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Genetic divergence between populations of the pocket gopher, *Thomomys umbrinus* (Richardson)

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Receipt of Ms. 11. 5. 1977

Introduction

The restrictions imposed on vertebrate species with fossorial life styles (such as low individual vagility, small population size, and strong environmental selective regimes) suggest that such species should display marked levels of population subdivision in genetic characters on a regional basis. Where this question has been examined, the observed patterns have followed the prediction.

Z. Säugetierkunde 43 (1978) 17—30

ISSN 0044—3468/ASTM-Coden ZSAEA 7

Genetic data of two kinds, chromosomal and genic (= allozymes), are now available for fossorial rodents of the Old World family Spalacidae (*Spalax:* Wahrman et al. 1968; Nevo and Shaw 1972) and the New World family Geomyidae (*Geomys:* Davis et al. 1971; Baker et al. 1973; Selander et al. 1974; Penney and Zimmermann 1976 and *Thomomys:* Patton 1972; Thaeler 1974; Patton et al. 1972; Nevo et al. 1974; Patton and Yang in press). While these species do show a higher level of interpopulation differentiation in both genetic characters than average rodent species, two quite distinct patterns of relationship between these variables have been noted (Patton and Yang, in press).

On the one hand, some species exhibit marked chromosomal differences associated with reproductive isolation and lower levels of both intra and interpopulation genic variation (such as *Spalax ehrenbergi* and the *Thomomys "talpoides"* complex). Contrasted to this pattern are species (*Geomys bursarius* and *Thomomys bottae)* in which chromosomal variation, while extensive within species, has been unrelated generally to development of genetic isolation. These latter species have average to quite high levels of genic variability within populations and show very marked interpopulation genic divergence patterns. Based on work with *T. bottae,* Patton and Yang (in press) concluded that the dominant mode of speciation in fossorial rodents has been by chromosomal reorganization and that change at structural gene loci has been generally independent of the process of speciation. The observed level of divergence in structured genes was related more to the time since cladistic events than to such events themselves.

The present report concerns patterns of geographic variation of genetic systems in the southern pocket gopher, *Thomomys umbrinus* (Richardson). Previous studies have shown that while this species is reproductively isolated from *T. bottae* in Arizona due to meiotic imbalances imposed by several chromosomal translocation differences (Patton 1973), the overall level of genic similarity between the two species is rather high (Patton et al. 1972). Indeed, sampled populations of *T. umbrinus* exhibit greater genic similarity to some geographically defined units of *T. bottae* than the latter do among themselves (Patton and Yang in press). Consequently, an effort has been made to examine differentiation patterns in karyotype and allozyme profile in *T. umbrinus* in greater detail, and to relate these to the basic patterns described for fossorial rodents in general.

Materials and methods

Twenty-three populations of *T. umbrinus,* predominantly from the western portions of the species range, have been examined. A total of 133 individuals representing 20 of these populations were karyotyped by a standard in vivo bone marrow or testis colchicine-hypotonic citrate sequence (Patton 1967). For the allozyme survey, 316 individuals from 18 populations were analyzed (see map, Fig. 1, and list of localities below). For each of these, blood samples and homogenates of kidney and liver were prepared according to the methods described by Selander et al. (1971). Procedures for starch-gel electrophoresis and staining were those of Selander et al. (1971) as modified by Patton et al. (1972). Protein systems used and tissue sources are described in other publications dealing with the *bottae*-group of *Thomomys* (Patton et al. 1972; Patton and Yang in press). The presumptive gene loci examined encode for 19 enzymatic and 4 general proteins, as follows; enzymatic proteins — malate dehydrogenase (MDH-1 and MDH-2), α-glycerophosphate dehydrogenase (αGPD), lactate dehydrogenase (LDH-1 and LDH-2); isocitrate dehydrogenase (IDH-1 and IDH-2), 6-phosphogluconate dehydrogenase (6PGD), alcohol dehydrogenase (ADH), sorbitol dehydrogenase (SDH), glutamic oxaloacetic transaminase (GOT-1 and GOT-2), phosphoglucomutase (PGM), phosphoglucose isomerase (PGI); indophenol oxidase (IPO), peptidase (Pept-1 and Pept-2) and esterase (Est-1 and Est-4); nonenzymatic proteins — erythrocytic protein (Pt-A), prealbumin (preAlb), albumin (Alb), and transferrin (Trf). Alleles have been

designated by mobility relative to the most common allele at a given locus in *T. bottae*, which was arbitrarily set at 100 (see PATTON and YANG, in press).

Both ROGERS' (1972) coefficient of genetic similarity (S-value) and NEI's (1971) genetic distance measure (D-value) were used as indices of interpopulation relatedness for the genic data. Cluster analysis of these matrices was performed by the unweighted pair-group method using arithmetic means (UPGMA; SNEATH and SOKAL 1973) with the NT-2 program of the Numerical Taxonomy Package adapted for the CDC 6400 computer by W. W. Moss.

The ecogeographic relationship of population samples to the observed patterns of genetic variation was examined by the connectedness method employed for *T. bottae* (PATTON and YANG in press). An index of ecogeographic distance between each population pair was calculated by employing the product of the airline mileage distance between each pair and the number of major habitat changes differentiating that pair. That is, two sampled populations 10 miles apart and connected by the same habitat type would have a distance score of 10 whereas those 10 miles apart but in elevationally contiguous and different habitats would have a score of 20. The rationale behind this measure is that migration, and hence gene flow, is more likely between populations adapted to similar environments (i. e., gross habitas in this case) than between those occurring in different ecological settings.

