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Thomomys bottae pocket gophers of the central Rio Grande Valley, New Mexico: local differentiation, gene flow, and historical biogeography

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ABSTRACT

Representatives of two strongly differentiated geographic units within *Thomomys bottae* come in contact along the Rio Grande south of Albuquerque, New Mexico. The two forms share an average genic similarity of only 69%, and differ in karyotype by as much as 17 pairs of uniarmed autosomes. This high level of genic and chromosomal differentiation might suggest extremely limited introgression, or perhaps none at all. However, diagnostic alleles at several strongly differentiated loci were detected in contact zone populations of the opposite group, indicating that some gene flow does occur. Suitable habitat and available land area are limited in the zone of contact, and these factors, in combination with the structure of local breeding populations of pocket gophers, contribute to restriction of gene flow through the contact zone. The measured width of the contact zone corresponds reasonably well with predictions derived from a neutral diffusion cline model under current estimates of gene flow rates and time of secondary contact.

INTRODUCTION

Strongly differentiated geographic units within the pocket gopher *Thomomys bottae* were described by Patton and Yang (1977) based on karyotypic and allozymic data. Through analyses of contact zones between these genetically defined geographic units (cf., Patton et al., 1979; Smith and Patton, 1980), we hope to gain a better understanding of the dynamics and evolutionary consequences of morphologic, karyotypic, and allozymic divergence within the species. Our current view of relationships among the genetic units is given in Fig. 1. A population group (labelled E in Fig. 1) representative of the low uniarmed karyotypic form of gopher with northern and western genic affinities comes in contact with a population group (labelled K in Fig. 1) representative of the high uniarmed, southern allozymic group along the Rio Grande south of Albuquerque, New Mexico. These two forms share an average genic similarity of only 0.687, a higher level of differentiation than that found between intraspecific units and even between species of most other mammals.

Thomomys b. connectens is a large gopher, with yellowish tan pelage, found along the Rio Grande in the Albuquerque Basin of central New Mexico. Hall (1936) considered *T. b. connectens* to be most closely related to *T. b. aureus,* found in the Four Corners area (junction of New Mexico, Colorado, Utah, and Arizona). It has a diploid number of 76 with all biarmed autosomes. *Thomomys b. opulentus* is a somewhat smaller, slightly more reddish–brown colored gopher found along the Rio Grande south of the Albuquerque Basin to

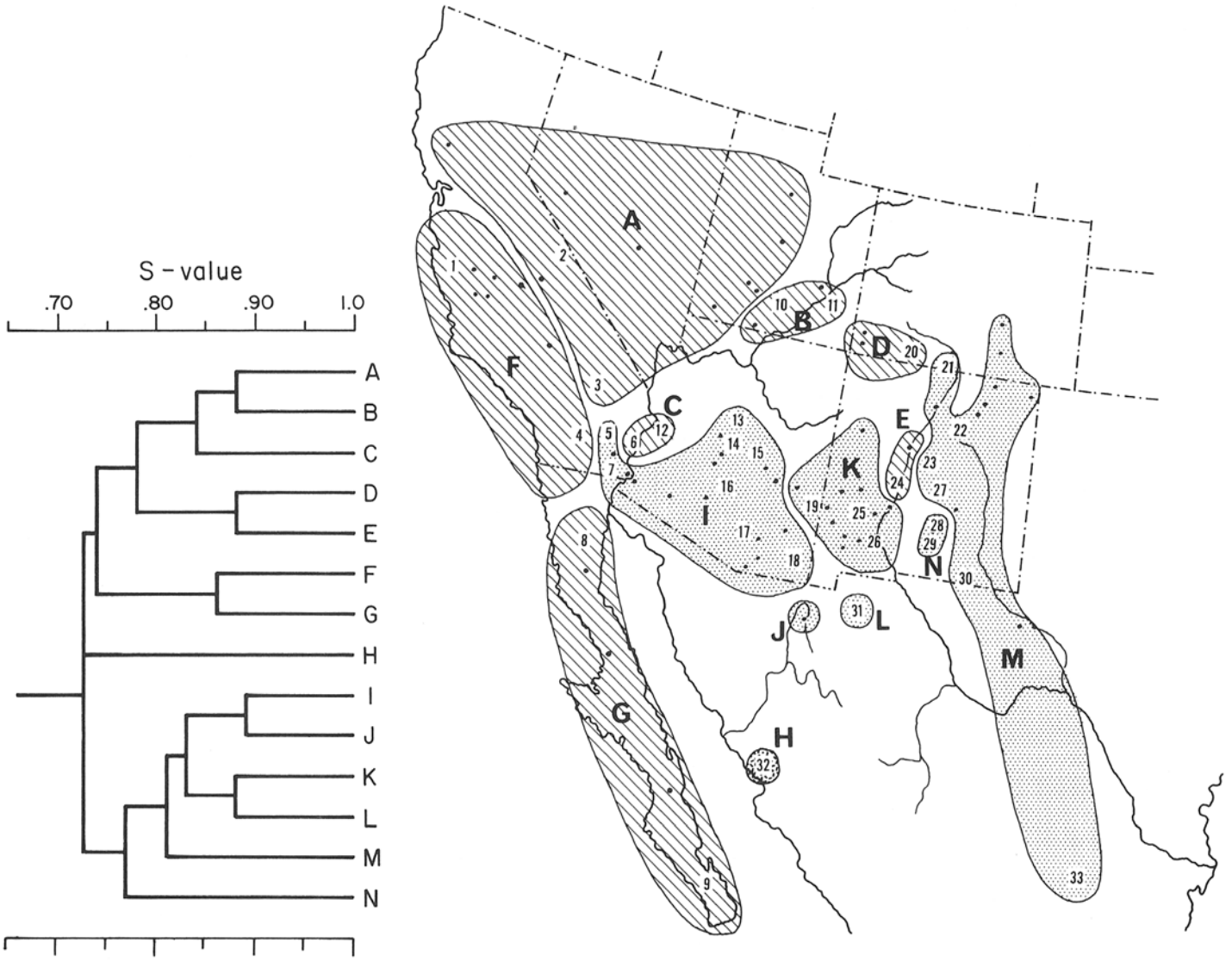

Fig. 1. Geographic units of *T. bottae* defined by electromorphic characters. Populations included within each major unit cluster by UPGMA at a level greater than 0.90 Rogers' similarity (S–value). UPGMA clustering of geographic units is shown in the phenogram.

Las Cruces. This form was considered by Goldman (1935) to be related to montane populations to the west *(T. b. fulvus)* and to the east *(T. b. ruidosae)*. This southern form also has a diploid number of 76, but with 24 to 34 uniarmed autosomes. Sampling along the Rio Grande Valley, Follingstad (cited in Findley et al., 1975:145–146) recorded sharp breaks in hind foot length and pelage color between populations of *T. b. connectens* and *T. b. opulentus*.

The extreme degree of chromosomal and genic differentiation between the two races suggests that they may be reproductively isolated. However, studies of other contact zones in *T. bottae* involving similar levels of karyotypic (Patton et al., 1979) and/or genic (Smith and Patton, 1980) differentiation demonstrate that such levels of divergence do not necessarily indicate reproductive incompatibility. Instead, even extreme levels of genetic differentiation may be due to the history and demography of the populations and to the geographic setting of the zone of contact between fully introgressing forms.

