluster analysis. The resulting phenogram indicated that *D. insularis* was electrophoretically most similar to *D. merriami* from Santa Rita; these populations clustered at a D-value of 0.05. The population of *D. merriami* from San Felipe joined the phenogram next (D = 0.09), followed by *D. nitratoides* (D = 0.18). The cophenetic correlation coefficient for this phenogram was 0.95. Phenetic relationships among populations were further summarized in an unrooted Fitch and Margoliash (1967) tree, in which branch lengths are indicative of the observed genetic distances among populations. The four populations clustered together as in the previous phenogram; *D. nitratoides* was the most genically divergent population, as indicated by this population having the longest branch in the tree (branch length = 0.12). The average percent standard deviation (Fitch and Margoliash, 1967) for the unrooted tree was 1.89.

Dipodomys insularis and the two populations of *D. merriami* clustered together at levels of genetic similarity consistent with these populations being conspecific. A D-value of 0.07 (range of 0.05 to 0.09) among *D. insularis* and the two populations of *D. merriami* correlates with the conclusions of Johnson and Selander (1971) that, within the genus *Dipodomys,* conspecific populations cluster together at values of genetic similarity ≥ 0.90 (D ≤ 0.10). *Dipodomys insularis* is geographically closest to *D. merriami* from Santa Rita, and these two populations also are most similar electrophoretically. *Dipodomys insularis* and *D. merriami* from Santa Rita shared two alleles at P-lll (Table 1) that were not represented in the population of *D. merriami* from San Felipe or in *D. nitratoides*. However, four alleles (Idh-2^{185}, Sod-1^{193}, Adh^{87}, P-lll^{85}) autapomorphic in the Santa Rita population were not represented in *D. insularis,* whereas *D. insularis* had one autapomorphic allele in Sdh^{85}. *Dipodomys nitratoides* is divergent from *D. merriami,* but was most similar electrophoretically to the population of *D. merriami* from San Felipe, which is geographically the closest population to *D. nitratoides*. These two populations shared allele P-lll^{63} that was not represented in the *D. merriami* population from Santa Rita or in *D. insularis*. Although our electrophoretic results are not unequivocal, our data indicate that *D. insularis* probably originated from a population of *D. merriami* that was derived from the adjacent mainland of Baja California. Considerable geographic variation in allozymes has been documented in conspecific populations of other species of *Dipodomys* (Best et al., 1986; Hamilton et al., 1987; Johnson and Selander, 1971).

Morphologic Data—No data on bacular morphology of *D. insularis* previously were available. Measurements (millimeters) for an adult and a subadult, respectively, are: length, 12.4, 10.7; height of base, 1.4, 1.4; and width of base, 1.2, 1.3. The baculum of the adult *D. insularis* is longer than the mean of 10.78 mm (range of 9.3 to 11.7 mm) for *D. merriami* and shorter than the mean of 13.34 mm (range of 13.0 to 13.7 mm) for *D. nitratoides* (Burt, 1960; Best and Schnell, 1974). Further comparisons of the baculum of *D. insularis* with these specimens indicate that the baculum of *D. insularis* is greater than *D. nitra-*

toides in height of base (average = 1.13, range of 1.0 to 1.2 mm) and width of base (average = 0.93, range of 0.9 to 1.0 mm). However, the baculum of *D. insularis* falls within the range of values for these characters in *D. merriami* (height of base, average = 1.26, range of 1.0 to 1.7 mm; width of base, average = 1.15, range of 0.8 to 1.3 mm; Burt, 1960; Best and Schnell, 1974).

Significant interpopulation variation ($P \leq 0.05$) was found in 16 of 19 external and cranial characters for males and 18 of 19 characters for females (Table 3). Neither sex differed significantly in interorbital width; males did not differ in length of tail and greatest width of cranium. *Dipodomys insularis* averaged larger than the three other populations in 13 characters for males and 10 for females, *D. merriami* from Santa Rita averaged larger in five characters for males and seven for females, and *D. nitratoides* averaged larger in one character for males and two for females. Conversely, *D. merriami* from San Felipe averaged smallest in seven characters for males and 10 for females, *D. nitratoides* averaged smallest in nine characters for males and seven for females, and *D. merriami* from Santa Rita averaged smallest in two characters for males and one for females.

Statistically significant differences separated the sample of *D. merriami* from San Felipe from the three other populations in five characters for males and six characters for females (Table 3). *Dipodomys merriami* from Santa Rita differed in nine characters for males and eight for females, *D. insularis* differed in 11 characters for males and nine for females, and *D. nitratoides* was significantly different in seven characters for males and eight for females.

Multivariate procedures used to cluster populations based upon phenetic distance for males and females had cophenetic correlation coefficients of 0.847 and 0.950, respectively. For males, *D. merriami* from San Felipe branched from *D. nitratoides* at a phenetic distance of 0.80, these two populations branched from the sample of *D. merriami* from Santa Rita at a phenetic distance of 1.23, and *D. insularis* was placed apart from the three other populations at a phenetic distance of 1.64. For females, *D. merriami* from San Felipe branched from *D. nitratoides* at a phenetic distance of 0.95, the sample of *D. merriami* from Santa Rita branched from *D. insularis* at a phenetic distance of 1.24, and the two pairs of populations branched from each other at a phenetic distance of 1.54. Thus, the population of *D. merriami* from San Felipe was most similar to *D. nitratoides* for both sexes, while the population of *D. merriami* from Santa Rita was intermediate between these two and *D. insularis* for males and most similar to *D. insularis* for females. Principal components analyses placed *D. nitratoides* and the population of *D. merriami* from San Felipe nearest to each other along components I and II. *Dipodomys insularis* and *D. merriami* from Santa Rita were separated from each other and from the two other populations along the first two components.

