THE SOUTHWESTERN NATURALIST 30(4):491-501 NOVEMBER 27, 1985

MORPHOLOGIC VARIATION AMONG ROCK POCKET MICE (*CHAETODIPUS INTERMEDIUS*) FROM NEW MEXICO LAVA FIELDS

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ABSTRACT.—Intraspecific variation in external and cranial measurements of rock pocket mice (*Chaetodipus intermedius*) was evaluated using 312 adult specimens (145 males and 167 females). Males were larger than females for 8 of 16 characters examined, and significant geographic variation occurred in 15 characters for one or both sexes. Generally, largest means of male and female characters were from specimens representing the Carrizozo malpais; the smallest mice were from the Afton lava flows. Specimens from the Pedro Armendariz lava field and the nearby Fra Cristobal Range were the closest geographically and the most similar morphologically.

Rock pocket mice (*Chaetodipus intermedius*) occur in northwestern Mexico and throughout much of Arizona and New Mexico (Hall, 1981). Of the 10 currently recognized subspecies of *C. intermedius* (Hall, 1981), three are confined to isolated black-lava outcrops, *C. i. nigrimontis* occurs on Black Mountain, Pima Co., Arizona; *C. i. ater* occupies the Carrizozo malpais, Lincoln and Otero Cos., New Mexico; and *C. i. rupestris* is found on the Afton lava flows, Dona Ana Co., New Mexico. In addition, an isolated population of *C. intermedius* inhabits the Pedro Armendariz lava field in Sierra and Socorro Cos., New Mexico (Weckerly, 1983). These geographic isolates differ markedly in coloration from populations of rock pocket mice in surrounding areas (Dice, 1929; Benson, 1932; Blossom, 1933; Weckerly, 1983). How much these populations differ morphologically from each other or from nearby populations has not been established. The restricted distribution and presumably intense natural selection for dark pelage coloration may also be associated with some selection for morphologic variation among the forms inhabiting lava fields. Best and James (1984) noted that some lava-dwelling rattlesnakes (*Crotalus*), in addition to being darker, were much smaller than other populations in New Mexico. Perhaps body size, as well as coloration, are affected by selection pressures on lava fields. However, Rogers and Schmidly (1981) found essentially no morphologic differentiation among similar populations of *Neotoma albigula*.

To determine if populations of *C. intermedius* differed between lava fields and an adjacent rocky outcrop, we studied morphologic variation in specimens collected from three lava fields and one mountain range in south-central New Mexico. Our purposes were to investigate the degree of sexual dimorphism, amount and pattern of interlocality variation within each character, and phenetic relationships among populations.

MATERIALS AND METHODS.—We analyzed 4 external and 12 cranial measurements (Fig. 1) for 312 adult *Chaetodipus intermedius*. Total length, tail length, hind foot length, and ear length were recorded to the nearest mm from the specimen tag. Nasal width and interparietal width were taken with an ocular micrometer in a stereo microscope at 10x, and the remaining cranial and mandible measurements were made to the nearest 0.1 mm using dial calipers. Specimens were

