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Martin L. Dobson
Cody, Wyoming

Clyde L. Pritchett
Brigham Young University

Jack W. Sites Jr.
Brigham Young University

GENETIC VARIATION AND POPULATION STRUCTURE IN THE CLIFF CHIPMUNK, *EUTAMIAS DORSALIS*, IN THE GREAT BASIN OF WESTERN UTAH

Martin L. Dobson[1], Clyde L. Pritchett[2], and Jack W. Sites, Jr.[2]

ABSTRACT.—Allelic variation at 21 of 39 electrophoretically resolved enzyme loci was used to examine patterns of geographic differentiation and population structure in six allopatric samples of *Eutamias dorsalis*. Coefficients of genetic similarity for paired combinations of *E. dorsalis* samples ranged from 0.955 to 0.975, except for one population that was 0.900. Conservative genic divergence among five populations is proposed to be the result of relatively recent isolation events. High positive F_{IS} values and chi-square analyses confirm a significant excess of homozygotes at several loci at the five localities for which sample sizes were statistically adequate. This may be partly attributable to inbreeding, a Wahlund effect, linkage disequilibrium, posttranslational modification, or some combination of these; but at present some of these alternatives cannot be excluded in favor of a single explanation. Some samples were collected across altitudinal gradients of over 800 m, suggesting that a Wahlund effect may be the most likely explanation for low levels of heterozygosity in these populations.

The distribution of montane mammals in the Great Basin of western Utah is disjunct, with populations isolated by low-elevation, cold desert valleys (Brown 1971a). The observed pattern has been explained by Pleistocene retreat (Late glacial to Late pleniglacial) of montane elements from pluvial valleys to higher elevation and more northern latitudes (Currey and James 1982, Wells 1983). At least four major glacial events occurred during the Pleistocene. The most recent, the Wisconsin, is suspected of having the greatest influence on existing boreal mammal faunas. Maximum glaciation occurred from the end of Early Pluvial (23,000 years B.P.) to Late Pluvial (12,500 years B.P.). During this time coniferous forests covered the foothills and piedmont, while low-elevation areas not covered by Lake Bonneville were dominated by sagebrush and juniper communities. Coniferous forests offered favorable dispersal habitat (Thompson and Mead 1982, Van Devender and King 1971, Wells and Berger 1967) in the intermountain valleys and low passes, which may have allowed exchange of montane faunal elements across the Great Basin.

The onset of xeric conditions during the Late Pluvial (12,500–7500 years B.P.) initiated major vegetation changes. Coniferous forests retreated upward in elevation and pinyon-juniper began to replace sagebrush communities from the south (Van Devender and Spaulding 1979). Continued warming during the Postpluvial (7,500–5,000 years B.P.) allowed range expansion of xeric mammal species in the low-elevation deserts, while ranges of small montane mammals followed vegetation shifts north and to montane uplands.

Recent biogeographic theory (Brown 1971a, 1978, Patterson 1980, 1982) suggests that distributions of small mammals can be explained as nonequilibrium extinctions without recolonization. Thus, the Great Basin environment and its insular montane mammal faunas offer interesting evolutionary "experiments" in which to assess the effects of isolation and possible recent population bottlenecking on levels of genetic divergence among conspecific montane mammal populations. The possibility of occasionally severe reductions in the sizes of insular mammal populations would be conducive to rapid fixation of alternate alleles and loss of overall genetic variability due to sampling error (Nei et al. 1975, Kilpatrick 1981), and this would facilitate divergence between populations despite their very recent isolation. This study reports on levels of genetic variability within and among samples of cliff chipmunks (*Eutamias dorsalis*) from six isolated mountain ranges in

[1]2437 Central Avenue, Cody, Wyoming 82414
[2]Department of Zoology, Brigham Young University, Provo, Utah 84602.

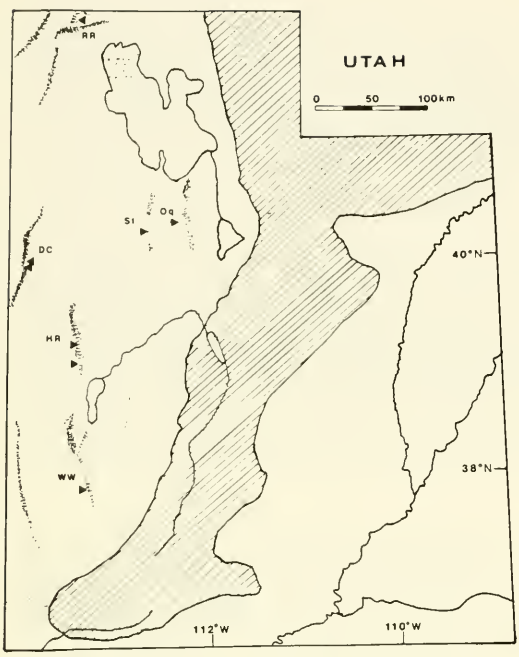

Fig. 1. Collection localities for *Eutamias dorsalis* from six mountain ranges in western Utah. Locality abbreviations are as in Table 1; stippled areas represent mountain ranges above 2,000 m; hatched region represents the Rocky Mountains.

western Utah, in an attempt to evaluate the effects of drift and recent insularization.

