EFFECTS OF ENVIRONMENT ON PHENOTYPIC VARIATION AND SEXUAL DIMORPHISM IN *DIPODOMYS SIMULANS* (RODENTIA: HETEROMYIDAE)

ROBERT MILES SULLIVAN AND TROY L. BEST

Department of Biology, Box 3AF, and Department of Fisheries and Wildlife Sciences, New Mexico State University, Las Cruces, NM 88003-8002 (RMS)
Department of Zoology and Wildlife Science and Alabama Agricultural Experiment Station, 331 Funchess Hall, Auburn University, AL 36849-5414 (TLB)

The magnitude of sexual dimorphism in size among populations of some small mammals living in different habitats may be a reflection of the degree of habitat partitioning between sexes or nutritional quality of available food. We tested these hypotheses by quantifying between-sex differences in size in populations of the Dulzura kangaroo rat (*Dipodomys simulans*) from several macrohabitat types at regional and local geographic scales. On a regional scale, our results indicated a significant shift in morphology of males and females along a north-south latitudinal gradient. Large kangaroo rats inhabited warm and arid southernmost latitudes, whereas small animals inhabited relatively cool and moist regions to the north. This morphologic gradient represented an increase in size with less seasonal variation in precipitation and temperature. This pattern was clearly counter to Bergmann's rule, but consistent with the hypothesis that temporal variation in availability of food may be an important factor leading to geographic variation in size. External and cranial measures of size dimorphism were not correlated significantly with any major geographic factor, and only cranial measures were associated significantly with variation in climate. At a local level, kangaroo rats living in different vegetation communities within the same latitudinal zone also exhibited significant sexual dimorphism in size; however, macrohabitat heterogeneity appeared to affect males and females equally. Both sexes were larger in Sierran Montane Conifer Forest and Californian Chaparral macrohabitats. Smaller animals occupied Californian Grassland and Coastal-scrub, and Vizcaino vegetation communities. This pattern of variation was observed in all three-way comparisons and suggests the possibility of habitat-mediated phenotypic responses. Finally, only one of eight comparisons involving kangaroo rats living in adjacent plant communities showed a significant two-way interaction between dimorphism and macrohabitat type. Our results, therefore, did not provide strong evidence to substantiate the hypotheses that the magnitude of dimorphism among populations of *D. simulans* living in different macrohabitats is a reflection of the degree of partitioning between sexes or nutritional quality of available food.

Key words: *Dipodomys*, geographic variation, morphology, sexual dimorphism, kangaroo rat, California, Baja California, Mexico

Several studies have shown that distributions of heteromyid rodents are correlated with structure of vegetation and differences exist in use of resources between co--existing species (Beatley, 1976; Brown and Lieberman, 1973; Kotler, 1985; Price, 1978; Reynolds, 1950; Rosenzweig, 1973; Rosenzweig and Winakur, 1969; Rosenzweig et al., 1975). Underlying these studies is the assumption that a functional relationship exists between use of habitat and morphology (Brown, 1975). Price (1978) suggested, that when this functional relationship is understood, it may be feasible to predict the morphology of resident rodents from assessments of vegetation or habitat

structure, and thus gain support for the theory that competitive divergence and availability of resources affect the structure of communities of competing species. Resources also may be partitioned by conspecific individuals of the opposite sex. Bowers and Smith (1979) showed that in heterogeneous communities, female *Peromyscus maniculatus* inhabited more favorable, moist habitats, whereas males occupied less favorable, xeric areas. Moreover, differences between sexes in external size and home-range size were correlated positively with structure of habitat. Dominance by females presumably functioned to maximize reproductive effort and survival of young. Bowers and Smith (1979) hypothesized that dimorphism in external size may arise from disruptive selection operating on sex-linked traits, and the magnitude of size dimorphism among populations living in different habitats is perhaps a reflection of the degree of habitat partitioning between sexes. Similarly, Smith and Patton (1980, 1984) suggested that nutritional quality of available food directly affects variation in external size among populations of *Thomomys bottae*; thus, factors that influence external size, such as quality of habitats, thereby influence levels of sexual dimorphism (Patton and Brylski, 1987).

Sexual dimorphism in *D. simulans* (previously, part of *D. agilis*) has been reported in some populations from southern California and Baja California (Best, 1978, 1983, 1993; Best et al., 1986). Additionally, the ecological distribution of *D. simulans* encompasses six major macrohabitats ranging from sparsely vegetated deserts to conifer forests (Fig. 1; Brown and Lowe, 1982). At several sites, vegetation changes in succession from coastal sage, chaparral, evergreen woodland, and pinyon pine, to conifer forest at higher elevations in the mountains (Cody et al., 1983). Thus, *D. simulans* provides a unique opportunity to test the pattern predicted by the hypotheses that differential use of resources by sexes (Bowers and Smith, 1979) or quality of habitats (Patton and Brylski, 1987) may promote sexual dimorphism in size. Herein, we use kangaroo rats as an index of quality of habitats. We assumed, based on studies by Daly and Patton (1986), Patton and Brylski (1987), and Smith and Patton (1980, 1984), that productive habitats are characterized by significantly larger animals compared to less productive areas that select for small size. Following the logic of Bowers and Smith (1979) and Patton and Brylski (1987), we predicted that the degree of sexual dimorphism in size would be largest in populations inhabiting these more productive vegetation communities. We realized, however, that the magnitude of these effects depends largely on availability of resources and the extent to which requirements of males and females overlap.