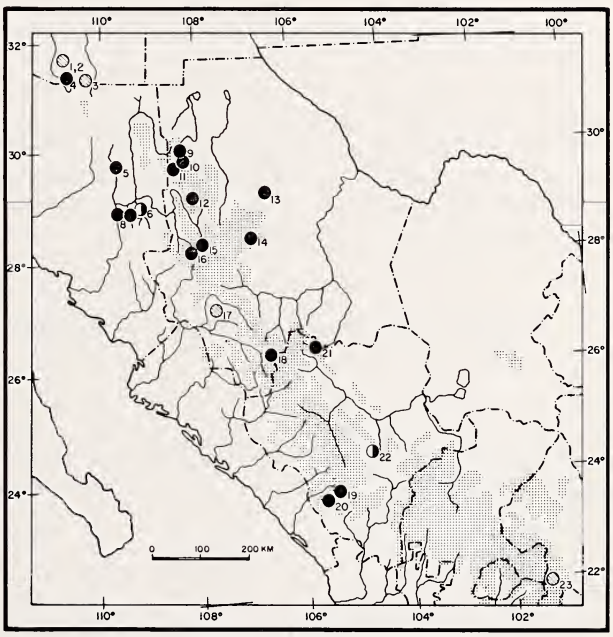

Fig. 1. Collecting localities for *Thomomys umbrinus* in the southwestern United States and western New Mexico (numbers refers to locality identification as given in text). Solid circles indicate localities for which both karyotypic and allozyme data are available; half-filled circles those for which only allozyme data are available; diagonally hatched circles are those for which only karyotypic data are available. The stippled region represents elevations above 6000 feet, the approximate lower boundary of pine forests.

Two measures have been employed to examine patterns of intrapopulation variability in genic characters: population type and population density. For the former each sampled population was ranked according to an estimation of the degree of geographic isolation exhibited with reference to adjacent populations located in the same general area. Populations which were well isolated in all directions, and hence which essentially existed as islands, were given a score of 1. Those which showed some level of interconnection, but in a more-or-less linear fashion (as along river courses), were given a rank of 2. And those occurring in broad areas of optimal habitat, and hence where genetic exchange would be relatively unrestricted in all directions were ranked as 3. Similarly, each sampled population was ranked according to the estimated density of animals per acre in the sample area. Density was determined by counting the number and placement of fresh earthen mounds present at the beginning of the sampling period.

Specimens representing 8 subspecies covering most of the northern and western distribution of *T. umbrinus* were examined by both methodologies (see map, Fig. 1). All specimens are preserved as standard museum vouchers (skin with skull) and are deposited in the mammal collections of the Museum of Vertebrate Zoology, University of California, Berke-

ley. Localites are given below; sample sizes for each technique are indicated (K = karyotype; A = allozyme). The numbers refer to geographic placement as indicated on the map, Fig. 1.

T. u. intermedius. — Arizona: [1] Madera Canyon, Santa Rita Mts. (K = 4); [2] Gardner Canyon, Santa Rita Mts. (K = 2); [3] Lyle Canyon Huachuca Mts. (K = 4); [4] Sycamore Canyon, Patagonia Mts. (K = 71; A = 43).

T. u. sonoriensis. — Sonora: [5] Moctezuma (K = 3; A = 24); [6] Sahuaripa (A = 6); [7] Bacanora (K = 1; A = 12); [8] El Novillo (K = 1; A = 21).

T. u. madrensis. — Chihuahua: [9] Colonia Garcia (K = 10; A = 26); [10] Valle Moctezuma (K = 6; A = 14); [11] Chuhuichupa (K = 1; A = 27); [12] Madera (A = 6).

T. u. juntae. — Chihuahua: [13] Sierra del Nido (K = 2; A = 2); [14] Cuauhtémoc (K = 3; A = 19).

T. u. chihuahuae. — Chihuahua: [15] Tomóchic (K = 3; A = 11); [16] Rancho El Pajarito (K = 3; A = 17); [17] Napuchis (K = 1); [18] El Vergel (K = 6; A = 16). Durango: [19] El Salto (K = 3; A = 22); [20] La Ciudad (K = 5; A = 23).

T. u. nelsoni. — Durango: [21] Las Nieves (K = 1; A = 14).

T. u. durangi. — Durango: [22] Morcillo (A = 13).

T. u. arriagensis. — San Luis Potosí: [23] Villa de Arriaga (K = 3).

Results and discussion

Karyotypic variation

Gross chromosomal characteristics are given for each of the 20 populations examined in Table 1. Although there is some variability within given sampled populations (e. g., Colonia Garcia [9]), the populations do break consistently into those with a diploid number of either 78 or 76. Within both of these groupings, however, considerable interpopulation variation may exist.

Table 1

Summary of karyotypic characteristics of populations of *Thomomys umbrinus*

Taxon	Locality Number	Number of ♂	Number of ♀	2n	Autosomes SM	Autosomes ST	Autosomes A	Autosomes micros	X	Y
intermedius	1	1	3	78	10	12	54	6	ST	dot
	2	2	0	78	8	12	56	6	ST	dot
	3	0	4	78	10	12	54	6	ST	-
	4	28	43	78	10	10	56	6	ST	dot
sonoriensis	5	1	2	78	10	12	54	6	ST	dot
	7	1	0	78	10	12	54	6	ST	dot
	8	1	0	78	10	12	54	6	ST	dot
madrensis	9	3	7	78	12	10-12	52-54	8-10	ST	dot
	10	0	6	76	42	32	0	0	ST	-
	11	0	1	76	42	32	0	0	ST	-
juntae	13	1	1	78	10	14	52	10	ST	dot
	14	0	3	78	10	14	52	10	ST	-
nelsoni	21	1	0	78	34	42	0	0	ST	dot
arriagensis	23	3	0	78	10	26	40	4	ST	dot
chihuahuae	15	1	2	76	42	32	0	0	ST	dot
	16	1	2	76	42	32	0	0	ST	dot
	17	1	0	76	20	24	30	0	SM	dot
	18	1	5	76	20	24	30	0	SM	dot
	19	0	3	76	40	34	0	0	ST	dot
	20	1	4	76	40	34	0	0	ST	dot