Materials and Methods

A total of 90 specimens representing six allopatric populations of *Eutamias dorsalis* in the Great Basin of western Utah (Fig. 1) was collected from May through September 1983. All 90 voucher specimens were deposited in the Brigham Young University mammal collection as standard museum mounts. Collection location, population abbreviations and sample sizes, and voucher specimen numbers are presented in Table 1.

Preferred habitat of cliff chipmunks is open canopy pinyon-juniper complex on granite substrate (Brown 1971b). Chipmunk densities were low in all sites except two: Indian Farm Canyon of the Deep Creek Mountains and Painter Creek of the House Range. Low density in the Stansbury Range reflects the small area of suitable habitat. Two locations were sampled from both the House Range and the Deep Creek Mountains (Table 1, Fig. 1), but in each case specimens were assumed to be from one breeding population because of site proximity and habitat uniformity. Heart, liver, and blood tissues were immediately removed from live-trapped specimens (killed by cervical dislocation) and transported in liquid nitrogen to the laboratory. Tissues were then homogenized in an equal volume of buffer (0.01 M Tris, 0.001 M EDTA, 5×10^{-5} M NADP, pH adjusted to 7.0 with HCl), centrifuged for 20 min at 4 C, and stored at −80 C. Hemolysate was maintained at 0–5 C until assayed. Methods of horizontal starch gel electrophoresis and biochemical staining were similar to those described by Selander et al. (1971) and Harris and Hopkinson (1976), with minor modifications. Gels were prepared using a 14% concentration of hydrolysed starch, which consisted of a 1:1 mix of starch from Sigma Chemical Co. (lot 31F-0135) and Otto Hillers's Electrostarch (lot 307). A total of 39 presumptive gene loci was consistently resolved across all populations, and the buffer/stain combinations used are summarized in Table 2. Enzyme nomenclature follows recommendations of the Nomenclature Committee of the International Union of Biochemistry (1984), with locus abbreviations following those suggested for lower vertebrates by Murphy and Crabtree (1985). We recognize that our nomenclature will depart from that used in most conventional mammal studies, but virtually all of these loci are either known (Fisher et al. 1980) or suspected of being homologous across all tetrapods (Harris and Hopkinson 1976).

Multilocus enzyme systems in which homologies are uncertain were simply designated numerically from most to least anodal (Est-"1", -"2", etc.). Alleles were designated numerically, with the most common allele assigned a value of 100 for anodal and −100 for cathodal migrants. Other allozymic bands and their corresponding alleles were designated as percentages of distances migrated relative to that of the 100 allele. Individual genotypes were inferred from enzyme phenotypes and statistically analyzed with the BIOSYS-1 program (Swofford and Selander 1981). Measures of genetic variability computed for each population include average locus heterozygosity (H, direct count), percent loci polymorphic (P), and mean number of alleles per locus (A).

TABLE 1. Summary of *Eutamias dorsalis* samples used in the study.

Locality	N	Elevation (m)	Museum deposition
DC = Deep Creek Mountains			
Indian Farm Canyon	22	1650–2400	BYU 7404–06,7409–28
Toms Creek	2	1800	BYU 7407–7408
HR = House Range			
Marjum Pass	18	1800–2100	BYU 7429–7446
Painter Creek	13	1800–2400	BYU 7447–7459
RR = Raft River Mountains			
Clear Creek	13	1800–2100	BYU 7471–7483
Oq = Oquirrh Mountains			
Ophir Canyon	11	1800–2250	BYU 7460–7470
WW = Wah Wah Mountains			
Pine Grove	9	1800–2250	BYU 7396–7403
St = Stansbury Mountains			
Johnson Pass	2	1800–1950	BYU 7484–7485

The genetic distance and similarity coefficients of Nei (1972, 1978) and Rogers (1972) were calculated for all pairwise comparisons of samples, and all such matrices were clustered by the UPGMA algorithm of Sneath and Sokal (1973). Wright's (1965, 1978) F-statistics were calculated for all variable loci, each population was tested for conformance to Hardy-Weinberg expectations using Levene's (1949) correction for small sample sizes, and intersample allele-frequency heterogeneity was evaluated by the contingency Chi-square method of Workman and Niswander (1970).