METHODS AND MATERIALS

Allozymic Analysis

Kidney extracts, and plasma and hemolysate fractions of blood were assayed using horizontal starch gel electrophoresis following the procedures of Selander et al. (1971), Patton et al. (1972), and Patton and Yang (1977). Twenty proteins encoded by 24 presumptive gene loci were analyzed. The loci examined were the same as those listed in Patton and Yang (1977) except

that Adh was scored in kidney rather than liver, Protein A and Peptidase–2 were eliminated, and three new loci were added: nucleoside phosphorylase (Np), aconitase–1 (Acon–1), and mannose phosphate isomerase (Mpi) (Harris and Hopkinson, 1976). A total of 280 individuals drawn from 14 populations of *T. b. connectens* and *T. b. opulentus* was examined.

Karyotypic Analysis

Forty–five individuals drawn from 12 populations were karyotyped using standard methods (Patton, 1967).

Morphometric Analysis

Thirteen cranial measurements taken with dial calipers from cleaned skulls and four external body measurements were used. The characters were the same as those described in Patton et al. (1979) except that ear length (EL) and bullar width (BuW) were eliminated, and body length (BL, total length minus tail length) and premaxillary length (PM, from anterior tip of nasals to posterior extension of premaxillae on dorsal surface of skull) were added. Only specimens judged to be adult by closure of the supraoccipital–exoccipital and basisphenoid–basioccipital sutures (Hoffmeister, 1969) were utilized in the analysis. A total of 145 individuals drawn from 15 localities was used in this analysis.

Pelage Color Analysis

Variation in middorsal pelage color of 166 individuals from 15 localities was examined by use of a Bausch and Lomb Spectronic 505 recording spectrophotometer equipped with a visible reflectance attachment. Measurements were made at 100% transmittance with a port size of 31 mm. Values for dominant wavelength (= hue), relative brightness (= value), and excitation purity (= chroma or saturation) were computed for each specimen judged to have adult pelage.

Statistical Procedures

The morphometric and pelage color data were analyzed independently using the discriminant analysis program of SPSS (Nie et al., 1975). Only those discriminant functions with eigenvalues greater than one were used in the analyses reported here (Gutman's lower bound criterion; Mulaik, 1972:141). Males and females were treated separately in the analysis of mensural characters due to secondary sexual variation. Estimates of genetic relatedness among populations were made using Rogers' (1972) genetic similarity coefficient (S–value). Clustering of the resulting similarity matrix was performed using the unweighted–pair–group method with arithmetic averages (UPGMA; Sneath and Sokal, 1973).

Specimens Examined

All specimens are preserved as standard museum vouchers (skin with skull, skull only, or skeleton only) and are deposited in the Museum of Vertebrate Zoology. Sample localities are listed below by number or letter and are indicated on the map (Fig. 2). Reference samples A–E are taken from Patton and Yang (1977); samples F–J are based on unpublished data. Sample sizes for each analysis are indicated (M = morphometric, P = pelage color, E = electrophoretic, K = karyotypic).

Thomomys bottae connectens

NEW MEXICO: [1] *SANDOVAL CO.:* Sandoval (M = 2, P = 2); [2] *BERNALILLO CO.:* Albuquerque, jct. N Coors Rd. and Paradise Hills Blvd. (M = 5, P = 6, E = 13); Albuquerque, 5 mi. N (M = 5, P = 5); Albuquerque, 4.5 mi. S (M = 1); Albuquerque, Simm's Farm, Rio Grande Blvd., 7 mi. NW Univ. New Mexico (M = 2, P = 2); Parjarito (M = 1, P = 2); *SOCORRO CO.:* [3] Bernardo, 1.2 mi. E (M = 11, P = 10, E = 19, K = 3); Bernardo, 1 mi. S (M = 2, P = 2); [4] La Joya, 1 mi. S (M = 13, P = 23, E = 23, K = 9); [5] La Joya, 2.5 mi. S (M = 19, P = 18, E = 32, K = 4); [6] La Joya, 4 mi. S (M = 7, P = 10, E = 20, K = 4); [7] La Joya, 3.5 mi. S, west side of Rio Grande (M = 18, P = 18, E = 37, K = 8).

Thomomys bottae opulentus

NEW MEXICO: *SOCORRO CO.:* [8] San Acacia Dam (M = 4, P = 4, E = 4); [9] San Acacia (M = 10, P = 11, E = 27, K = 1); [10] Escondida (M = 5, P = 5, E = 8, K = 1); [11] Socorro (M = 7, P = 11, E = 15, K = 5); [12] San Antonio (M = 5, P = 8, E = 11, K = 2); [13] San Marcial (M = 9, P = 9, E = 17, K = 2); [14] *SIERRA CO.:* Truth or Consequences (M = 7, P = 8, E = 16, K = 3); [15] *DOÑA ANA CO.:* Radium Springs (M = 12, P = 12, E = 26, K = 3).

Thomomys bottae fulvus

NEW MEXICO: *GRANT CO.:* [A] Iron Creek, Black Range (E = 30); [B] Rocky Canyon, Black Range (E = 12); [C] *MCKINLEY CO.:* Zuni Mts., Sawmill Canyon (E = 6).