SM=metacentric and submetacentric; ST=subtelocentric; A=acrocentric

The major pattern found within the 2n = 78 group is one characterized by a low number of biarmed autosomes (20—24) and a large number of uniarmed autosomes (52—56), including 6 to 10 minute acrocentrics. The microelements are unique to these gophers among all populations of *T. bottae* and *T. umbrinus* examined (Patton 1972, 1973). This karyotypic class characterizes animals distributed largely from low to mid elevations in Sonora north through Arizona, New Mexico (C. S. Thaeler, Jr., pers. communication), and then south through central Chihuahua (Fig. 1). A slight modification of this theme was found in southwestern San Luis Potosí, where *T. u. arriagensis* typically has somewhat fewer acrocentrics (including only 4 minute acrocentrics) and more subtelocentric autosomes (Table 1). The sample from Las Nieves [21] (allocated to *T. u. nelsoni)* had a totally biarmed autosomal complement with no minute autosomal elements (Table 1).

The 2n = 76 group of *T. umbrinus* is similar in every respect to the general karyotype found in *T. bottae*. The pattern of interpopulation variation within both species is also similar. In *T. bottae,* populations are known which span the range in number of acrocentric autosomes from 0 to 19 pairs. The *T. umbrinus* 2n = 76 karyotypes reported here contained either 0 or 15 pairs of uniarmed autosomes.

Animals with the 2n = 76 karyotype were only found in the boreal forest zones of the Sierra Madre Occidental of Mexico from central Durango to northern Chihuahua. Interestingly, populations form the northern and southern portions of this sampled range share more gross karyotypic similarity (i. e., all have zero uniarmed autosomes and a subtelocentric X-chromosome) than those more centrally located (30 uniarmed autosomes and a submetacentric X-chromosome; see Table 1 and Fig. 1). It should be stressed that it is a member of the 2n = 78 group of *T. umbrinus (intermedius*; Patagonia Mts., Arizona) which is known to hybridize limitedly with *T. bottae* but with largely infertile offspring (Patton 1973). The degree of reproductive incompatability between the 2n = 76 *umbrinus* and the karyotypically similar *bottae* is not known. There is no area known where the two forms might be in contact.

In northern Chihuahua, the two diploid number classes of *T. umbrinus* probably meet. We have samples from within 6 airline miles of one another in the continuously forested northern extent of the Sierra Madre (2n = 76, Valle Moctezuma [10] and 2n = 78, Colonia Garcia [9]) without indication of genetic exchange between them (see below).

Allozyme analysis

Of the 23 loci examined electrophoretically, 19 were polymorphic in one or more population samples. Of the variable loci, 15 contained a major allele with a frequency of .95 or less (Table 2). Monomorphic loci included MDH-2, PGI, IPO, and Pt-A. Only four loci were consistently variable in the majority of populations (PGM, Est-1, Est-4, and preAlb); all other variable loci were polymorphic in only one or a few populations.

Intrapopulation variability. Table 2 provides estimates of overall genic variability in those 15 populations for which sample size is 10 or greater. The proportion of loci polymorphic per population ranges from 13 percent (Las Nieves [21]) to 44 percent (Rancho El Pajarito [16]) with an unweighted mean of 29 percent. The proportion of loci heterozygous per individual per population ranges from 2.2 percent (Las Nieves) to 10 percent (Rancho El Pajarito) with an unweighted mean across all samples of 5.9 percent. These estimates are equivalent to those of other rodents (Selander and Kaufman 1973; Selander et al. 1974). In comparison to other pocket grophers, *T. umbrinus* is intermediate in levels of intrapopulation varia-

Table 2

Allele frequencies for all polymorphic loci, where $p < .95$, for those population samples with N greater than 10. P is the total percentage of loci polymorphic per population sample and H is the percentage of loci heterozygous per indidual per population sample