RESULTS

PATTERNS OF VARIABILITY.—Of the 39 loci scored in *E. dorsalis*, the following 18 loci were monomorphic for the same allele in all six populations: Adh-A, Ap-A, M-Aat-A, S-Aat-A, Pep-B, Pep-D, Esterases 1, 2, 4, and 5, Gpi-A, Gtdh-A, G3pdh-A, M-Icdh-A, Ldh-B, M-Mdh-A, Sod-"2", and P-alb. Allelic frequencies of the 21 polymorphic loci are given in Table 3. The Stansbury Mountain sample was fixed for S-Mdh-A, M-Me-A, and Xdh-A alleles that were rare or absent from the other samples. The Deep Creek sample varied at four loci, M-Acon-A, S-Icdh-A, Ldh-A, and Pgm-A, which were monomorphic for the common allele across all other samples. The remaining loci are characterized by differing degrees of polymorphism in different samples.

POLYMORPHISM AND HETEROZYGOSITY.—Table 3 summarizes estimates of the average proportion of polymorphic loci per sample (P), the average number of loci heterozygous per individual for each sample (H), and the mean number of alleles per locus (A). Estimates of P were calculated using both the .01 and .05 criteria in order to facilitate comparison with other investigators. The proportion of polymorphic loci per sample (P) averaged 0.15 (range: 0.05–0.25) and 0.20 (range: 0.05–0.33) for the .05 and .01 levels, respectively. Heterozygosity estimates averaged 0.010 and ranged from 0.005 in the Oquirrh sample to a high of 0.013 in the House Range sample. These estimates appear lower than other reports for this genus, H = 0.061 for *E. panamintus* (Kaufman et al. 1973). Estimates of A ranged from 1.143 for the Stansbury sample, which may be an artifact of small sample size, to a high of 1.857 for the Deep Creek sample. The average across all samples was 1.524.

GENETIC SIMILARITY AND DISTANCE.—Coefficients of genetic similarity, S (Rogers 1972), and genetic distance, D (Nei 1978), based on the 39 loci assayed were calculated for all pairwise sample comparisons (Table 4). Values of S ranged from 0.891 to 0.976 and for D from 0.001 to 0.086. The Stansbury sample consistently had the lowest S and highest D values. Values from the matrices of intersample genetic similarities and distances were clustered by the UPGMA option of BIOSYS-1, and dendrograms are presented in Figure 2 (dendrograms of Nei's [1978] I matrix and Nei's [1972] earlier I and D coefficients are available from the senior author upon

TABLE 2. Enzymes and electrophoretic conditions used in the analysis of *Eutamias dorsalis* populations. Locus prefixes M and S refer to mitochondrial and supernatant (= cytosolic) loci, respectively; and tissue abbreviations H, He, L, and P refer to heart, hemolysate, liver, and plasma, respectively. Abbreviations of enzymes in parentheses are older names found in most mammal literature.

Enzyme	Enzyme commission number[1]	Locus	Buffer conditions[2]	Tissue
Aconitate hydratase	4.2.1.3	M-Acon-A	B	L
Alcohol dehydrogenase	1.1.1.1	Adh-A	B	L
Aminopeptidase ("Lap")	3.4.11.1	Ap-A	A	P
Aspartate aminotransferase ("Got-2")	2.6.1.1	M-Aat-A	B	L
Aspartate aminotransferase ("Got-1")	2.6.1.1	S-Aat-A	B	L
Dipeptidase[3]	3.4.12.9	Pep-A	B	L
Dipeptidase	3.4.13.9	Pep-B	B	L
Dipeptidase	3.4.13.9	Pep-D	B	L
Esterases (non-specific)	—	Est. "1"-"6"	D	L,P
Fumarate hydratase	4.2.1.2	Fum-A	B	L
Glucose dehydrogenase	1.1.1.47	Gcdh-A	B,C	L
Glucose-6-phosphate isomerase ("Pgi")	5.3.1.9	Gpi-A	B	L
Glucose-6-phosphate dehydrogenase	1.1.1.49	G6pdh-A	B	L
Glutamate dehydrogenase	1.4.1.2	Gtdh-A	B	L
Glycerol-3-phosphate dehydrogenase ("-Gpd")	1.1.1.8	G3pdh-A	B	L
L-Iditol dehydrogenase ("Sdh")	1.1.1.14	Iddh-A	B	L
Isocitrate dehydrogenase ("Idh-2")	1.1.1.42	M-Icdh-A	B	L
Isocitrate dehydrogenase ("Idh-1")	1.1.1.42	S-Icdh-A	B	L
Lactate dehydrogenase ("Ldh-2")	1.1.1.27	Ldh-A	C	L
Lactate dehydrogenase ("Ldh-1")	1.1.1.27	Ldh-B	C	L
Malate dehydrogenase ("Mdh-2")	1.1.1.37	M-Mdh-A	B	L
Malate dehydrogenase ("Mdh-1")	1.1.1.37	S-Mdh-A	B	L
"Malic enzyme"[4] ("Me-2")	1.1.1.40	M-Me-A	B	L
"Malic enzyme" ("Me-1")	1.1.1.40	S-Me-A	B	L
Mannose-6-phosphate isomerase	5.3.1.8	Mpi-A	B	L
Phosphoglucomutase	5.4.2.2	Pgm-A	B	L
Phosphogluconate dehydrogenase	1.1.1.44	Pgdh-A	B	L
Superoxide dismutase ("Ipo")	1.15.1.1	Sod-"1"[5]	B	L
Superoxide dismutase ("1po")	1.15.1.1	Sod-"2"	D	L
Xanthine dehydrogenase	1.2.1.37	Xdh-A	B	L
General proteins:				
Albumin	—	Alb	A	L,H
Hemoglobin[6]	—	Hb-"1"	A	He
Post-albumin	—	P-alb	A	L,H
Transferin	—	Trf	A	L,H