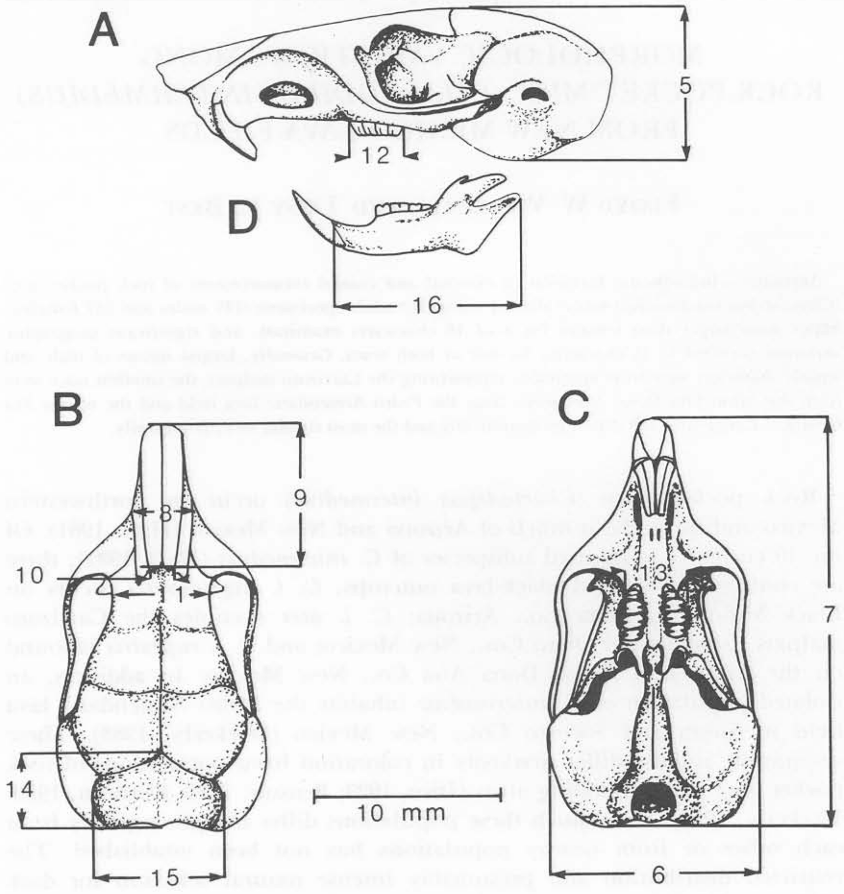

FIG. 1.—Cranial elements of *Chaetodipus intermedius* illustrating the 12 skull measurements taken. A, skull, lateral view; B, skull, dorsal view; C, skull, ventral view; D, mandible, lateral view. Numbers correspond to the characters listed in Table 1.

aged according to the criteria of Hoffmeister and Lee (1967) for *C. penicillatus*; only age classes 1-4 were used in the analyses.

Specimens used in the analyses were from the following areas (code name and sample size are included for each group); 1) Pedro Armendariz lava field, Sierra and Socorro Cos., PEDRO A. (68 males, 82 females); 2) Fra Cristobal Mountain Range, Sierra and Socorro Cos., FRA CRIS. (11, 16); 3) Carrizozo malpais, Lincoln and Otero Cos., CARRIZOZO (16, 14); and 4) Afton lava flows, Dona Ana Co., AFTON (50, 55). The Fra Cristabol Range is separated from the Pedro Armendariz lava field by about 5 km of sandy soil, which is not inhabited by *C. intermedius*.

Character heterogeneity (between sexes and among the four localities) was tested using a one-way analysis of variance, and a sums of squares simultaneous test procedure to determine maximally nonsignificant subsets (SS-STP—Gabriel and Sokal, 1969). Mean measurements of each character for each locality were used in the mulitvariate procedures. Characters were standardized (so that each had a mean of 0 and a standard deviation of 1 across localities), and correlation and distance matrices (Sneath and Sokal, 1973) were calculated. Clusters of localities and characters were obtained with the unweighted pair-group method using arithmetic averages (UPGMA). Principal components were calculated from a correlation matrix among characters, and projections of the localities were plotted on the first three components. To elucidate

TABLE 1.—*Secondary sexual dimorphism in size for 16 morphologic characters of* Chaetodipus intermedius *from four localities in New Mexico.*

Character	Char. no.	Character-state means[1]		Analysis of variance[2]	
		males (N=145)	females (N=167)	*d.f.*	*F*-ratio
External					
Total length	1	168.1	163.6	1,265	20.042**
Tail length	2	93.8	91.5	1,264	7.387**
Hind foot length	3	20.4	20.0	1,303	6.297*
Ear length	4	6.8	6.7	1,280	0.912
Cranium and mandible					
Greatest depth	5	8.6	8.5	1,303	16.305**
Mastoid width	6	13.0	12.8	1,303	21.378**
Greatest length	7	23.9	23.6	1,284	24.231**
Rostral width	8	3.8	3.8	1,302	0.060
Nasal length	9	8.6	8.5	1,291	15.721**
Nasal width	10	2.1	2.1	1,306	1.676
Interorbital width	11	6.2	6.2	1,308	1.396
Maxillary toothrow length	12	3.6	3.7	1,309	0.341
Maxillary toothrow width	13	4.2	4.2	1,304	0.202
Interparietal length	14	3.5	3.5	1,303	0.747
Interparietal width	15	7.5	7.4	1,299	3.043
Mandible length	16	11.0	10.9	1,285	9.088**

[1]Dimensions in mm; N = number of specimens.
[2]Single-classification analysis of variance, sexes compared pairwise for each character.
[3]Minimally significant sexual dimorphism assumed where *P* c 0.05 (one asterisk); two asterisks indicate *P* c 0.01.

correlations between characters, dendrograms were constructed from correlation matrices of the 16 standardized characters for males and females.