Locus	Allele	Patagonia Mts. (4)	Moctezuma (5)	Bacanora (7)	El Novillo (8)	Colonia García(9)	Valle Moctezuma (10)	Chuhuichupa (11)	Cuauhtémoc (14)	Tomóchic (15)	Rancho El Pajarito (16)	El Vergel (18)	El Salto (19)	La Ciudad (20)	Las Nieves (21)	Moncillo (22)
LDH-1	104			.08							.09	.03				
	102					.04	.14									
	100	1.0	1.0	.92	1.0	.96	.86	1.0	1.0	1.0	.91	.97	1.0	1.0	1.0	1.0
MDH-1	100	1.0	1.0	1.0	.60	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.98	1.0	1.0	1.0
	64				.40								.02			
IDH-2	138							.02					.14	.11		
	100	1.0	1.0	1.0	1.0	1.0	1.0	.98	1.0	1.0	1.0	1.0	.86	.89	1.0	1.0
GOT-1	119															.08
	100	1.0	.94	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.97	1.0	1.0	1.0	.92
	89		.06													
	85											.03				
∝GPD	181		.02													
	154		.29		.17	.29				.64	.88					
	119	1.0	.69	1.0	.83	.71	1.0	1.0	.92	.36	.12	.72	1.0	1.0	1.0	1.0
	109								.08			.28				
Pept-1	106					.10										
	100	.89	1.0	1.0	1.0	.90	1.0	1.0	1.0	1.0	1.0	.94	.18		1.0	1.0
	89	.11										.06	.82	1.0		
SDH	-80								.03							
	-100	1.0	1.0	1.0	1.0	1.0			.97		.09					
	-129						1.0	1.0		1.0	.91	1.0	1.0	1.0	1.0	1.0
ADH	-100	1.0	1.0	.23	.31	.75			1.0					.02		
	-114			.77	.69	.25	1.0	1.0		1.0	1.0	1.0	.91	.98	1.0	1.0
	-121												.09			
6PGD	143					.04					.12					
	113	.01														
	100	.99	1.0	1.0	1.0	.90	1.0	.98	1.0	1.0	.88	1.0	1.0	.91	1.0	1.0
	86					.06										
	67							.02						.09		
PGM	145						.71	.65		.27		.13				
	131					.04	.29	.35		.09	.17	.03				
	100	1.0	1.0	1.0	.93	.96			1.0	.64	.68	.84	1.0	1.0	1.0	.96
	69															.04
	46				.07						.15					
Est-1	106						1.0	1.0	.14	.05	.12	.53	.59	.57	.08	.27
	100	1.0	1.0	1.0	.80	.69			.83	.75	.79	.47	.41	.43	.56	.68
	94				.20	.31			.03	.20	.09				.36	.05
Est-4	110								.08			.03				
	106	.02											.05			
	102	.02			.41											
	100	.05				.17	.11	.42	.31	.05	.27	.91	.84	.87	.92	.86
	96	.01														
	95	.88	.90	.99	.52	.08	.89	.41	.47	.86	.50	.06	.11	.13	.08	.14
	89	.01		.01	.07	.73		.17	.14	.09	.23					
	84		.10													
	80					.02										
Alb	104								.03					.02		1.0
	103.5	1.0	.73	.71	1.0	.79		.09	.97	.14	.15				1.0	
	103					.21	1.0	.91		.86	.85	1.0	1.0	.98		
	100		.27	.29												
preAlb	101					.17							.23	.23		
	100					.77			.41			.44	.77	.77	1.0	.89
	98	1.0	.57	.87	1.0	.06	.96	.91	.50	1.0	1.0	.56				.11
	97		.43	.13			.04	.09	.09							
Trf	132	1.0	1.0	1.0	1.0					.05	.06	1.0	1.0	1.0	1.0	1.0
	121					1.0	1.0	1.0	1.0	.95	.94					
P		22.2	26.1	26.1	26.1	39.1	21.8	34.8	34.8	26.1	43.5	34.8	30.4	30.4	13.0	21.8
H		2.7	5.6	6.1	9.5	7.4	3.4	6.8	6.0	5.2	10.0	7.1	8.3	5.9	2.2	3.0

bility between a high in *T. bottae* ($\bar{H}$ = 9.3 percent; PATTON and YANG in press) and a low in *T. "talpoides"* ($\bar{H}$ = 4.7 percent; NEVO et al. 1974).

While the factors involved in the maintenance of protein polymorphism in natural populations remain unclear (see review by LEWONTIN 1974), two general hypotheses have been advanced to explain patterns observed in pocket gophers and other fossorial rodents. NEVO (NEVO and SHAW 1972; NEVO et al. 1974) has argued that the relatively low genic variability values often characterizing fossorial rodents in general are best explained as an adaptive strategy for homozygosis in response to the relatively uniform subterranean environment encountered (niche width variation hypothesis). An alternative explanation was put forward recently (PATTON and YANG in press) based on the interaction between the breeding structure and effective size of populations. It is basically a random genetic drift model with large populations occupying broadly contiguous areas able to maintain higher levels of variability than small, well-isolated ones.

Since all obligate fossorial rodents (e. g. members of the families Geomyidae and Spalacidae, for example) live in constant burrow micro-environments, the niche width-variability hypothesis would predict a consistently low level of genic variability in all species. Exceptions to this predicted relationship would prove fatal to the model. While such a relationship has indeed been found for *Spalax* (NEVO and SHAW 1972) and for the "*talpoides*" group of *Thomomys* (NEVO et al. 1974), such is decidedly not the case for *T. bottae* (PATTON and YANG in press). The latter species has twice the average intrapopulation variability than other fossorial species and is one of the most variable mammals known. The data presented here for *T. umbrinus* also do not support the narrow niche-low variability expectation. While the species is less variable on the average than *T. bottae,* it is fully as variable as non-fossorial rodents (overall mean $\bar{H} \sim 5.5$ percent; SELANDER et al. 1974). Indeed, with the total data base now available for fossorial rodents (including *Spalax, Thomomys,* and *Geomys),* the mean and distribution of heterozygosity values (unweighted $\bar{H}$ = .053; range, .037—.093) is not significantly different from that of non-fossorial rodents (see SELANDER et al. 1974). Hence, the niche width-variability hypothesis cannot by itself account for the observed levels of intrapopulation genic variability in fossorial rodents.

On the other hand, data available for *T. umbrinus* are consistent with a random genetic drift model with the degree of population connectedness (i. e., gene flow) and population size the key determinants. Of a series of geographic, ecologic, and demographic factors examined to explain heterozygosity patterns in *T. bottae,* only a qualitative assessment of the breeding structure of populations and an estimation of population density showed significant relationships (PATTON and YANG in press). These same two parameters are also important features of the population variability pattern of *T. umbrinus.* The relationship between $\bar{H}$ and both breeding structure

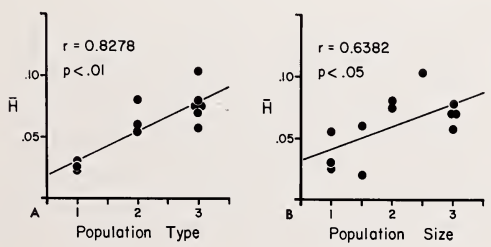

Fig. 2. Relationship between average individual heterozygosity per population sample (H) and population type (A) and population size (B). Lines have been fitted by the least squares method. „Population Type" is a measure of the estimated degree of connectedness (= gene flow) between populations over geography (see PATTON and YANG, in press, and text). „Population size" is the ranked estimated density per acre of pocket gophers at each collecting locality (see text).