[1]Nomenclature and E.C. numbers follow recommendations of the Nomenclature Committee of the International Union of Biochemistry (1984).
[2]Buffers used: A—Tris-hydrochloric acid pH 8.5, 50 ma for 5 hr; B—Tris-citrate pH 8.0, 75 ma for 6 hr; C—Tris-citrate pH 6.7, 50 ma for 6 hr; D—Poulik pH 8.7, 50 ma for 10 hr.
[3]Substrates for dipeptidases A, B, and D were glycyl-L-leucine, DL-leucylglycylglycine, and L-phenylalynyl-L-proline, respectively.
[4]NADP-dependent malate dehydrogenase
[5]Locus homologies with lower vertebrates uncertain
[6]*Eutamias* hemoglobin is encoded by two loci (Jensen et al. 1975), but the single locus resolved in this study is arbitrarily designated Hb-"1".

request). In all dendrograms generated, five samples are very similar (S values 0.94–0.98) and consistently cluster in one branch, whereas the Stansbury Mountain sample is comparatively very divergent (average S = 0.90).

POPULATION STRUCTURE.—A summary of F statistics for all variable loci is presented in Table 5, excluding those for the small Stansbury sample. The inbreeding coefficients (F_{IS}) ranged from −0.016 to 1.000 with a mean of 0.320. The standardized gene frequency variance (F_{ST}) values ranged from 0.013 to 0.196 with a mean of 0.094.

Chi-square tests were performed to test for deviation of genotypes from Hardy-Weinberg expectations for all variable loci in all but the Stansbury sample, and surprisingly, all samples showed significant deviation at some loci, due to the presence of rare homozygotes. The House Range sample, for example, had no heterozygotes at G-6–pdh (30 100/100 and 1

TABLE 3. Allele frequencies and estimates of genic variability in six samples of *Eutamias dorsalis*. Locality abbreviations are from Table 1 and Figure 1.