Discriminant analysis (considering all 16 characters) was used to characterize each of the four localities. Then, all specimens were reclassified to give an estimate of the accuracy of the original separation of localities.

Statistical analyses were performed at The University of New Mexico Computer Center using the following programs: UNIVAR (D. M. Power, unpublished), NT-SYS (Rohlf et al., 1972), and SPSS (Nie et al., 1975).

RESULTS AND DISCUSSION.—*Character correlations.*—For males, mandible length and nasal length, greatest length of cranium and interparietal width, greatest depth of cranium and mastoid width, and maxillary toothrow length and interparietal length were the most highly correlated pairs of characters (*r* *b* 0.95). Total length, interorbital width, hind foot length, and ear length were the least correlated with other characters (*r* *c* 0.79). Females had highest correlations (*r* *b* 0.95) for tail length and greatest length of cranium, mandible length and nasal length, greatest depth of cranium and mastoid width, hind foot length and rostral width, and interorbital width and interparietal width. Only maxillary toothrow length was not highly correlated with another character (*r* *c* 0.56).

For both sexes the correlations among characters were quite high. Our character set was not as heterogeneous as has been reported for other heteromyids; for example, *Dipodomys ordii* (Kennedy and Schnell, 1978) and *D. agilis* (Best, 1983*b*).

Sexual dimorphism.—When all males were compared with all females, we found that eight characters of *C. intermedius* exhibited significant secondary sexual dimorphism in size (Table 1). Of the dimorphic characters,

TABLE 2.—*Variation in means of 16 morphologic characters of* Chaetodipus intermedius *from four localities in New Mexico. Statistically homogeneous subsets derived from SS-STP analyses are shown by lines below the sample number and ranked means.*

Character	Males: Results of SS-STP				Females: Results of SS-STP			
External								
Total length	3	1	4	2	3	2	1	4
	172.9	168.3	167.1	165.7	175.3	165.6	163.4	160.1
Tail length	2	3	4	1	3	2	1	4
	98.2	96.6	93.1	93.0	98.6	96.2	91.0	89.0
Hind foot length	4	3	2	1	4	3	2	1
	21.6	21.1	20.1	19.5	21.4	21.0	19.9	18.9
Ear length	1	2	4	3	2	1	4	3
	7.1	6.9	6.6	5.6	7.0	6.9	6.5	5.9
Cranium and mandible								
Greatest depth	3	2	1	4	3	1	2	4
	8.7	8.7	8.6	8.5	8.7	8.5	8.5	8.3
Mastoid width	2	3	1	4	3	1	2	4
	13.2	13.2	13.1	12.8	13.1	12.9	12.9	12.6
Greatest length	3	2	1	4	3	2	1	4
	24.6	24.2	23.9	23.8	24.3	24.0	23.6	23.5
Rostral width	3	2	1	4	3	2	1	4
	4.0	4.0	3.8	3.8	4.0	3.9	3.8	3.7
Nasal length	3	2	4	1	3	2	4	1
	9.0	8.7	8.7	8.5	8.8	8.7	8.5	8.3
Nasal width	3	1	2	4	3	1	2	4
	2.2	2.1	2.1	2.0	2.1	2.1	2.1	2.0
Interorbital width	2	3	4	1	3	1	2	4
	6.3	6.3	6.3	6.2	6.3	6.2	6.2	6.2
Maxillary toothrow length	2	3	1	4	2	1	3	4
	3.8	3.7	3.7	3.6	3.7	3.7	3.6	3.6
Maxillary toothrow width	3	1	2	4	3	1	2	4
	4.3	4.2	4.2	4.1	4.2	4.2	4.2	4.1
Interparietal length	2	1	3	4	2	1	3	4
	3.9	3.5	3.5	3.3	3.7	3.5	3.4	3.3

Interparietal width	3	2	1	4	3	1	2	4
	7.9	7.5	7.4	7.3	7.8	7.5	7.3	7.3
Mandible length	3	2	4	1	3	2	4	1
	11.3	11.1	11.0	10.9	11.3	11.0	10.8	10.8

all except hind foot length (*P c* 0.05) were significant at *P c* 0.01. Males were larger for all of the significantly dimorphic characters. Maxillary toothrow length was the only mean value that indicated females may be larger. Sexual dimorphism in the genus *Chaetodipus* has been studied by several investigators (e.g., Anderson, 1964; Wilkins and Schmidly, 1979).