and density is shown in Fig. 2. As can be noted, a strong, positive relationship exists in both cases such that $\bar{H}$ is predictably higher in large, rather continuously distributed populations than in small, well-isolated ones. In a general sense, the

Table 3

Coefficients of genic similarity (S-values) above the diagonal and genetic distance (D-values) below the diagonal between 18 populations of *Thomomys umbrinus*

Numbers identifying samples are as indicated on the map, Fig. 1 and in the text

	Patagonia Mts. (4)	Moctezuma (5)	Bacanora (7)	Sahuaripa (6)	El Novillo (8)	Colonia Garcia (9)	Sierra del Nido (13)	Cuauhtémoc (14)	Las Nieves (21)	Moncillo (22)	Valle Moctezuma (10)	Chuhuichupa (11)	Madera (12)	Tomochic (15)	Rancho El Pajarito (16)	El Vergel (18)	El Salto (19)	La Ciudad (20)
4	----	.945	.936	.942	.928	.826	.800	.857	.859	.810	.684	.672	.733	.774	.750	.767	.734	.725
5	.017	----	.929	.901	.901	.844	.783	.839	.841	.810	.686	.679	.733	.774	.750	.769	.723	.714
7	.033	.038	----	.965	.903	.816	.808	.876	.881	.849	.724	.711	.764	.807	.788	.803	.763	.754
6	.035	.053	.007	----	.914	.813	.813	.883	.889	.840	.717	.703	.762	.805	.790	.794	.754	.745
8	.022	.036	.035	.033	----	.843	.797	.847	.857	.812	.682	.686	.734	.779	.763	.771	.723	.711
9	.131	.122	.146	.143	.125	----	.870	.880	.843	.815	.702	.721	.744	.786	.786	.747	.723	.729
13	.192	.197	.171	.168	.181	.073	----	.892	.909	.845	.698	.724	.749	.763	.763	.775	.759	.748
14	.116	.125	.074	.070	.104	.060	.055	----	.891	.842	.748	.767	.804	.830	.830	.804	.756	.761
21	.129	.131	.088	.085	.110	.115	.068	.075	----	.930	.675	.699	.721	.751	.751	.852	.836	.840
22	.181	.172	.125	.135	.158	.157	.126	.126	.051	----	.670	.693	.711	.745	.740	.847	.826	.830
10	.366	.341	.299	.311	.334	.304	.323	.248	.368	.376	----	.964	.929	.901	.886	.800	.722	.731
11	.371	.347	.309	.316	.328	.273	.277	.232	.330	.341	.010	----	.926	.891	.898	.815	.744	.750
12	.287	.266	.227	.238	.261	.234	.254	.184	.302	.305	.045	.046	----	.934	.937	.817	.738	.745
15	.215	.206	.158	.166	.196	.185	.229	.128	.249	.254	.060	.067	.022	----	.947	.842	.765	.771
16	.233	.217	.176	.178	.204	.173	.217	.132	.241	.248	.068	.061	.020	.012	----	.833	.760	.761
18	.219	.219	.164	.171	.197	.231	.200	.180	.121	.123	.174	.149	.150	.118	.115	----	.902	.908
19	.273	.274	.225	.238	.267	.256	.222	.223	.140	.148	.266	.240	.247	.198	.200	.061	----	.979
20	.288	.293	.241	.253	.286	.274	.241	.237	.155	.161	.284	.258	.253	.214	.216	.046	.002	----

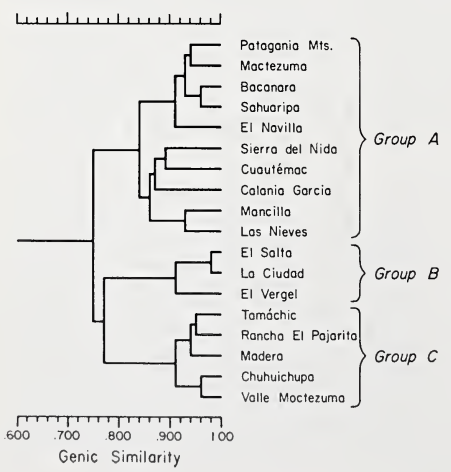

Fig. 3. Phenogram of population relatedness based on UPGMA clustering of Rogers' genic similarity coefficients (S-values) for the allozyme data. The samples are divided into three nearly equally distinct yet internally homogeneous clusters at the 80 percent similarity level.

same pattern was observed by PENNEY and ZIMMERMANN (1976) for the pocket gopher, *Geomys bursarius,* although they curiously attributed the observed H levels in that species to both selection for a uniform niche and random events.

Interpopulation variability. Estimates of genetic relatedness between all population pairs were made using both ROGERS' (1972) similarity and NEI's (1971) distance measures (S and D-value, respectively). These data are given in Table 3 and a phenogram based on S-values and clustered by the unweighted pair group method is presented in Fig. 3.

Two features are quite apparent from these data. Most striking is the low level of genic similarity between the sampled populations of *T. umbrinus.* The average population pair shares only 80 percent similarity with a range between all pairs of 67 to 98 percent (NEI's $\bar{D}$ = .181, range .002 [El Salto-La Ciudad] to .376 [Valle Moctezuma-Morcillo]). While these values are generally low for conspecific populations of most rodent or other mammal species, they are very comparable to interpopulation similarity measures observed in 50 populations of *T. bottae* (PATTON and YANG in press). In the latter, the average population pair shares 79 percent similarity with an overall range of 63 to 97 percent.