		Sample sizes and localities					
Locus	Allele	(N=9) WW	(N=24) DC	(N=11) Oq	(N=13) RR	(N=31) HR	(N=2) St
M-Acon-A	88	0.0	0.042	0.0	0.0	0.0	0.0
	100	1.000	0.958	1.000	1.000	1.000	1.000
Est-"3"	86	0.167	0.125	0.0	0.0	0.0	0.0
	100	0.556	0.875	0.545	1.000	0.871	0.500
	107	0.222	0.0	0.455	0.0	0.129	0.250
	105	0.056	0.0	0.0	0.0	0.0	0.000
	110	0.0	0.0	0.0	0.0	0.0	0.250
Est-"6"	90	0.278	0.083	0.091	0.154	0.194	0.0
	100	0.556	0.792	0.545	0.692	0.710	0.500
	105	0.167	0.083	0.364	0.077	0.097	0.500
	110	0.0	0.042	0.0	0.077	0.0	0.0
Fum-A	100	1.000	0.875	1.000	0.962	0.887	1.000
	188	0.0	0.125	0.0	0.038	0.113	0.0
Gcdh-A	100	1.000	1.000	1.000	1.000	0.968	1.000
	110	0.0	0.0	0.0	0.0	0.032	0.0
G6pdh-A	100	1.000	1.000	1.000	1.000	0.968	1.000
	108	0.0	0.0	0.0	0.0	0.032	0.0
S-Icdh-A	100	1.000	0.979	1.000	1.000	1.000	1.000
	112	0.0	0.021	0.0	0.0	0.0	0.0
Iddh-A	100	1.000	0.938	1.000	0.962	1.000	1.000
	387	0.0	0.062	0.0	0.038	0.0	0.0
Ldh-A	100	1.000	0.958	1.000	1.000	1.000	1.000
	125	0.0	0.042	0.0	0.0	0.0	0.0
S-Mdh-A	84	0.0	0.0	0.0	0.038	0.0	1.000
	100	1.000	1.000	1.000	0.924	1.000	0.0
	105	0.0	0.0	0.0	0.038	0.0	0.0
M-Me-A	75	0.0	0.167	0.091	0.077	0.0	1.000
	100	1.000	0.813	0.909	0.923	1.000	0.0
	110	0.0	0.020	0.0	0.0	0.0	0.0
S-Me-A	50	0.0	0.208	0.0	0.0	0.065	0.0
	100	1.000	0.792	1.000	1.000	0.935	1.000
Mpi-A	100	1.000	1.000	0.955	1.000	0.935	1.000
	115	0.0	0.0	0.045	0.0	0.065	0.0
Pep-A	100	1.000	1.000	1.000	1.000	0.984	1.000
	120	0.0	0.0	0.0	0.0	0.016	0.0
Pgm-A	35	0.0	0.083	0.0	0.0	0.0	0.0
	100	1.000	0.917	1.000	1.000	1.000	1.000
Pgdh-A	118	0.333	0.0	0.0	0.0	0.0	0.0
	100	0.667	1.000	1.000	1.000	1.000	1.000
Sod-"1"	60	0.111	0.0	0.143	0.0	0.0	0.0
	100	0.889	0.771	0.714	0.846	0.968	1.000
	130	0.0	0.229	0.143	0.154	0.032	0.0
Xdh-A	40	0.0	0.166	0.182	0.077	0.0	1.000
	100	1.000	0.792	0.818	0.923	1.000	0.0
	110	0.0	0.042	0.0	0.0	0.0	0.0
Alb	100	0.889	1.000	1.000	1.000	1.000	1.000
	110	0.111	0.0	0.0	0.0	0.0	0.0
Hb-"1"	80	0.056	0.020	0.0	0.0	0.065	0.0
	100	0.944	0.917	0.955	0.923	0.903	1.000
	120	0.0	0.063	0.045	0.077	0.032	0.0

Table 3 continued.

Locus	Allele	Sample sizes and localities (N=9) WW	(N=24) DC	(N=11) Oq	(N=13) RR	(N=31) HR	(N=2) St
Trf	100	0.889	1.000	1.000	1.000	0.968	1.000
	120	0.111	0.0	0.0	0.0	0.032	0.0
Polymorphic per sample (P)*	(.05)	0.179	0.256	0.128	0.154	0.154	0.051
	(.01)	0.179	0.325	0.175	0.200	0.275	0.051
Average heterozygosity per individual (H)**		0.048	0.024	0.042	0.028	0.036	0.050
Mean number of alleles per locus (A)		1.476	1.857	1.478	1.571	1.619	1.143

*A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95 (.05 criterion) or 0.99 (.01 criterion).
**Estimate of H determined by direct count.

TABLE 4. Matrix of genetic similarity S (Rogers 1972) above the diagonal and genetic distance D (Nei 1978) below the diagonal for six samples of *E. dorsalis*. Abbreviations of populations follow Table 1.

Population	WW	DC	Oq	RR	HR	St
Wah Wah Mtns.	—	0.941	0.962	0.963	0.965	0.891
Deep Creek Mtns.	0.010	—	0.959	0.969	0.964	0.891
Oquirrh Mtns.	0.004	0.007	—	0.969	0.964	0.912
Raft River Mtns.	0.006	0.002	0.006	—	0.976	0.901
House Range	0.005	0.003	0.005	0.001	—	0.894
Stansbury Mtns.	0.086	0.071	0.066	0.075	0.085	—

108/108 genotypes) and Sod-"1" (30 100/100 and 1 130/130), $X^2 = 61.02$ (1 df), $P < .001$. Samples from the Oquirrh, Raft River, and Wah-Wah Mountains had no heterozygotes at three loci each, as follows: (1) Oq—M-Me-A (10 100/100 and 1 75/75, $X^2 = 21.05$ with 1 df), Sod-"1" (5 100/100, 1 60/60, and 1 130/130; 4 individuals unscorable; $X^2 = 26.22$ with 1 df), Xdh-A (9 100/100 and 2 40/40, $X^2 = 14.12$ with 1 df), $P < .001$; (2) RR—M-Me-A (12 100/100 and 1 75/75, $X^2 = 25.04$ with 1 df), Sod-"1" (11 100/100 and 2 130/130, $X^2 = 16.76$ with 1 df), Xdh-A (12 100/100 and 1 40/40, $X^2 = 14.12$ with 1 df), $P < .001$; (3) WW—Pgdh-A (6 100/100 and 3 118/118, $X^2 = 10.47$ with 1 df), Sod-"1" (8 100/100 and 1 60/60, $X^2 = 17.01$ with 1 df), Trf (8 100/100 and 1 120/120, $X^2 = 17.01$ with 1 df), $P < .001$. The same trend was evident in 8 of 13 polymorphic loci in the Deep Creek sample: M-Acon-A (23 100/100 and 1 88/88, $X^2 = 47.02$ with 1 df), Ldh-A (23 100/100 and 1 125/125, $X^2 = 47.02$ with 1 df), Pgm-A (22 100/100 and 2 35/35, $X^2 = 31.38$ with 1 df), Fum-A (21 100/100 and 3 188/188, $X^2 = 28.27$ with 1 df), S-Me-A (19 100/100 and 5 50/50, $X^2 = 26.25$ with 1 df), Sod-"1" (19 100/100 and 5 130/130, $X^2 = 26.25$ with 1 df); M-Me-A (19 100/100, 4 75/75, and 1 100/110, $X^2 = 26.96$ with 3 df); Xdh-A (19 100/100, 4 40/40, and 1 110/110, $X^2 = 73.99$ with 3 df); $P < .001$ in all cases.