For the Pedro Armendariz lava field, eight characters showed significant size dimorphism (*P c* 0.05, *d.f.* = 1,127-1,147); total length, hind foot length, ear length, greatest depth of cranium, mastoid width, greatest length of cranium, rostral width, and nasal length. The Fra Cristobal sample showed significant size dimorphism in greatest depth of cranium, mastoid width, and interparietal width *P c* 0.05, *d.f.* = 1,25). No characters were sexually dimorphic for the Carrizozo malpais (*d.f.* = 1,19-1,28). Specimens from the Afton lava flows showed significant size dimorphism in six characters; total length, tail length, greatest depth of cranium, mastoid width, rostral width, and nasal length (*P c* 0.05, *d.f.* = 1,86-1,102). Males were largest for all of the dimorphic characters for each locality. Thus, there was considerable variability in the number of characters that were dimorphic among the four localities. Best (1983*b*) suggested that sample size may affect the detection of sexually dimorphic characters in *Dipodomys*. While this may partially be true for the *C. intermedius* studied here, these results indicate there is geographic variation in sexual dimorphism among our samples. Of the sexually dimorphic characters, it appears that variability between sexes for total length was contributed mostly be the Pedro Armendariz and Afton samples, for tail length by the Afton sample, for hind foot length, ear length, and greatest length of cranium by the Pedro Armendariz sample, for greatest depth of cranium and mastoid width by the Pedro Armendariz, Fra Cristobal, and Afton samples, and interparietal width by the Fra Cristobal sample. When all samples had been grouped by sex, ear length and rostral width did not show significant secondary sexual size dimorphism (Table 1).

Interlocality variation.—Significant interlocality heterogeneity was shown by one or both sexes for all characters (*P c* 0.05), except interorbital width (Table 2). Only males showed significant interlocality variation for rostral width (*F* = 19.63, *P c* 0.001), and only females showed significant variability for total length (*F* = 12.50, *P c* 0.001), and mandible length (*F* = 8.60, *P c* 0.01). As evidenced by the *F*-ratios for males, mastoid width, rostral width, nasal width, interparietal length, and interparietal width exhibited the most interlocality variation (*F*-ratio > 15), whereas tail length, hind foot length, and nasal length exhibited the least (*F*-ratio < 6). For females, hind foot length and interparietal length showed the most variation (F-ratio > 25), and the two measurements of the maxillary toothrow the least (F-ratio < 5).

Except for interparietal length and greatest length and depth of cranium, the F-ratios for each character were very different between sexes. Males had much higher values for ear length, mastoid width, rostral width, nasal width, maxillary toothrow length, maxillary toothrow width, and interparietal width. Females were much higher for total length, tail length, hind foot length, nasal length, and mandible length. The differing degrees in interlocality variability between sexes further elucidates the sexual dimorphism in the characters examined.

For both sexes the largest individuals for most of the 16 characters were from the Carrizozo malpais, the smallest were from the Afton lava flows, and the Pedro Armendariz and Fra Cristobal populations were intermediate (Table 2). Mice from the Afton lava flow were significantly smaller than those of other samples for greatest depth of cranium and mastoid width for both sexes, and maxillary toothrow length and interparietal length for males only. The Carrizozo malpais pocket mice were smaller than the other samples in ear length for males, larger for nasal width and interparietal width for males, and larger in total length for females. The Fra Cristobal mice were largest in interparietal length for males, and the Pedro Armendariz specimens were the smallest in hind foot length for females.

Multivariate analyses.—Phenograms for both sexes, constructed from correlation and distance matrices of the 16 characters are presented in Figs. 2A-2D. Each of the correlation phenograms (Figs. 2A and 2B) can be divided into three clusters at a correlation of about 0.15. For both sexes the upper cluster contains the Pedro Armendariz and the Fra Cristobal samples, and the two others are made of the Afton and Carrizozo samples.