The other major feature apparent from Fig. 3 is the obvious separation of *T. umbrinus* populations into three quite distinct but internally homogeneous clusters. These groupings have both geographic consistency and internal karyotypic homogeneity. The most divergent cluster (labeled Group A in Fig. 3) contains all of the 2n = 78 populations whereas the 2n = 76 populations are divided into two groups of nearly equivalent level of divergence (Groups B and C, Fig. 3). The average within group S-values are quite high ($\bar{S}$ = .864 ± .047 st. dev., .930 ± 043, and .930 ± .032 for within Group A, B, and C comparisons, respectively) while the between group average similarity is significantly lower ($\bar{S}$ = .751 ± .004 for comparisons between Groups A, B, and C).

The major phenetic clusters depicted in Fig. 3 are composed of populations which are distributed in a circumscribed geographic fashion. Group A, the 2n = 78 cluster, occurs generally at low to mid elevations in desertscrub-desert grassland-woodland habitats to the west, north, and east of the Sierra Madre Occidental. Both 2n = 76 groups are confined to the boreal forest zones of the Sierra Madre proper: Group B is largely south of the Barranca del Cobre (the "Grand Canyon of Mexico") of south-central Chihuahua, and Group C is north of that potential barrier. Populations of Groups A and C are in very close proximity at the extreme northern end of the Sierra Madre in Chihuahua (see Fig. 1).

The concordance between the chromosomal and genic divergence data strongly suggest that the sampled populations of *T. umbrinus* represent more than one species. In particular, the magnitude of the chromosomal differences recorded (Table 1) is equivalent to that known to differentiate *T. umbrinus* (subspecies *intermedius)* and *T. bottae.* Although these populations are known to hybridize, the hybrids are largely sterile due to meiotic imbalances, and genic introgression is non-existent (PATTON et al. 1972; PATTON 1973).

A definitive analysis of the level of reproductive compatability between contact populations of any of the *T. umbrinus* genetic groups is not now available. Nevertheless, three aspects of the current data set do bear on this question. Frist, the pattern of regional differentiation at individual loci is not one of high between-locus concordance. This is to say, the geographic units distinguished at one locus are not necessarily the same delineated by other loci. Examples of this between loci pattern difference are given in Fig. 4. Here, for example, while the 2n = 76 populations are largely distinguished from the 2n = 78 samples at the Alb and SDH loci, the groupings of populations are quite different at the αGPD and Trf loci.

A pattern of greater concordance at individual loci would be expected if the overall genetic groupings do represent more than one species. Similarly, even at those loci which do generally distinguish regional groups, the distinctive alleles are often shared by other genetic units (for example, Alb-103.5 is dominant in Group A yet found in moderate to low frequency in populations of Group C; αGPD-109 is shared between a 2n = 76 [Group B] and a 2n = 78 group population; and so forth, see Fig. 4).

A second way to examine for potential interbreeding ability between genetic groups is to relate the overall pair-wise similarity level to a measure of ecogeographic distance between the populations sampled (see above). The pattern of geographic relationship at the genic level is often strongly influenced by the distance between populations, particularly over regions of somewhat uniform habitat (see Levin and Kerster 1974; Selander and Kaufman 1975; Patton and Yang in press). In the present situation, a negative relationship should be seen between genic similarity and distance within given genetic groups,

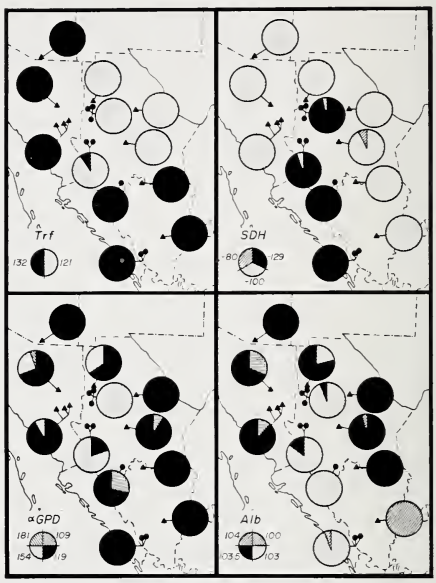

Fig. 4. Geographic pattern of allele frequency variation at four genetic loci (Trf, SDH, α GPD, and Alb). Triangles represent 2n = 78 population samples; circles represent 2n = 76 samples.

if they are reproductively internally compatible, while such a relationship should not be expected between populations belonging to different reproductive units, if isolation is indeed complete. This prediction is based on the likelihood that gene flow between gopher populations follows an isolation by distance model (Wright 1943). Hence, adjacent interbreeding populations should be more similar than non-adjacent but potentially interbreeding ones while the level of genic similarity will be independent of distance if the populations are reproductively isolated.

Figure 5 illustrates the relationship between pair-wise population genic distance which incorporates both airline and ecologic distance (see above and Patton and Yang in press). Three relationships are plotted; within the 2n = 78 group, within the 2n = 76 group, and between populations of both groups. Note that for both of the within-group comparisons there is a very strong negative relationship, such that S decreases with an increase in distance between populations. These relations are not strictly linear, but rather suggestive of an exponential relationship, and thus match expectations of an isolation by distance model. The steeper slope for the 2n = 76 group is a function of the observed sharp changes in overall similarity across a region of relatively uniform habitat. In reality, however, this section of the Sierra Madre Occidental is deeply dissected by mayor canyon systems (see Fig. 1) so that the populations examined are not nearly as continuous as our measure of ecogeographic distance would suggest.