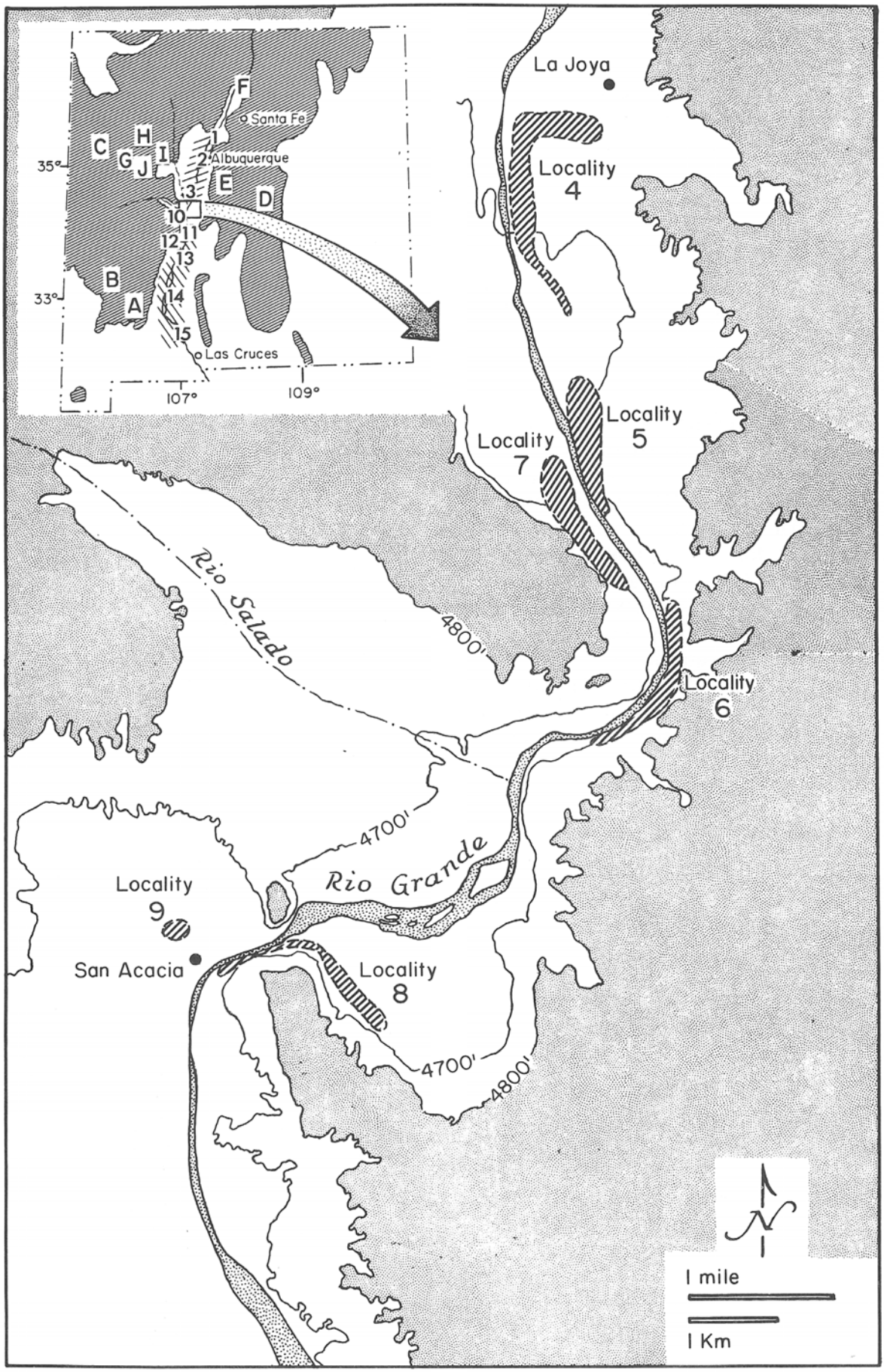

Fig. 2. Sample localities of pocket gophers, *Thomomys bottae,* from New Mexico. Localities are indicated by number (Rio Grande Valley samples), or by letter (reference samples from elsewhere in New Mexico; see Specimens Examined). In the inset map of New Mexico, the area above the 6000 foot contour is shaded. Sample localities 1–7 are of *T. b. connectens* and 8–15 are *T. b. opulentus*.

Thomomys bottae actuosus

NEW MEXICO: [D] *LINCOLN CO.:* Gallinas Mts., Red Cloud Canyon, 2 mi. S Rough Mt. (E = 20); [E] *TORRANCE CO.:* Manzano Mts., 7 mi. NW Tajique (E = 19).

Thomomys bottae pervagus

NEW MEXICO: [F] *RIO ARRIBA CO.:* Alcalde (E = 11).

Thomomys bottae morulus

NEW MEXICO: [G] *VALENCIA CO.:* San Rafael, 13.1 mi. S (E = 14).

Thomomys bottae planorum

NEW MEXICO: [H] *VALENCIA CO.:* San Mateo (E = 12).

Thomomys bottae paguatae

NEW MEXICO: [I] *VALENCIA CO.:* Cebolleta (E = 10).

Thomomys bottae collis

NEW MEXICO: [J] *VALENCIA CO.:* Cebolita Creek, 16.3 mi. S Grants (E = 27).

RESULTS

Overall Genic Differentiation

Relationships between the major units along the Rio Grande and related reference populations elsewhere in New Mexico are shown on a contour map with 5% similarity level contours (Fig. 3), based on a UPGMA cluster of Rogers' similarity values (Table 1). As is evident from the figure, *T. b. connectens* is closely related genically to subspecies to the west of Albuquerque in an area of lava flows near Grants, New Mexico, and to populations in the Four Corners area. *Thomomys b. opulentus* does not form a discrete unit by itself, but is associated with populations of *T. b. fulvus,* found in the mountains to the west of the Rio Grande Valley, and with *T. b. morulus,* distributed to the west of the lava flows south of Grants, New Mexico. The southern Rio Grande populations are also fairly closely related to populations of *T. b. actuosus* in the Manzano and Gallinas Mountains, and to *T. b. pervagus* along the Rio Grande north of Santa Fe (both members of geographic unit M; see Fig. 1).

The 14 sampled populations of *T. b. connectens* and *T. b. opulentus* along the Rio Grande were monomorphic for the same allele at seven of the

Table 1. Coefficients of genic similarity (Rogers' S) for 20 populations of *Thomomys bottae* in New Mexico. Representative populations of *T. b. connectens* (localities 2–4) and *T. b. opulentus* (localities 9–15) from along the Rio Grande are included, as well as reference populations from elsewhere in New Mexico (localities A–J). Numbers and letters are designated as in Specimens Examined and Fig. 2.

	T. b. connectens			*T. b. opulentus*														
	2	3	4	9	10	11	12	13	14	15	A	B	C	D	E	F	G	H	I
3	.977																		
4	.975	.963																	
9	.716	.726	.700																
10	.691	.702	.674	.933															
11	.692	.707	.682	.918	.940														
12	.679	.693	.668	.938	.941	.932													
13	.663	.678	.650	.901	.914	.943	.919												
14	.666	.685	.655	.936	.920	.915	.942	.922											
15	.680	.694	.665	.889	.917	.925	.896	.928	.895										
A	.673	.691	.664	.874	.898	.905	.892	.905	.890	.923									
B	.691	.708	.682	.889	.911	.947	.917	.926	.904	.906	.933								
C	.643	.657	.637	.867	.887	.904	.900	.900	.893	.881	.913	.920							
D	.714	.729	.706	.874	.881	.906	.894	.875	.864	.876	.894	.903	.896						
E	.707	.720	.701	.858	.861	.893	.884	.878	.850	.870	.878	.896	.894	.970					
F	.705	.718	.699	.875	.875	.899	.893	.870	.874	.871	.888	.894	.896	.985	.969				
G	.638	.646	.626	.853	.876	.879	.874	.869	.872	.863	.879	.873	.932	.855	.842	.861			
H	.953	.951	.947	.706	.680	.681	.668	.652	.655	.670	.663	.681	.636	.705	.701	.698	.629		
I	.963	.963	.953	.718	.692	.698	.686	.668	.674	.682	.680	.699	.650	.722	.714	.711	.639	.970	
J	.938	.942	.938	.717	.686	.684	.688	.683	.676	.690	.684	.683	.663	.722	.730	.717	.651	.921	.927