Distance phenograms show the same clusters (Figs. 2C and 2D). Thus, the Pedro Armendariz and Fra Cristobal samples are the most similar, and the Afton and Carrizozo samples are different. The Afton sample appears somewhat intermediate between the Carrizozo and the two other samples.

Loadings of characters on the first three component axes are presented in Table 3, and three-dimensional projections are depicted in Figs. 2E and 2F. Character loadings on principal component I for both sexes are high for all characters except total length, interorbital width, and interparietal length for males, rostal width and maxillary toothrow width for females, and hind foot length for both sexes. Following the reasoning of Johnston and Selander (1971), Niles (1973), and Kennedy and Schnell (1978), this component may be taken to represent overall size in both sexes because it accounts for most of the covariation among characters. For both sexes, the Carrizozo sample has the highest loading along component I, and the Afton sample has the lowest (Figs. 2E and 2F). This component accounts for about 60% of the phenetic variation (Table 3). The Carrizozo sample is the largest for most characters (Table 2); thus, the larger animals are to the right side of Figs. 2E and 2F.

On principal component II, hind foot length for both sexes, ear length, and interparietal length for males, and rostral width and maxillary toothrow width for females, have higher loadings than on component I

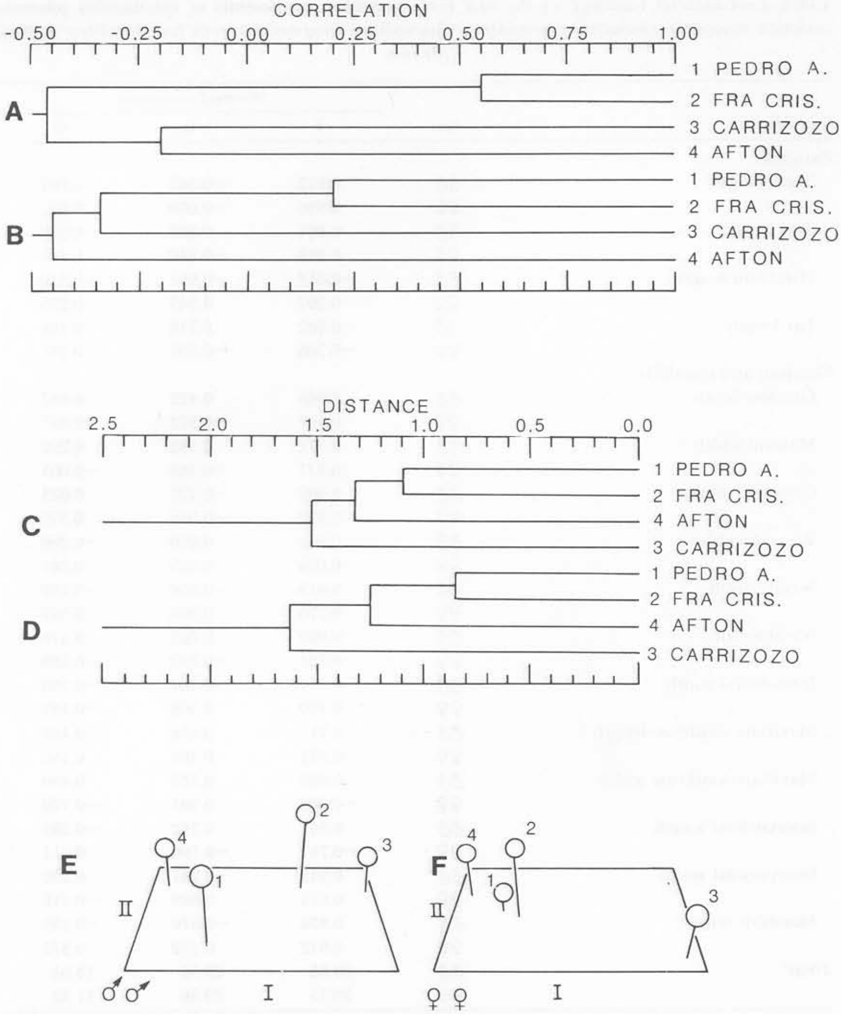

FIG. 2.—Phenograms (A-D) constructed from correlation and distance matrices and three-dimensional projections (E and F) of OTUs onto the first three principal component axes of variation in the matrix of correlations of 16 morphologic characters for *Chaetodipus intermedius*. Analyses for males are depicted in A, C, and D, and for females in B, D, and F. Accuracy of the phenograms in depicting interlocality relationships increases from left to right. The cophenetic correlation coefficients for A-D are 0.982, 0.931, 0.615, and 0.947, respectively.