If the between-group relationship, however, is compared to both of the within-group patterns, the picture is considerably different. For the former, the majority of

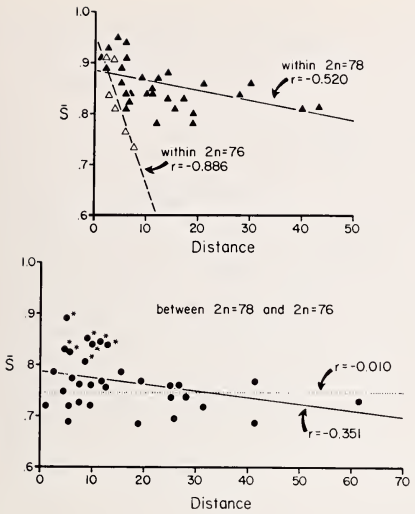

Fig. 5. Relationship of the between-pair genic similarity value (S) and a measure of the ecogeographic distance between each population pair (see text). Uper figure illustrates this relationship for the within 2n = 78 and within 2n = 76 group comparisons. The lower figure shows the relationship between the 2n = 78 and 2n = 76 population pairs. For the latter, the asterisks distinguish the 8 population pair comparisons in southern Chihuahua and Durango. The solid line represents the relationship between all points on the lower graph; the dotted line represents that relationship excluding the 8 pairs indicated by asterisks. All lines were fitted by the least squares method.

S-values are about 10 percent lower and there is very little relationship between genetic and ecogeographic distance. In other words, the average between-group pairwise S-value is about .750 regardless of ecogeographic distance. This observation fits the expectation if indeed the 2n = 76 and 2n = 78 groups are genetically isolated. However, one series of population comparisons do provide exceptions to this general picture. The comparisons of Cuauhtémoc [14], Las Nieves [21], and Morcillo [22] (of the 2n = 78 group) with the Tomóchic-Rancho El Pajarito [15–16], El Vergel [18], and El Salto-La Ciudad [19–20] samples (2n = 76 group) show distinctly higher levels of similarity relative to other between-group pairs (see Fig. 5). This pattern is significant since the two sets of populations involved occur geographically adjacent from central Chihuahua south into Durango, thus suggesting some gene exchange along the eastern slope of the Sierra Madre in this region. The somewhat lower genic similarity for this set of populations as a group compared to within 2n = 78 or 2n = 76 group populations of the same ecogeographic distance may either be a result of very limited occasional contact, and hence opportunity for gene flow, or the development of partial levels of reproductive isolation between the two forms in question.

Finally, the data for the 2n = 78 and 2n = 76 populations which are in near contact in the northern Sierra Madre (Colonia Garcia [9] versus Valle Moctezuma [10] and Chuhuichupa [11]) also suggest some degree of reproductive incompatability between these chromosomal forms. The Colonia Garcia sample is approximately 6 airline miles north of Valle Moctezuma, yet the two share only 70 percent genic similarity (Table 2). The two populations are apparently fixed for different alleles at both the SDH and Est-1 loci, although in both cases the Colonia Garcia allele is found in other 2n = 76 populations (e. g., Madera [12]). Hence, while these data are strongly suggestive of a high degree of reproductive isolation between the 2n = 78 and 2n = 76 chromosomal groups in the region, they are not conclusive.

Despite indications of gene flow in certain areas, the overall pattern of population divergence suggests that the level of reproductive isolation achieved by the different chromosomal groups may be largely a function of which pair of adjacent populations is involved. It would not necessarily be unexpected, therefore, to find with additional studies that the 2n = 78 and 2n = 76 populations are rather completely isolated in

the northern Sierra Madre but much less so further to the south in southern Chihuahua and Durango. Future field tests are necessary to clarify the possibility and extent of gene flow between the various geographic segments of these chromosomal units.

Genetic versus phenetic similarity

The concordance between both chromosomal and genic similarity measures strongly suggests that the sampled populations of *T. umbrinus* represent more than one species. The surprising fact, however, is the rather inconsistent relationship between these two measures of genetic divergence and exomorphological differentiation based on standard external and cranial morphology and pelage color variation. The only area for which a comparable modern systematic treatment of variation within and between *T. umbrinus* populations has been undertaken is the Mexican state of Chihuahua. Here, Anderson (1972) has thoroughly reviewed the patterns of morphological variation and recognizes six subspecies, each of which is internally rather homogeneous from a morphological standpoint. The suggested relationship between populations based on genetic data presented here and the morphological criteria used by Anderson deviate from one another in several significant features. Specifically, Anderson allocates populations representing both the Group A and C or Group B and C genetic units into the same subspecies (*madrensis* and *chihuahuae*, respectively). This implies that, in terms of gross morphology, there is little external difference between the populations so allocated yet the underlying genetic distance may be extreme. While a complete understanding of this lack of concordance between genetic and phenetic patterns of similarity remains to be achieved, we would suggest that the discordance is largely due to the radically different selective regimes (or lack thereof) impinging upon the expression of variability pattern at each organizational level. Specifically, overall pelage color, body size, and conceivably cranial shape are likely to vary directly with external environmental characters, such as soil color, depth, and friability. On the other hand, variation at the chromosome and genic levels are likely to be more independent of these pressures and perhaps related more to demographic features, mode of divergence, and time since divergence. Thus, populations inhabiting rather uniform habitat conditions over distance may indeed be very similar in external morphology yet, because of historical accident, be quite divergent genetically.

Acknowledgements

Appreciation is extended to Suh Y. Yang, John W. Wright, Michael D. Robinson, and Donald O. Straney for valuable suggestions and/or critical examination of the manuscript. Carol P. Patton and John W. Wright provided invaluable aid in the field and Margaret F. Smith provided laboratory assistance. Collecting permits were kindly made available by the State of Arizona Department of Game and Fish and the Dirección Generál de la Fauna Silvestre, Departmento de Conservación, México, D. F., México. Financial assistance was provided by the National Science Foundation (DEB 76-09685 to JLP).