DISCUSSION

Allopatric populations of cliff chipmunks sampled had weak interpopulational divergence (average D = 0.028), with the Stansbury sample strongly divergent from others (average D = 0.74) while the remaining samples are only slightly divergent from each other (average D = 0.005, Fig. 2). The small D values are consistent with those calculated for other mountain-top species of small rodents (Mewaldt and Jenkins 1986, Sullivan 1985). The divergence of the Stansbury Mountain sample is primarily due to the fixation of three alleles, S-Mdh-A (84), M-Me-A (75), and Xdh-A (40) (Table 3) that were rare or absent in the rest of the samples. This sample also had a unique Est-3 (110) allele at 0.25 frequency, but because of its small size (2 individuals), some of this difference may simply be a function of a large sampling error. However, the Stansbury population is likely

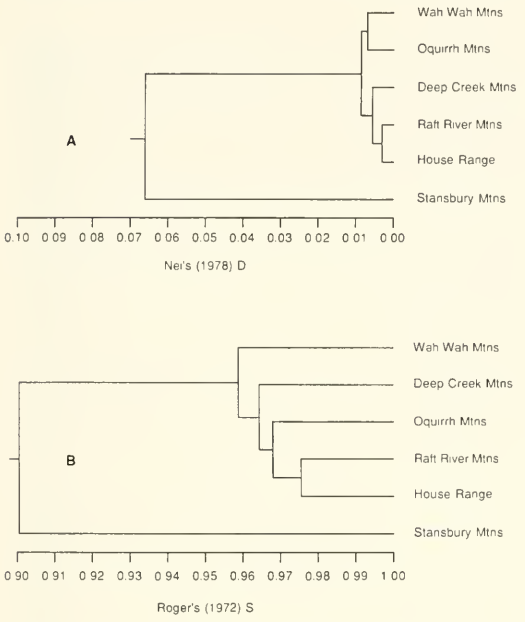

Fig. 2. UPGMA dendrograms of genetic distance values (Nei 1978), A, and similarity values (Rogers 1972), B, for six samples of *Eutamias dorsalis*. Sample localities are those shown in Figure 1; cophenetic correlation values are 0.991 and 0.975, respectively.

TABLE 5. Summary of F-statistics for all variable loci across all examined samples of *Eutamias dorsalis* except Stansbury Mountains.

Locus	F_{IS}	F_{IT}	F_{ST}
M-Acon-A	1.000	1.000	0.034
Est-"3"	−0.259	−0.002	0.196
Est-"6"	−0.211	−0.148	0.052
Fum-A	0.517	0.544	0.056
Gcdh-A	−0.033	−0.006	0.026
G-6-pdh-A	1.000	1.000	0.027
S-Icdh-A	−0.021	−0.004	0.017
Iddh-A	−0.056	−0.021	0.034
Ldh-A	1.000	1.000	0.034
S-Mdh-A	−0.061	0.012	0.047
M-Me-A	0.933	0.937	0.066
S-Me-A	0.714	0.750	0.127
Mpi-A	−0.060	−0.022	0.035
Pep-A	−0.016	−0.003	0.013
Pgm-A	1.000	1.000	0.068
Pgdh-A	1.000	1.000	0.286
Sod-"1"	1.000	1.000	0.068
Xdh-A	1.000	1.000	0.083
Alb	−0.125	−0.023	0.091
Hb-"1"	−0.072	−0.058	0.013
Trf	0.752	0.770	0.071
Mean	0.320	0.384	0.094

very small, as evidenced by very low capture success per unit effort compared to other samples, and it appears to be restricted to one canyon. Thus, the relatively large level of genetic divergence may also reflect the influence of a recent population bottleneck and/or pronounced genetic drift.