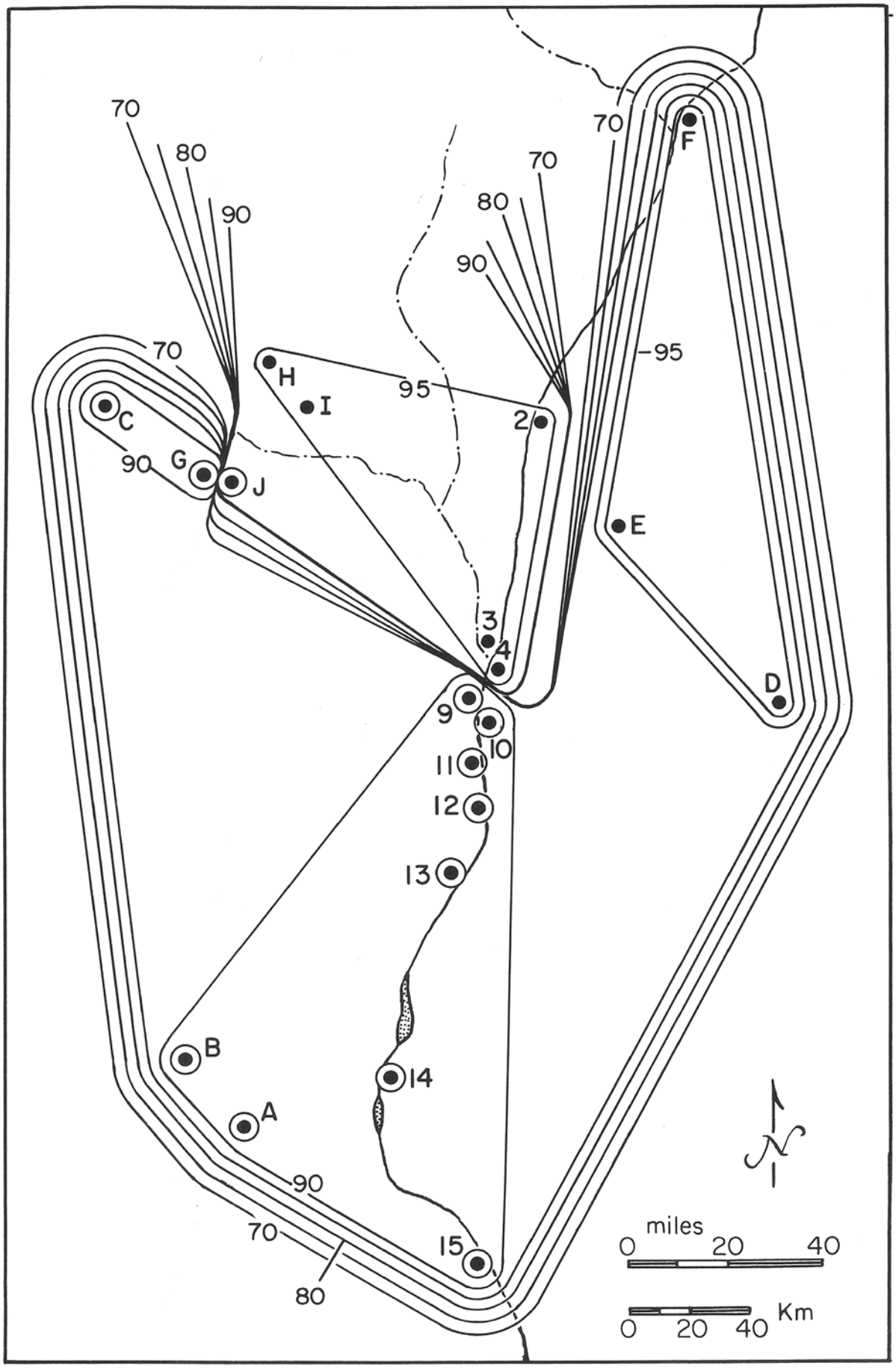

Fig. 3. Genic similarity among representative populations of *Thomomys bottae* from New Mexico. The contour lines, at intervals of 5% similarity, are drawn from a UPGMA cluster of Rogers' coefficient of genic similarity. All samples are joined at a contour level of 65%.

24 loci examined: Mdh–1, Mdh–2, Idh–2, Got–2, Pgi, Ipo, and Pept–1. One additional locus, Sdh, was essentially monomorphic, with a variant occurring at a frequency of less than 0.05 in one population. Allele frequencies for the 16 polymorphic loci are given in Table 2. Eight of the variable loci (Ldh–2, Idh–1, Got–1, αGpd, Pgm, Adh, Acon–1, and Np) can be characterized as showing a low to moderate level of differentiation between populations of *T. b. connectens* (localities 2–7) and *T. b. opulentus* (localities 8–15). For these loci the same allele is the common one (frequency > 0.50) in all populations, except for Adh, where the common allele in all other populations occurs at a frequency of 0.29 in population 15. The less common alleles at these loci are not shared between the two subspecies. The remaining eight loci (Ldh–1, 6Pgd, Est–1, Est–4, Alb, preAlb, Trf, and Mpi) exhibit major differences in allele frequency between populations of *T. b. connectens* and *T. b. opulentus*. At the most strongly differentiated loci, populations of these two subspecies away from the point of contact are fixed for different alleles (Table 2).

Genetic similarity is high within both *T. b. connectens* ($\bar{S}$ = 0.973 for localities 2–7) and *T. b. opulentus* ($\bar{S}$ = 0.912 for localities 8–15), but the two units share only a remote relationship ($\bar{S}$ = 0.687). This is about the same level of differentiation as that found between the units of *T. bottae* that meet along the Colorado River (Smith and Patton, 1980), and is a higher level of differentiation than that found between *T. b. actuosus* and *T. b. ruidosae* where the two come in contact in south central New Mexico (Patton et al., 1979).

Genic Characterization of Contact Zone

The eight loci which differentially characterize *T. b. connectens* and *T. b. opulentus* identify a zone of contact and can be used to analyze the extent of gene exchange between the two races. Major shifts in allele presence or frequency occur along an 8 km distance, between-population samples 4 and 9. For example, at the Est–1 locus, populations 2 through 5 *(T. b. connectens)* are fixed for the Est–1^{106} allele, while populations 8 through 15 *(T. b. opulentus)* are fixed for the Est–1^{100} allele (Fig. 4a, 4b, and Table 2). The *opulentus* allele was detected in low frequency in two of the *connectens* populations (localities 6 and 7) in the zone of contact. Similar patterns are found for several other alleles (Ldh–1^{96}, $6Pgd^{100}$, Trf^{100}; see Fig. 4 and Table 2). The opposite pattern of allele distribution, with *connectens* alleles found in contact zone populations of *opulentus,* is also observed ($6Pgd^{79}$, $preAlb^{101}$, Mpi^{60}; Fig. 4 and Table 2).

The remaining alleles at these strongly differentiated loci fit into two categories. The first category includes alleles restricted to one or the other subspecies. Most of these alleles ($6Pgd^{88}$, Est–4^{102}, Est–4^{95}, $preAlb^{100}$, Mpi^{117}, Mpi^{107}, Mpi^{80}, Mpi^{70}) occur in low frequency. However, the Alb^{100} allele occurs in a frequency of 0.81 or greater in all sampled populations of *T. b. opulentus,* but was not detected in any populations of *T. b. connectens*. The second category includes alleles found in both subspecies. Some of these alleles (Ldh–1^{100}, Est–4^{100}, Est–4^{96}) were found in most or all populations of both subspecies. The Est–4^{106} allele was found in low frequency in two populations of each subspecies. The last four alleles (Alb^{103}, $preAlb^{98}$, Trf^{121}, Mpi^{100}) were found in all populations of one subspecies and in scattered populations of the other subspecies, including localities at some distance from the zone of contact.

The low level of apparent gene exchange in the zone of contact can be further characterized in order to shed some light on the question of potential gene flow between the two strongly differentiated units. A genic index (or hybrid index; see Anderson, 1949; Patton et al., 1979) was constructed based on the seven most strongly differentiated loci (Ldh–1, 6Pgd, Est–1, Alb, preAlb, Trf, and Mpi). Each individual from the contact region was assigned a value of +1 for each allele characteristic of *T. b. connectens,* and a value of −1 for each allele characteristic of *T. b. opulentus*. The distribution of genic index scores in contact and near contact localities (4–11) is given in Table 3. Although no individuals identifiable as F_1 hybrids (genic index score of zero) were observed, a tendency towards intermediate scores in contact zone populations is indicated.

Karyotypic Variation

Individuals of *T. b. connectens* typically have a karyotype with all biarmed autosomes. There are a few exceptions in individuals from contact

Table 2. Allele frequencies at 16 polymorphic loci in populations of *Thomomys bottae* along the Rio Grande in New Mexico. (Numbers in the upper row correspond to the listing in Specimens Examined and Fig. 2; those in parentheses indicate sample size.)