Previous analyses of intraspecific morphologic variation in *Dipodomys* have shown significant amounts of interpopulation heterogeneity. These studies have shown intraspecific geographic variation in morphologic characters similar to the levels we found when we compared *D. insularis* with *D. merriami*; e.g., *D. gravipes* (Best, 1983*a*), *D. elator* (Best, 1987), *D. agilis* (Best, 1978, 1983*b*; Best et al., 1986), *D. microps* (Csuti, 1979), *D. phillipsii* (Genoways and Jones, 1971), *D. ordii* (Kennedy and Schnell, 1978), *D. spectabilis,* and *D. deserti* (Nader, 1978).

Because *D. nitratoides, D. insularis,* and *D. merriami* are similar in size, it was expected that they would overlap in external and cranial characters. Determining species-level differences among these taxa would be difficult based only upon variation in dimensions of external and cranial characters. However, data are available that differentiate these species. The elongated baculum of *D. nitratoides* (Burt, 1960; Best and Schnell, 1974), its greater number of chromosomes (Stock, 1974), and the difference at Ldh-2 (found in the present study) aid in distinguishing this species from *D. merriami* and *D. insularis*. Although *D. insularis* shows greater divergence from other populations of *D. merriami* than is found among any of the subspecies of *D. merriami* (Lidicker, 1960), no single character can be used reliably to separate them. Although it is not clear what characters he used, Lidicker (1960) noted that *D. insularis* and *D. merriami* were sufficiently distinct so that all individuals could be readily recognized.

Taxonomic Conclusions—Based upon similarities in proteins and the similar degree of morphologic variation between *D. merriami* and *D. insularis* compared with that within other species of *Dipodomys, D. insularis* probably is a subspecies of *D. merriami*. However, *D. merriami insularis* is geographically isolated from other populations of *D. merriami* and is statistically significantly dif-

TABLE 3—Variation in means (in millimeters) of 19 morphologic characters of four populations of *Dipodomys*. Statistically homogeneous subsets derived from Student-Newman-Keuls tests are shown by lines below the population number (1 = *D. merriami* from San Felipe, 2 = *D. merriami* from Santa Rita, 3 = *D. insularis*, 4 = *D. nitratoides*) and ranked means for each character.

Character	Males				Females			
External								
Total length	3	2	4	1	2	4	3	1
	258.6	252.6	244.3	243.8	250.1	241.0	239.5	233.2
Length of body	3	2	4	1	4	2	3	1
	108.6	102.4	101.4	96.7	103.7	101.4	95.1	94.3
Length of tail	2	3	1	4	2	3	1	4
	150.2	150.0	147.2	142.9	148.7	144.4	139.0	137.3
Length of hind foot	2	3	1	4	2	3	1	4
	40.3	37.9	37.6	35.4	37.7	37.7	37.2	35.4
Length of ear	2	3	4	1	2	3	4	1
	14.7	13.0	12.5	10.4	14.6	13.1	12.4	10.3
Cranium								
Basal length	3	2	4	1	3	2	4	1
	21.1	20.0	19.0	18.9	20.6	19.9	18.9	18.9
Greatest length	3	2	1	4	3	2	1	4
	21.1	20.0	19.0	18.9	21.2	19.9	18.5	19.0
Maxillary arch spread	3	2	4	1	3	2	4	1
	21.2	19.9	19.0	18.5	20.7	19.7	19.0	18.3
Interorbital width	3	4	1	2	3	2	1	4
	11.3	11.0	10.8	10.8	11.2	10.9	10.8	10.7
Nasal length	3	2	1	4	3	2	1	4
	13.7	13.1	12.9	12.6	13.6	13.0	12.7	12.2
Intermaxillary width	3	2	1	4	3	2	4	1
	7.4	7.2	6.9	6.8	7.2	7.2	6.9	6.7
Alveolar length	3	2	1	4	2	1	3	4
	4.9	4.8	4.6	4.6	4.9	4.6	4.6	4.5
Lacrimal length	3	2	4	1	3	2	4	1
	3.5	3.3	3.0	2.9	3.5	3.3	3.1	2.9
Maxillary arch width	3	2	1	4	3	2	1	4
	5.8	5.2	4.9	4.7	5.7	5.1	4.9	4.7
Basioccipital length	4	1	3	2	4	1	3	2
	5.1	4.9	4.8	4.7	5.1	4.7	4.7	4.6
Greatest depth	2	1	4	3	2	1	4	3
	12.1	11.8	11.8	11.6	12.0	11.7	11.7	11.4
Greatest width	2	1	3	4	2	3	4	1
	23.1	23.0	22.9	22.8	22.8	22.5	22.5	22.4
Zygomatic width	3	2	1	4	3	2	4	1
	17.9	17.0	16.5	16.2	17.4	16.9	16.3	16.2
Nasal width	3	4	2	1	3	2	4	1
	3.7	3.2	3.1	3.1	3.5	3.1	3.1	3.0

ferent in several morphological characters. These morphological traits are likely the result of the prolonged isolation of *D. m. insularis* on San José Island. Although the karyotype of *D. m. insularis* may be identical to that of other subspecies of *D. merriami,* it (along with additional genic information, including analyses of DNA) ultimately may be important in verifying the species-level designation of kangaroo rats on San José Island.

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