The overall mean F_{ST} value of 0.094 (Table 5) suggests an appreciable level of subdivision between the montane populations, although much higher levels are known in other small mammals (F_{ST} = 0.412 for *Thomomys bottae*, for example; see Patton and Yang 1977). Appreciable substructuring in populations may result from population bottlenecks and the ensuing influence of drift (Schwartz and Armitage 1980), and the winter of 1982–83 was one of the most severe on record in Utah (NOAA 1983). This may have reduced population sizes, forcing inbreeding and fostering a breeding structure in which drift could have a pronounced influence. However, if we invoke an explanation of differentiation by climatically caused population bottlenecking and subsequent drift for the Stansbury sample, we must also account for the extensive polymorphism observed in the other samples (e.g., DC and HR), which presumably were also subject to the same severe conditions. It is unlikely that the observed polymorphism of alternate alleles could have been accumulated in each population in the short time since the Postpluvial, 7500 years B.P., when desert advancement last isolated mountain ranges. Two alternate explanations are proposed. First, one large, genetically variable population may have been widely distributed across the Great Basin and subsequently became fragmented and restricted to mountain ranges by the Pleistocene climatic shifts. This is the vicariance explanation proposed by Patterson (1980, 1982) for montane mammal populations in New Mexico. This hypothesis would predict near genetic uniformity and very low between-population divergence in the absence of drift, isolation by distance (Wright 1965), or some behavioral mechanism contributing to small, effective breeding sizes and nonrandom mating. Alternately, since chipmunks are reported from the Pliocene of North America (Black 1972), *E. dorsalis* as a species may predate the Pleistocene and may have entered the Great Basin from the Rocky Mountains or some other center of origin. Pleistocene ice ages repeatedly forced floral

and faunal elements to lower elevations and may have facilitated intermittent gene flow among chipmunk populations. This may have been sufficient to maintain allelic variants in most populations. Without additional genetic information from hypothesized source populations (i.e., Wasatch Range) and others more distantly isolated in Great Basin mountain ranges, we cannot choose among these alternatives.

Ecological and behavioral factors may be as important as historical events in determining the genetic structure of chipmunk populations. For example, in addition to the dispersal barriers between populations (i.e., desert valleys, lakes, rivers, and distance), chipmunks also face problems of short-distance dispersal imposed by complex, interspecific competition, interspecific territoriality (Broadbooks 1970, Brown 1971b, Heller 1971), habitat requirements (Sharples 1983), predation, altitudinal zonation (Chappell 1978, Heller 1971), and philopatry to home range (Broadbooks 1970, Martinsen 1968, Sheppard 1972). Broadbooks (1970), Martinsen (1968), and Sheppard (1971) found three significant behavioral characteristics of yellow-pine chipmunks (*E. amoenus*) and least (*E. minimus*) chipmunks that would influence the geographic distribution of allele frequencies: (1) chipmunks have a well-defined home range in which they remain from year to year, (2) a high percentage (8 of 11) of the offspring remain in the area of the parent, and (3) 67.4% of chipmunks released .4 km from their home range returned within 1–3 days after release.

If similar behavior is typical of *E. dorsalis* populations, then breeding units may be characterized by high incidences of parent-offspring or sib matings. Some evidence of inbreeding is given by the F-statistics. For example, when averaged across all samples, F_{IS} values were mostly high and positive, an indication of heterozygote deficiency for many loci (Table 5). This is due to the complete absence of heterozygotes at some loci in the five localities for which sample sizes were statistically "adequate" (all but Stansbury). The F_{IS} values may reflect either high levels of inbreeding or further levels of subdivision within our "samples" of *E. dorsalis*, but other explanations are possible. For example, the frequent occurrence of double homozygotes in some loci segregating three alleles (Xdh-A and S-Me-A in the Deep Creek sample, and Sod-"1" in the Oquirrh Mountain sample) also suggests the possibility of linkage disequilibrium in small, nonrandom mating populations. Several other studies have shown that small population size per se is not always accompanied by strong inbreeding, as various species of mammals avoid consanguinous matings by a number of behavioral mechanisms (Foltz and Hoogland 1983, Hoogland 1982, Patton and Feder 1981, Schwartz and Armitage 1980). Patton and Feder (1981), for example, found a paradoxical situation in which high heterozygosity was maintained in apparently very small breeding units of the gopher *Thomomys bottae*, and this was explained as an equilibrium achieved between the rate of migration (either recolonization following extinction or individual recruitment into groups) and the effective number of individuals that are contributing to the breeding effort each year. We do not have the ecological or pedigree information necessary to evaluate the importance of these factors in *E. dorsalis*, but their prevalence in other rodents, and the previously mentioned behavioral traits of other *Eutamias*, collectively suggest that inbreeding alone cannot explain all of the observed heterozygote absences in these populations. If it did, it should have a more or less equal influence across all variable loci, and this is not the case (Table 3).