		T. b. connectens						*T. b. opulentus*							
		2	3	4	5	6	7	8	9	10	11	12	13	14	15
Locus	Allele	(13)	(19)	(35)	(32)	(20)	(37)	(4)	(27)	(8)	(15)	(11)	(17)	(16)	(26)
Ldh-2	500	0.04	0.03	0.19	0.20	0.05									
	100	0.96	0.97	0.81	0.80	0.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Idh-1	148										0.03				
	100	1.00	1.00	0.93	0.86	0.80	0.92	1.00	1.00	1.00	0.97	1.00	1.00	1.00	1.00
	78			0.07	0.14	0.20	0.08								
Got-1	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	1.00	0.88	0.97	1.00
	83										0.03		0.12	0.03	
αGpd	119									0.06	0.13		0.15		0.04
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94	0.87	1.00	0.85	1.00	0.87
	80														0.10
Pgm	131										0.03	0.09	0.06		
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	0.91	0.91	1.00	0.98
	69												0.03		
	46														0.02
Adh	−114	0.96	0.87	1.00	1.00	1.00	1.00	1.00	0.93	0.87	0.87	0.95	0.62	0.66	0.29
	−107	0.04	0.13												
	−100								0.07	0.13	0.13	0.05	0.38	0.34	0.46
	−71														0.25
Acon-1	144	0.10													
	100	0.90	1.00	1.00	1.00	1.00	1.00	0.75	0.85	0.75	0.97	1.00	0.96	1.00	0.85
	70							0.25	0.15	0.25	0.03		0.04		0.15
Np	107				0.03	0.08									
	100	1.00	1.00	1.00	0.97	0.92	1.00	0.75	0.98	1.00	1.00	1.00	0.92	0.78	1.00
	85							0.25	0.02				0.08	0.22	
Ldh-1	100	1.00	1.00	1.00	0.98	0.97	0.89	0.50	0.19	0.38	0.20	0.09	0.21	0.25	0.60
	96				0.02	0.03	0.11	0.50	0.81	0.62	0.80	0.91	0.79	0.75	0.40
6Pgd	100						0.01	0.50	0.83	1.00	1.00	0.95	0.97	0.91	0.98
	88								0.09			0.05	0.03	0.09	0.02
	79	1.00	1.00	1.00	1.00	1.00	0.99	0.50	0.07						
Est-1	106	1.00	1.00	1.00	1.00	0.95	0.96								
	100					0.05	0.04	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Est-4	106				0.03	0.03			0.02			0.15			
	102											0.10	0.06		0.15
	100		0.16	0.03	0.02	0.03	0.10	0.50	0.87	0.75	0.54	0.70	0.53	1.00	0.60
	96	1.00	0.84	0.97	0.95	0.95	0.90	0.50	0.11	0.25	0.46				
	95											0.05	0.41		0.25
Alb	103	1.00	1.00	1.00	1.00	1.00	1.00		0.15	0.06	0.13				0.19
	100							1.00	0.85	0.94	0.87	1.00	1.00	1.00	0.81
preAlb	101	0.89	0.87	1.00	1.00	1.00	1.00		0.09						
	100							0.13	0.24	0.14	0.60	0.18	0.62	0.31	0.65
	98	0.11	0.13					0.87	0.67	0.86	0.40	0.82	0.38	0.69	0.35
Trf	121	1.00	1.00	1.00	0.98	1.00	0.97	0.38	0.32	0.07			0.15		
	100				0.02		0.03	0.62	0.68	0.93	1.00	1.00	0.85	1.00	1.00
Mpi	117							0.37	0.35		0.03	0.23	0.04	0.38	0.05
	107							0.25	0.07	0.06	0.07		0.04		
	100		0.10					0.37	0.52	0.94	0.90	0.77	0.92	0.59	0.95
	80	0.10	0.20		0.09										
	70													0.03	
	60	0.90	0.70	1.00	0.91	1.00	1.00		0.06						

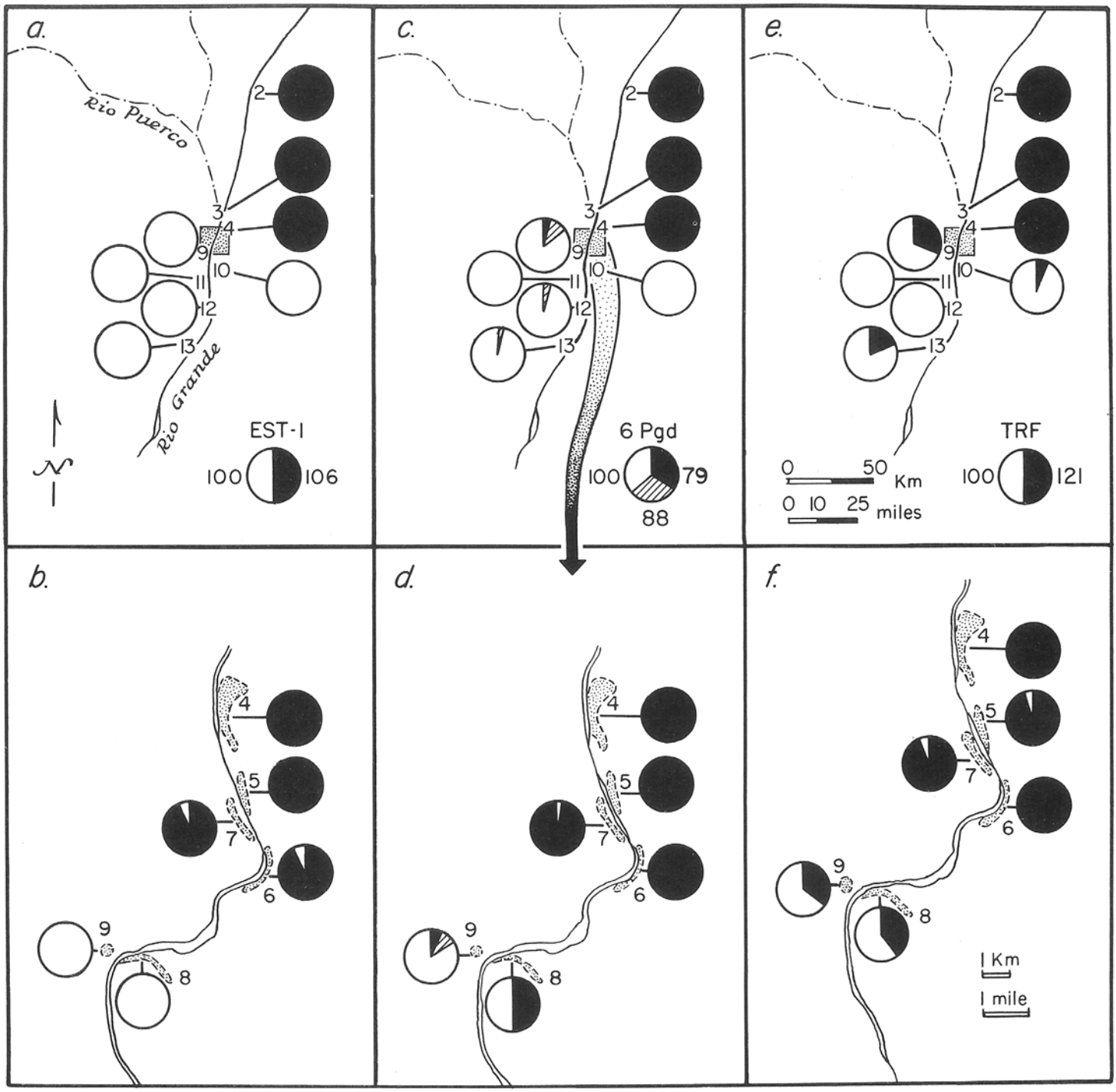

Fig. 4. Allele frequency variation at three loci in *Thomomys bottae*. Fig. 4a shows variation at the Est–1 locus from Albuquerque to San Marcial; Fig. 4b is a detailed picture of the pattern for Est–1 in the zone of contact; Fig. 4c shows the broad scale pattern for 6Pgd; Fig. 4d shows details for 6Pgd in the contact zone; Fig. 4e shows the broad scale pattern for Trf; and Fig. 4f shows details for Trf in the contact zone.