(Table 3). Other characters for both sexes have only weak associations. The 26% of the variance accounted for by this component for males and the 29% for females (Table 3) is shown by a separation of the Pedro Armendariz sample toward the front of the plots for males (Fig. 2E) and the placement of the Carrizozo sample toward the front of the plot for females (Fig. 2F).

The third principal component for males has highest loadings for total length, tail length, and interorbital width (Table 3). Females have highest

TABLE 3.—*Character loadings*[1] *of the first three principal components of interlocality phenetic variation among 16 characters representing* Chaetodipus intermedius *from four localities in New Mexico.*

Character	Sex	Principal components		
		I	II	III
External				
Total length	♂♂	0.612	−0.507	0.607
	♀♀	0.996	−0.060	0.071
Tail length	♂♂	0.804	0.203	−0.559
	♀♀	0.863	−0.240	0.445
Hind foot length	♂♂	−0.012	−0.951	−0.310
	♀♀	0.207	0.945	0.255
Ear length	♂♂	−0.682	0.718	−0.136
	♀♀	−0.766	−0.595	0.241
Cranium and mandible				
Greatest depth	♂♂	0.905	0.422	0.047
	♀♀	0.927	−0.372	−0.037
Mastoid width	♂♂	0.772	0.592	0.232
	♀♀	0.871	−0.488	−0.063
Greatest length	♂♂	0.992	−0.127	0.023
	♀♀	0.922	−0.086	0.379
Rostral width	♂♂	0.965	0.030	−0.260
	♀♀	−0.094	0.955	0.281
Nasal length	♂♂	0.819	−0.556	−0.139
	♀♀	0.776	0.206	0.597
Nasal width	♂♂	0.909	0.023	0.416
	♀♀	0.861	−0.332	−0.386
Interorbital width	♂♂	0.574	−0.307	−0.759
	♀♀	0.799	0.568	−0.197
Maxillary toothrow length	♂♂	0.717	0.678	−0.163
	♀♀	−0.872	0.464	0.156
Maxillary toothrow width	♂♂	0.805	0.337	0.489
	♀♀	−0.089	0.981	−0.170
Interparietal length	♂♂	0.541	0.742	−0.395
	♀♀	−0.767	−0.198	0.611
Interparietal width	♂♂	0.943	−0.267	0.200
	♀♀	0.675	0.609	−0.416
Mandible length	♂♂	0.876	−0.470	−0.105
	♀♀	0.912	0.170	0.373
Total[2]	♂♂	60.96	25.53	13.51
	♀♀	59.16	29.36	11.48

[1]Correlations of locality mean values of individual characters with the component axes.
[2]Percent of total phenetic variance explained.

loadings for nasal length and interparietal width and much lower loadings for all other characters. About 14% of the phenetic variance is explained by this component for males and 11% for females; no particular trends can be detected along this third component (Figs. 2E and 2F).

The three components explain 100% of the character variation for each sex (Table 3). Thus, distortion of the phenetic distances between localities is minimal when the character space is reduced to three dimensions. Previous principal components analyses of variation in heteromyids have explained a much smaller percentage of the total character variation; for example, in *Dipodomys* (Best, 1978, 1983*b*; Kennedy and Schnell, 1978).

TABLE 4.—*Discriminant analyses between* Chaetodipus intermedius *from four localities in New Mexico.*[1]

Actual group	N cases	Predicted group membership			
		Pedro Armendariz	Fra Cristobal	Carrizozo	Afton
Males					
Pedro Armendariz	68	56(82.4%)	9(13.2%)	0	3(4.4%)
Fra Cristobal	11	0	10(90.9%)	0	1(9.1%)
Carrizozo	16	4(25.0%)	1(6.3%)	10(62.5%)	1(6.3%)
Afton	50	0	0	0	50(100%)
Females					
Pedro Armendariz	82	64(78.0%)	13(15.9%)	2(2.4%)	3(3.7%)
Fra Cristobal	16	4(25.0%)	9(56.3%)	1(6.3%)	2(12.5%)
Carrizozo	14	1(7.1%)	2(14.3%)	10(71.4%)	1(7.1%)
Afton	55	1(1.8%)	2(3.6%)	0	52(84.6%)

[1]86.9% of the males and 80.8% of the females were correctly classified based upon 16 morphologic characters.