Summary

Data on chromosomal and genic (= allozyme) variability are given for populations of the pocket gopher, *Thomomys umbrinus*, in the northern and western portion of the species range. Two distinct karyotypic patterns are represented with populations having either 2n = 78 od 2n = 76, although there is interpopulation variation in both diploid number groups. These two chromosomal units correspond as well to sets of populations delimited by electrophoretic criteria. For the allozyme data, however, while the 2n = 78 group shows genic homogeneity, two very distinctive units with 2n = 76 are recognizable. If all samples are considered, there is a wide range in observed levels of genic similarity between populations (mean, 80 percent; range, 67—97 percent). However, similarity values

between populations belonging to each chromosomal type are considerably higher (within-group genic similarity averages 90 percent; between-group average similarity is 75 percent).

The concordance of these data suggest that the populations examined belong to more than one biological species. Although this hypothesis must be tested by analysis of the genetic consequences of populations in contact, the allozyme data do suggest at least occasional gene exchange between some member populations of each differentiated group. Gene flow appears to be more probable along the eastern slope of the Sierra Madre Occidental in southern Chihuahua and Durango than in the Sierra Madre of northern Chihuahua. In the latter area, samples of the 2n = 78 and 2n = 76 chromosomal forms were collected within 6 airline miles of one another.

Average individual heterozygosity is 5.9 percent. This level of intrapopulation variation is equivalent to that recorded for rodents in general. Hence, the data argue against the narrow niche-low variability hypothesis developed by Nevo (Nevo et al. 1974) as a general model predicting genic variability in fossorial rodents. Indeed, the pattern of variability observed for *T. umbrinus* is identical to that recorded earlier for *T. bottae* (Patton and Yang in press). For both species, the best predictors of overall population genic variation are the density and breeding structure of the populations sampled. This suggests that random events are particularly important in the genic structuring of gopher populations, regardless of whether the alleles involved are under natural selection or not.

Zusammenfassung

Genetische Unterschiede zwischen Populationen von Thomomys umbrinus (Richardson)

Es werden Daten über die chromosomale und genetische Variabilität von Populationen von *Thomomys umbrinus* aus dem nördlichen und westlichen Teil des Verbreitungsgebietes der Art mitgeteilt. Die Populationen weisen mit entweder 2n = 78 oder 2n = 76 zwei deutlich unterscheidbare Karyotypen auf, obgleich zwischen den Populationen innerhalb dieser beiden Gruppen erhebliche chromosomale Unterschiede vorkommen. Die durch den Karyotypus gekennzeichneten zwei Gruppen entsprechen solchen, die sich auch durch elektrophoretische Kriterien abgrenzen lassen. In bezug auf die Allozymdaten zerfällt die Gruppe mit 2n = 76 in zwei verschiedene Untergruppen, während die Gruppe mit 2n = 78 in dieser Hinsicht homogen ist. Bei Berücksichtigung aller Proben ist erkennbar, daß genetische Ähnlichkeit zwischen den Populationen in sehr unterschiedlichem Ausmaß vorliegt (Homogenitätsgrad im Mittel: 80 %; Bereich: 67 % bis 97 %). Zwischen den Populationen innerhalb jeweils einer der beiden durch den Karyotypus gekennzeichneten Gruppen jedoch ist die genetische Homogenität beträchtlich höher (innerhalb einer Gruppe durchschnittlich 90 %, zwischen den Gruppen durchschnittlich 75 %).

Die Übereinstimmung der Befunde weist darauf hin, daß unter den untersuchten Populationen mehr als eine biologische Spezies vertreten ist. Diese Hypothese muß jedoch noch durch Untersuchung der genetischen Konsequenzen, die sich bei untereinander in Kontakt stehenden Populationen ergeben, geprüft werden. Die Allozymdaten deuten bereits auf einen zumindest gelegentlichen Genaustausch zwischen Populationen innerhalb der einen oder anderen Gruppe hin. Ein solcher Genaustausch ist längs des östlichen Hanges der Sierra Madre Occidental im südlichen Chihuahua und im Durango wahrscheinlicher als in der Sierra Madre der nördlichen Chihuahua. In diesem zuletzt genannten Gebiet wurden Proben der Gruppen mit 2n = 78 und 2n = 76 in einer Entfernung von 6 Flugmeilen voneinder gesammelt. Der durchschnittliche indiviuelle Heterozygotiegrad beträgt 5,9 %. Dieses Ausmaß an Variabilität innerhalb einer Population gleicht derjenigen, die für Nager im allgemeinen gilt. Diese Befunde lassen die Richtigkeit der von Nevo entwickelten Hypothese (Nevo et al. 1974) in Zweifel ziehen; danach soll die Beziehung: „enge Nische = geringe Variabilität" als ein allgemeines Modell Vorhersagen über die genetische Variabilität bei grabenden Nagern erlauben. Die Variabilität, die hier für *Thomomys umbrinus* beobachtet wurde, entspricht in der Tat vollkommen der früher für *Thomomys bottae* nachgewiesenen (Patton und Yang, im Druck). Für beide Spezies erfolgt die Vorhersage der generellen genetischen Variabilität einer Population am besten unter Berücksichtigung ihrer Dichte und Fortpflanzungsverhältnisse. Dieses deutet darauf hin, daß Zufallsereignisse für die genetische Struktur von *Thomomys*-Populationen von besonderer Wichtigkeit sind, gleichgültig, ob die betreffenden Allele selektiv bevorteilt sind oder nicht.

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