zone populations, as follows: locality 5—one individual with one acrocentric autosome out of four individuals sampled; locality 7—one individual with two acrocentrics out of eight individuals sampled.

There is a broader range in the number of acrocentric autosomes in populations of *T. b. opulentus,* with the number increasing somewhat between southern and northern populations, as follows: locality15—24 acrocentrics (N = 3); locality 14—28 acrocentrics (N = 3); locality 13—between 28 and 34 acrocentrics (N = 2); locality 12—between 30 and 33 acrocentrics (N = 2); locality 11—between 28 and 32 acrocentrics (N = 5); locality 10—32 acrocentrics (N = 1); locality 9—28 or 30 acrocentrics (N = 1)

Table 3. Genic index scores for contact and near contact populations of *T. b. connectens* (localities 4–7) and *T. b. opulentus* (localities 8–11).

Locality	Sample size	Genic Index Score													
		−14	−12	−10	−8	−6	−4	−2	0	+2	+4	+6	+8	+10	+12	+14
4	35															35
5	32														2	30
6	19														3	16
7	37													2	10	25
8	4			2	1	1										
9	27	7	7	4	5	3	1									
10	7	1	5	1												
11	15	7	6	2												

The variation in number of acrocentric chromosomes within and between populations of *T. b. opulentus* makes it difficult to attribute biarmed elements to introgression from *T. b. connectens* with any certainty. The three individuals of *T. b. connectens* with one or two acrocentric autosomes may indicate a low level of genetic exchange, similar to that suggested by the allozymic data. The genic index scores of these three individuals are all +14, allozymically "pure" *T. b. connectens*. Thus different individuals give an indication of a low level of genetic exchange in the chromosomal and allozymic data sets.

Morphological Variation

Discriminant function analyses were performed on: 1) the cranial and external morphometric characters, and 2) the pelage color values to achieve maximum separation of all of the populations. In the analysis of cranial and external characters in males, the first two discriminant functions explain 83.6% of the variance. For female pocket gophers, the first two discriminant functions account for 67.1% of the variance. The results are presented graphically in Fig. 5. Each population is represented by a polygon enclosing the plotted points of all individuals in the population, with locality numbers marking the group centroids. For both males and females, the populations separate out by subspecies along the first discriminant axis. The single male from locality 14 (Truth or Consequences) appears to be somewhat intermediate morphologically. Contact zone populations (unshaded polygons), however, do not exhibit morphological intermediacy; rather, they are aligned with samples of the same subspecies collected away from the zone of contact.

In contrast to the abrupt nature of the contact indicated by allozymic, karyotypic, and cranial and external morphometric data, strong differentiation between the two subspecies is lacking in pelage color. A histogram for each population showing individual values along the first discriminant function for pelage color (accounting for 70.2% of the variance) is given in Fig. 6. Individuals of *T. b. connectens* tend to fall on the negative end of the scale, while individual scores of *T. b. opulentus* are more positive. However, there is considerable overlap between the two groups, and the overlap is not restricted to contact zone populations. A few individuals stand out particularly as having pelage color characteristics more typical of the other subspecies. For example, one individual from Escondida (locality 10) has a discriminant score of −3.00, more typical of *T. b. connectens*. However, the genic index score for this individual is −14, which would be considered genetically "pure" *T. b. opulentus*.

DISCUSSION

Patterns of Allele Distribution along the Rio Grande

Electrophoretic, karyotyic, and cranial morphometric analyses all indicate a steep, narrow zone of contact between *T. b. opulentus* and *T. b. connectens*. The electrophoretic data in this case provide the most detailed information on potential interaction between the two groups. Although the groups are strongly differentiated electrophoretically, some alleles are shared between the two. A pattern in which an allele is present in some populations of both genetic units along the Rio Grande can be explained in three ways:

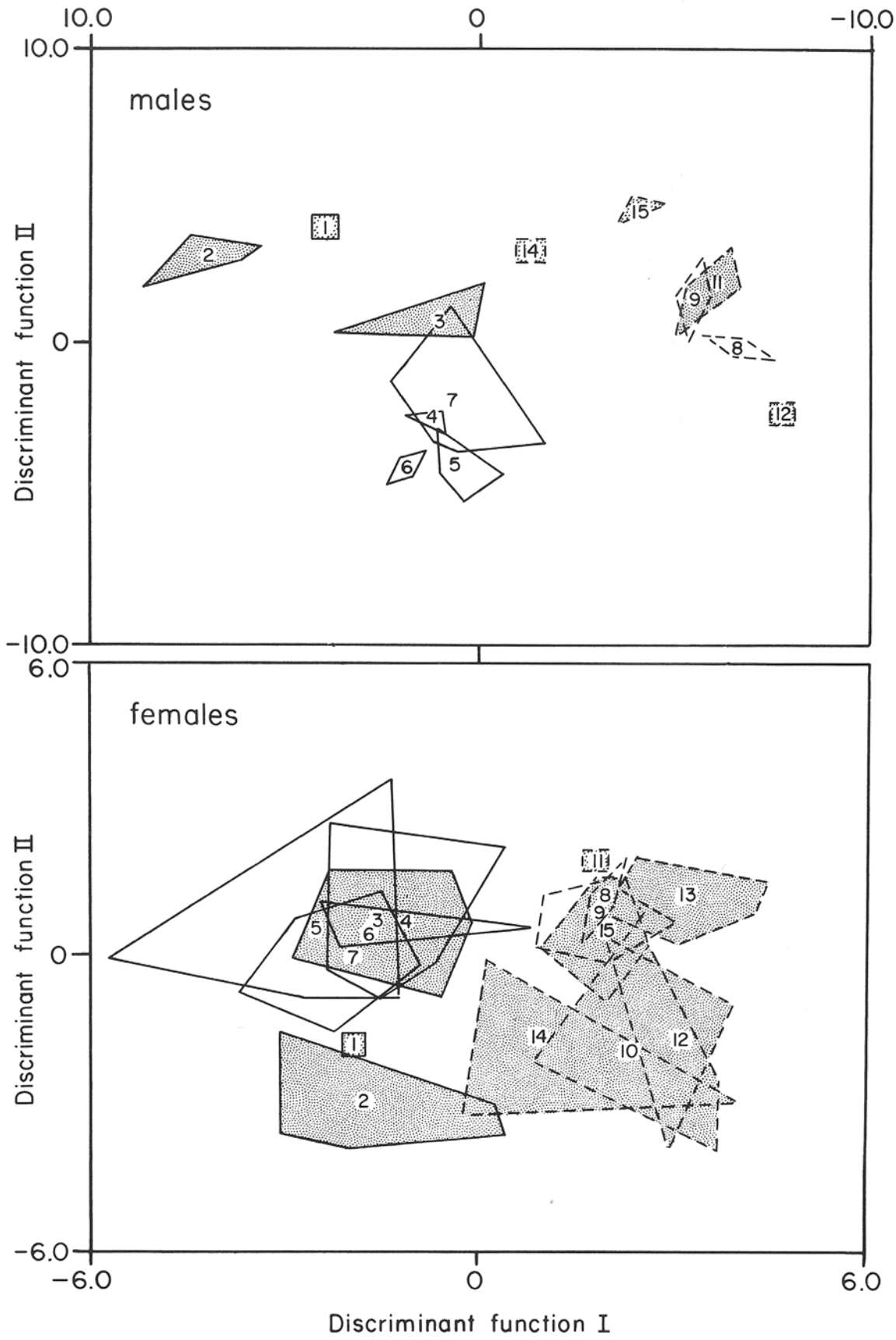

Fig. 5. Plots of the first and second discriminant functions based on cranial and external body measurements for populations of *Thomomys bottae* from the Rio Grande Valley. Males are shown in the upper plot, females in the lower. Each polygon surrounds the individual points for one population. Populations of *T.b. connectens* are shown with solid outlines; populations of *T. b. opulentus* have dashed outlines. Polygons representing populations from the contact zone are unshaded; those from outside the zone of contact are shaded. Group centroids are marked by locality numbers (identified under Specimens Examined).

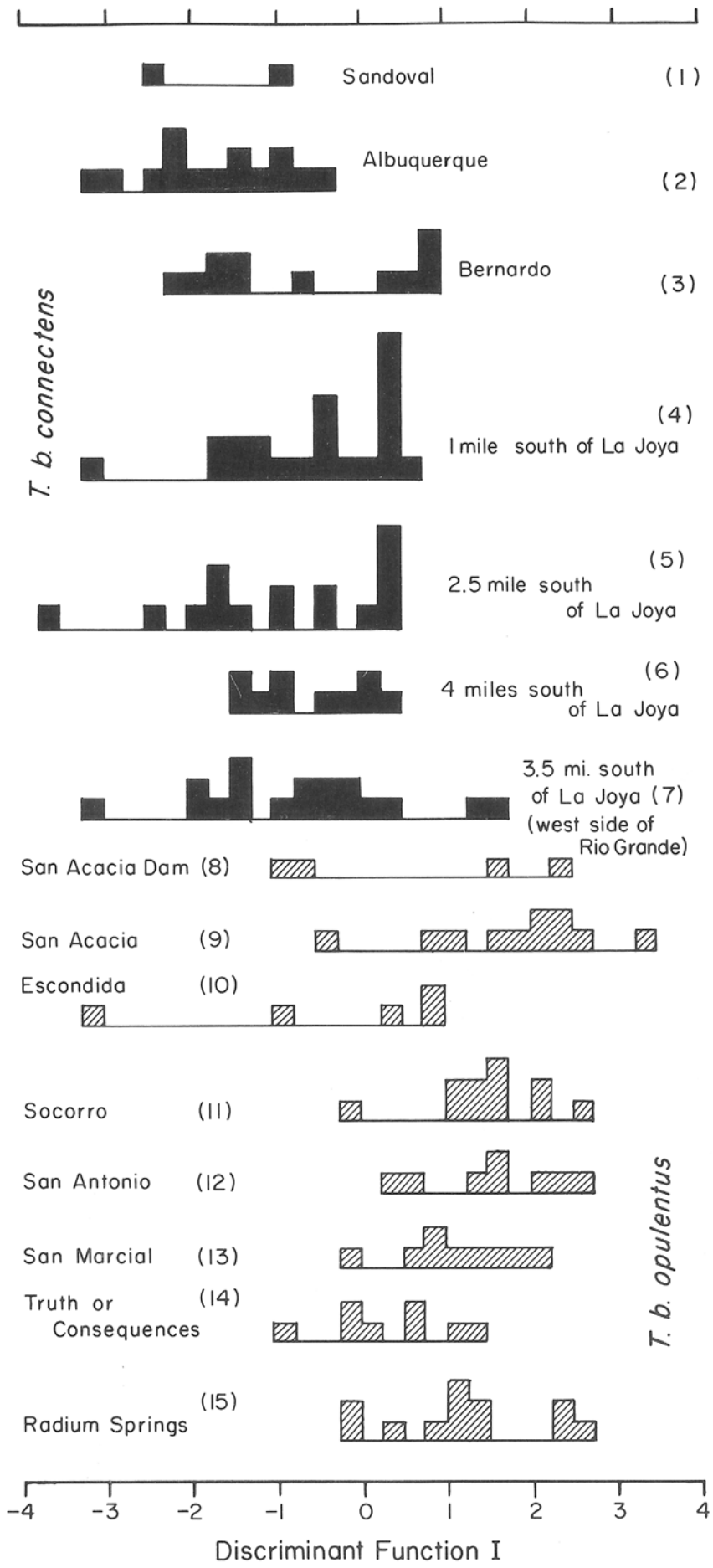

Fig. 6. Distribution of values along the first discriminant function axis for the pelage color analysis of individual specimens of *T. b. connectens* (solid) and *T. b. opulentus* (striped) along the Rio Grande.

1) as introgression of an allele that evolved in one population group during isolation and spread to the other population group through introgressive hybridization following contact; 2) as the retention of an ancestral polymorphism common to both *T. b. opulentus* and *T. b. connectens;* or 3) as convergent evolution of alleles with the same mobility in the two groups. Patterns such as those described above for the $6Pgd^{100}$ and $6Pgd^{79}$ alleles, where an allele is present in high frequency in one subspecies and is also found in a few contact populations of the other subspecies, are most readily interpreted as evidence for introgression. Other patterns of allele distribution, however, are not as helpful in characterizing the genetic interaction between the two units because they may easily be interpreted in more than one way. While the presence of the Alb^{103} allele in scattered populations of *T. b. opulentus* as far south as Radium Springs (locality 15) could be interpreted as evidence for a far reaching result of introgression, it is equally likely that both Alb alleles were present in an ancestral population and that during a period of isolation populations of *T. b. connectens* lost the Alb^{100} allele while most populations of *T. b. opulentus* lost the Alb^{103} allele. Although convergent evolution of electromorphs remains a possibility, such an explanation is less likely in the present case, with populations of the same subspecies, and more likely in a case concerning taxa that have been separated for a relatively long time.

The genic index, based on the most strongly differentiated loci, suggests that interaction between the two genetic units is not limited to the production of F_1 individuals, a situation in which genetic isolation would be complete even though reproductive isolation is not (cf., Patton, 1973). Instead, the presence of individuals resulting from apparent multiple filial and backcross generations indicates that hybrids are not at a disadvantage. If there is no reproductive barrier to interbreeding, it is not immediately clear why there is such a low level of introgression in this situation, particularly since the valley of a major river might be expected to provide a broad corridor for gene flow. In order to understand the dynamics of the contact zone, it is important to consider the past history and the present environmental conditions of the region as well as the population structure and movement potential of pocket gophers themselves.