This difference is due mostly to the greater percentages of variation represented on principal components II and III.

The placement of the Carrizozo and Afton samples somewhat distant from the other samples in the univariate analyses (Table 2), dendograms (Figs. 2A-2D), and three-dimensional plots (Figs. 2E and 2F) prompted us to use discriminant analyses in separating localities. The discriminant analyses showed reasonably good separations among localities (Table 4). The Afton sample was classified with the greatest accuracy for both sexes; the least accurate classifications were of the Carrizozo sample for males and the Fra Cristobal and Carrizozo samples for females (Table 4). Overall, 87% of the males and 81% of the females were correctly classified in the analyses. Characters contributing the most to the separation of localities were hind foot length, interparietal length, nasal width, and ear length for both sexes. Mastoid width and interparietal width for males, and depth of cranium and nasal length for females also contributed to the separation.

SIGNIFICANCE.—Sexual dimorphism is pronounced in *C. intermedius* from south-central New Mexico. Detection of sexual dimorphism may be related to sample size, but there seems to be considerable geographic variation in the secondary sexual size dimorphism. Perhaps age of the lava fields or the selective pressures of climate, vegetative cover, food, physiology, reproduction, competition, etc., have differentially affected the sexes and localities.

Considering that our samples came from a relatively small area of New Mexico, it was surprising to find 15 of 16 characters exhibited interlocality variation. Among the heteromyids, such a high degree of variability within a small area has been shown in *D. gravipes* (Best, 1983*a*) and *D. ordii* (Schmidly, 1971; Kennedy et al., 1980). We would not expect *C. intermedius* to consistently vary this much throughout its range since our samples are from isolated populations that likely face differing selective pressures and probably have little gene flow with other populations.

Our sample from the Pedro Armendariz lava field showed closest affinities with the Fra Cristobal population. The two populations are separated by sandy habitat that is only 5 km wide. There is either some gene exchange between these two populations or they have not been isolated for very long, or both. Mice from the Afton lava flows, which did not group closely with the other samples, are surrounded by a sandy desert (Elder, 1977). However, the west side of the Afton flows may be no more than 3-5 km from suitable habitats which are also volcanic, but much older (F. F. B. Elder, pers. comm.). Conversely, the Carrizozo malpais, which also did not group closely with the other samples, abutes favorable habitat for *C. intermedius* (Bradt, 1932). However, we were unable to locate specimens from this adjacent area.

Chaetodipus intermedius is closely associated with rocky habitats (Bailey, 1931); in the southwestern deserts these are sometimes widely separated by large expanses of unsuitable substrates. *C. intermedius* appears to be an ideal candidate for investigations of variation between populations isolated on islands of suitable habitat. Perhaps, size of the favorable habitat and proximity to other such areas could be compared to give an idea of the degree and pattern of selection and gene exchange that has taken place.

We are grateful to A. L. Gennaro for assistance during the early phases of this project and for providing facilities at the Eastern New Mexico University Natural History Museum. Funding was provided by the New Mexico Department of Game and Fish Endangered Species Program. Melvin and Felicia Beard collected a large number of the specimens from the Pedro Armendariz lava field. The following persons also provided valuable assistance during the study. G. Oty, D. Weckerly, N. Oty, D. Beard, H. Pierce, H. James, and C. Sanford. We thank the curators and museum assistants at the following collections for access to specimens and equipment: Museum of Southwestern Biology, University of New Mexico, Albuquerque; Museum of Vertebrate Zoology, University of California, Berkeley; Museum of Zoology, University of Michigan, Ann Arbor; Natural History Museum, Eastern New Mexico University, Portales; and The Museum, Texas Tech University, Lubbock. Y. Ramsey prepared the figures, S. A. Reza assisted in proofreading, and F. F. B. Elder, D. F. Williams, M. L. Kennedy, G. D. Baumgardner, and two anonymous reviewers critically evaluated the manuscript.

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