Alternatively, the high frequency of fixed allelic differences among different individuals within the same sample suggests that we may well have pooled breeding units that differed drastically in their allelic composition (Wahlund effect). The Deep Creek sample displayed heterozygote deficiencies at eight loci and was comprised of collections from two different localities (Table 1, Fig. 1), but the excess number of homozygotes in the total sample did not correlate with the numbers of individuals from either of these two sites. In other words, this effect did not disappear when these samples were analyzed separately. Similarly, the House Range sample was collected from two localities and showed heterozygote deficiencies at five loci; again the phenomenon was independent of sample localities. The Oquirrh and Raft River samples were collected from one canyon each, and both samples showed heterozygote deficiencies at the same three loci (S-Me-A,

Sod-"1", and Xdh-A). Chesser (1983) has shown that important patterns of genetic variability may be obscured when breeding units are pooled together, and we suspect that our "samples" of *E. dorsalis* may include separate Mendelian units that may differ drastically in allelic composition at some loci.

We recognize the risk of over-analyzing these data in light of the small sample sizes but feel that at least some other possible explanations for the complete absence of heterozygotes at many loci can be ruled out. The possibilities include: (1) inadvertant inclusion of a second species of *Eutamias* in the samples, (2) scoring of multiple loci for some enzyme systems in only select individuals from each sample, and (3) enzyme denaturation and/or posttranslational modification of gene products in select individuals.

Eutamias minimus is sympatric with *E. dorsalis* at all localities sampled, but the latter is very distinct, and CLP and MLD have had considerable experience with both species. Museum voucher specimens were prepared for all individuals used in this study, and a recheck confirmed their identification as *E. dorsalis*. We conclude that there is almost no chance of "mistaken identity" and that this explanation would not, by itself, account for the different locus *combinations* displaying heterozygote absence at the five localities tested.

Second, we can rule out the likelihood of scoring different loci from a multilocus enzyme in different individuals from the same populations, because the number of loci encoding the enzymes used in this study is well known in mammalian systems (Harris and Hopkinson 1976). A single tissue type was used in most electrophoretic runs (liver, see Table 2), but even when others were used, multilocus systems were evident either as two zones of activity on the same gel, or as different patterns of variability evident in different tissues of the same individual. The rare homozygotes we resolved were scored as such from zones of different mobility in one or a few individuals on gels that otherwise contained a single electromorph common to all other specimens, with the *same* tissue type being used throughout.

The problem of enzyme denaturation and/or posttranslational modification is more difficult to assess. Moore and Yates (1983) evaluated rates of protein inactivation (for 27 enzymes) under controlled conditions in four species of mammals of varying body size (*Antilocapra americana*, *Plecotus townsendii*, *Dipodomys ordii*, and *Peromyscus boylii*) and found that 95% of the proteins routinely examined electrophoretically are still stable (i.e., not denatured and showing mobilities identical to controls) in unfrozen tissues for a minimum of 12 hrs after death. The locus Sod-"1" had no heterozygotes in all five of the *E. dorsalis* samples but was one of the most stable systems studied by Moore and Yates (1983); the least stable system examined by them, ADH, was not included in our protocol (Table 2). Further, our method of obtaining animals from the field insured that tissues were taken from specimens and frozen in liquid nitrogen within 30 min of capture. Laboratory protocol for homogenizing and storing tissue samples was consistent throughout the study, so there seems to have been little opportunity for extensive contamination or denaturation of the samples.

The possibility of epigenetically or posttranslationally modified electromorph mobilities (see Lebherz 1983) in some *E. dorsalis* specimens is one that we cannot evaluate with the information we have. Some classes of these alterations are known to have a genetic basis in some organisms (Womack 1983, Dykhuizen et al. 1985), and in at least one rodent species, mobility differences in two different loci (Trf and Ap-A) seem to vary with the physiological state of the animal (McGovern and Tracy 1981). If this is the explanation for most or all of the rare homozygotes we encountered, then the physiologically or genetically based phenomenon for such electromorph mobility alterations must be widespread in *E. dorsalis* populations. Elimination of these individuals from our analyses would lower the mean inbreeding coefficient (F_{IS}) and perhaps slightly decrease mean D and F_{ST} values, although our conclusions about a moderate level of population subdivision and minimum genetic divergence would be virtually unaltered.

We suggest that the montane mammal populations of the Great Basin offer excellent model systems for addressing issues in island biogeography and population biology, but that future sampling strategies be designed to collect an adequate number of individuals

(n = 25, if possible) from a single ecologically homogenous site, and that, for larger mountain ranges at least, two or more localities be collected and analyzed as separate population samples in order to assess within, as well as between, mountain range divergence. Such control in sampling will allow for a more rigorous assessment of macrogeographic patterns of gene flow and population structure.

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