The Rio Grande Valley, Past and Present

The headwaters of the Rio Grande are in the San Juan and Sangre de Cristo ranges in southern Colorado and northern New Mexico. The Rio Grande is a complex stream that flows through a series of linked intermontane basins, variously referred to as the Rio Grande rift or the Rio Grande structural depression (see discussion in Baltz, 1978). Bachman and Mehnert (1978) used potassium–argon dating of volcanic rocks in association with ancestral stream deposits to show that the Rio Grande in central New Mexico became a throughflowing drainage system during the late Pliocene (between 3.0 and 4.5 m.y.a.). The oldest date comes from San Acacia where a basaltic flow dated at 4.5 ± 0.1 million years old underlies ancestral Rio Grande deposits.

The Rio Grande did not carve the depression through which it flows, except in a minor way. Instead, throughout most of its geologic history, the river has been depositing sediment to fill in the trough (Kelley, 1969). About 20,000 feet of sedimentary rock underlies the Albuquerque region, the upper half of which consists of sediments deposited by the river during subsidence of the trough (Kelley, 1969). The river would have meandered over a broad floodplain while these sediments were being deposited. Then, in relatively late geologic time, the Rio Grande cut a series of terraces in the thick basin fill. Data on the ages of soils associated with various geomorphic surfaces (Machette, 1978) and vertebrate fossil evidence (Lambert, 1969, 1978) indicate that the cutting of the Valley of the Rio Grande near Albuquerque probably began in the mid–Pleistocene. Intermediate terraces bordering the valley are thought to be of middle to late Pleistocene age, while the innermost valley is late Wisconsin to Recent in age (Lambert, 1969). Following the interval of valley cutting, the river began filling in again, so that presently lowlands in the vicinity of Albuquerque contain about 75 feet of fill that the river has returned to its Inner Valley (Kelley, 1969).

The Rio Grande is subject to flooding in the springtime, especially in years of heavy snow pack in the headwater mountains. Later summer or fall floods may also occur if heavy rains fill normally dry tributaries such as the Rio Puerco and the Rio Salado. Prior to the construction of

Elephant Butte Dam in 1916 and other smaller dams along the valley, the Rio Grande shifted its course with every major spring flood. Even with the engineered controls, the river sometimes cuts new channels during floods and deposits loads of sediment as the high water recedes (Kottlowski, 1967). At San Acacia (mid–contact area) the greatest flooding in this century took place in late summer and fall of 1929 (Patterson, 1965). The original USDA soil survey along the Rio Grande in the Socorro area north to San Acacia was done earlier that same summer, and soil maps had to be revised because sediments ranging from a few inches to more than three feet were deposited throughout the area. Buildings in the town of San Acacia were damaged, and the railroad, roads, ditches, and dikes were washed out or buried in many places (Poulson and Fitzpatrick, 1929). In a flood such as this, much or all of the available habitat for pocket gophers between La Joya and San Acacia would undoubtedly be covered by water.

Contact between the two differentiated units of pocket gophers is coincident with a marked transition in vegetation adjacent to the Rio Grande (Bailey, 1913; Kuchler, 1964). The area of contact is in a narrow, short segment of the Rio Grande Valley situated between two broader basins. The width of the Inner Valley of the Rio Grande at Albuquerque is 15 km (Kelley, 1969); at San Acacia the river flows thorugh a gap approximately 300 m wide between basaltic andesite–capped bluffs. This is the narrowest segment of the inner Rio Grande Valley between White Rock Canyon (near Santa Fe) and Elephant Butte Dam (near Truth or Consequences) (Chapin et al., 1978). The extent of relatively flat land adjacent to the river is very limited in the area of contact, and much of the land that would appear to be available may not provide suitable habitat for gophers. Reconnaissance during field work in May of 1980 revealed no visible signs of gopher activity in the area on the west side of the river at the mouth of the Rio Salado, an area that is covered by fine sand with the vegetation limited largely to a salt cedar bosque. The area on the east side of the river to the east and north of locality 8 is a broad and barren salt flat, again with no visible gopher activity. In fact, sample localities 5 through 8 were the only areas within the contact zone where we found evidence of gopher activity during our field work. Animals are found primarily along the river, with only an occasional individual on the immediately adjacent bajadas or open desert. Thus, although flooding has been controlled by dams along the river and irrigated fields north and south of the contact zone provide a large reservoir of potential immigrants, gophers are not distributed continuously throughout the zone. Rather, at any one time, animals are found in patches, with their numbers ranging between less than one to upwards of 15 individuals per acre, with substantial distances between patches.

Population Structure and Gene Flow in **Thomomys bottae**

Local *Thomomys bottae* populations are characterized by an unequal breeding sex ratio favoring females, with a high variance in male reproductive success (Patton and Feder, 1981). These two factors coupled with dispersal distances measured in tens of meters per generation (Howard and Childs, 1959; Vaughan, 1963) contribute to a very small genetically effective population, and impose additional significant constraints on gene flow through the Rio Grande contact zone. Here, we envision a situation in which only an occasional parental type individual succeeds in passing the barriers imposed by both topography and by the population structure of these animals, and interbreeds successfully. Due to unbalanced dispersal into a local site, F_1 offspring would be surrounded by parental individuals of the local type, and would backcross to these parentals. Thus, at any single sample point in time, evidence for introgression would be limited to a few individuals which appear as backcross recombinants in genic index score.

Various parameters involved in contact dynamics can be investigated using simple mathematical models. Endler (1977:91) gives an expression for the width of a cline as a function of the time since neutral secondary contact as:

$$w = 1.68\ \ell\ \sqrt{T}$$

where w is the width of the cline, ℓ is a gene flow parameter, and T is time (measured in generations, or in years if there is one generation per year) since contact. In a study of a hybrid zone in *Dendroica* warblers, Barrowclough (1980) used 10^3 meters/year as an estimate of gene flow for

passerine birds, and 7500 years as an estimate of time since contact for the warbler zone to obtain an estimate of 145 km for the width of the hybrid zone, remarkably close to the measured width of the zone based on plumage characters. Gene flow in *Thomomys bottae* is probably closer to 10^2 meters/year, an order of magnitude less than in passerine birds. Vaughan (1963) gave mean dispersal distances for *T. bottae* in Colorado as young males (66 m), adult males (111 m), young females (31 m), and adult females (136 m). Howard and Childs (1959) recorded movements of 30 to 120 m for *T. bottae* in California. If we were to assume that *T. b. connectens* and *T. b. opulentus* have been in contact along the Rio Grande for a long time, say 100,000 years, the predicted width of the hybrid zone would be 53 km. However, it is unlikely that the two subspecies have been in continuous contact for such a long period of time. Shifting distribution of the six species of pocket gophers currently found in New Mexico (Findley et al., 1975) during late and post–Pleistocene times in response to climatic and vegetation changes renders it likely that these two races of *T. bottae* achieved their present contact only in more recent times. Thus, if we take a post–Wisconsin estimate of 10,000 years as the time since secondary contact of *T. b. connectens* and *T. b. opulentus,* the estimated width of the contact zone would be 17 km. However, this cline model assumes large populations and homogeneous gene flow, whereas pocket gophers have small effective population sizes and there are both topographic and edaphic constraints on gene flow in the contact area. The measured width of the contact zone, approximately 8 km, thus appears to be reasonably consistent with a model of neutral secondary contact. Although there is no apparent reproductive isolation between the two subspecies, extensive introgression is not possible, even over time, since populations through the zone are at continual low density, have patchy distributions, and are subjected to strong temporal perturbations due to periodic flooding.

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