Materials and Methods

Morphologic characters and statistical techniques.—A series of 18 external and cranial characters (Table 1) was measured for 1,554 adults from throughout the range of *D. simulans* (818 males and 736 females; Fig. 1). Characters used included length of body, length of tail, length of hind foot, length of ear, basal length of cranium, greatest length of cranium, spread of maxillary arch, interorbital width, nasal length, intermaxillary width, length of alveolar toothrow, width of maxillary arch, basioccipital length, greatest depth of cranium, greatest width of cranium, zygomatic width, and nasal width. Methods of measuring and aging techniques followed Best (1978, 1983, 1993). All statistical procedures used the BIOΣTAT I and II computer packages (Pimentel and Smith, 1986*a*, 1986*b*). Because size relationships are characteristically allometric (Bookstein et al., 1985), characters were transformed to their natural logarithms. Log-transformation results in a high degree of linearity of the size component of the data (Owen, 1988), legitimizes linear statistics used in the analysis (Humphries et al., 1981), and approximates independence from the relative magnitude of the original variables (Pimentel, 1979). Characters were tested for univariate normality by use of the Kolmogorov-Smirnov *D*-statistic.

Separate multivariate analyses were performed on suites of both external and cranial

TABLE 1.—*Single-classification analysis of variance (ANOVA) of the differences in external and cranial characters among female and male* Dipodomys simulans, *average ± 1SD in parentheses,* D *= generalized distance (Mahalanobis' distance—Pimentel, 1979);* d.f. *= 1,549. Extent of geographic variation among males and females;* F*-ratio derived from single-classification ANOVA,* d.f. *= 21,793 (for males) and 21,714 (for females);* n *= sample size.*

	Extent of dimorphism between males and females (ANOVA)				Extent of geographic variation among populations of each sex (ANOVA)	
	Males	Females			Males	Females
Character	(n = 851)	(n = 736)	F-ratio	D	F-ratio	F-ratio
Length of body	115.0 (6.6)	113.4 (5.4)	24.0***	0.249	4.1***	4.1***
Length of tail	170.2 (11.0)	167.2 (11.0)	19.5***	0.224	6.6***	5.4***
Length of hind foot	41.6 (1.6)	41.1 (1.4)	44.4***	0.339	7.4***	8.4***
Length of ear	14.7 (2.2)	14.5 (2.0)	7.5**	0.139	8.3***	7.8***
Basal length of cranium	21.8 (0.6)	21.6 (0.6)	34.9***	0.300	6.6***	7.8***
Greatest length of cranium	39.3 (1.0)	38.9 (1.0)	4.4*	0.107	7.5***	7.4***
Spread of maxillary arch	20.8 (0.7)	20.6 (0.8)	1.5	0.061	7.5***	7.5***
Interorbital width	10.6 (0.7)	10.5 (0.5)	1.7	0.066	2.6***	2.0***
Nasal length	14.1 (0.5)	13.9 (0.6)	2.8	0.085	3.1***	2.4***
Intermaxillary width	7.4 (0.3)	7.4 (0.3)	0.3	0.029	11.8***	7.1***
Length of alveolar toothrow	4.9 (0.3)	4.9 (0.3)	0.3	0.027	3.8***	4.5***
Lacrimal length	3.6 (0.3)	3.6 (0.3)	1.3	0.058	4.0***	3.8***
Width of maxillary arch	4.9 (0.3)	4.9 (0.3)	1.0	0.058	3.7***	4.6***
Basioccipital length	5.7 (0.3)	5.6 (0.3)	31.0***	0.280	3.7***	4.2***
Greatest depth of cranium	13.3 (0.3)	13.2 (0.3)	29.6***	0.277	10.8***	11.5***
Greatest width of cranium	24.6 (0.8)	24.4 (0.7)	30.4***	0.279	21.3***	21.8***
Zygomatic width	10.9 (0.7)	18.8 (0.6)	12.1**	0.177	5.3***	5.0***
Nasal width	3.7 (0.2)	3.6 (0.2)	19.9***	0.227	9.8***	7.8***

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

characters. Multivariate analysis of variance (MANOVA) was used to assess the statistical significance of interpopulation variation. Principal-components analysis, employing the variance-covariance matrix (Patton and Brylski, 1987), was used to generate a reduced set of orthogonal vectors from log-transformed characters. A multivariate measure of geographic variation was obtained for each sex by use of canonical analysis of discriminance, by reducing the multidimensional character space to one dimension.

Multivariate measures of sexual dimorphism in size were obtained in two ways. First, an overall measure of dimorphism was obtained by use of MANOVA to separate maximally the sexes on a sample-by-sample basis. Discriminant-function analysis using Geisser classification probabilities quantified overlap between males and females, with prior probabilities based on sizes of samples. Discriminant-space distances (D^2, Mahalanobis' distances), in standard-deviation units between centroids, were constructed between the sexes for each site; the greater the magnitude of the distance the greater the difference between males and females (Pimentel, 1979; Pimentel and Smith, 1986*b*). As a second measure of dimorphism, we used the difference between values of the factor scores of centroids for males and females for each sample on the first principal component (Price, 1984). Separate MANOVAs and principal-components analyses were preformed on external (external-size index) and cranial characters (cranial-size index). Body mass was not used in estimating dimorphism, because it is more subject to variation in nutritional status, health, age, or reproductive condition than other characters (Alexander et al., 1979; Ralls, 1976, 1977).

Measures of macrohabitat heterogeneity.—Populations of *D. simulans* were grouped into samples obtained from six major biotic communities, including Sierran Montane Conifer Forest (forest formation), Californian Chaparral

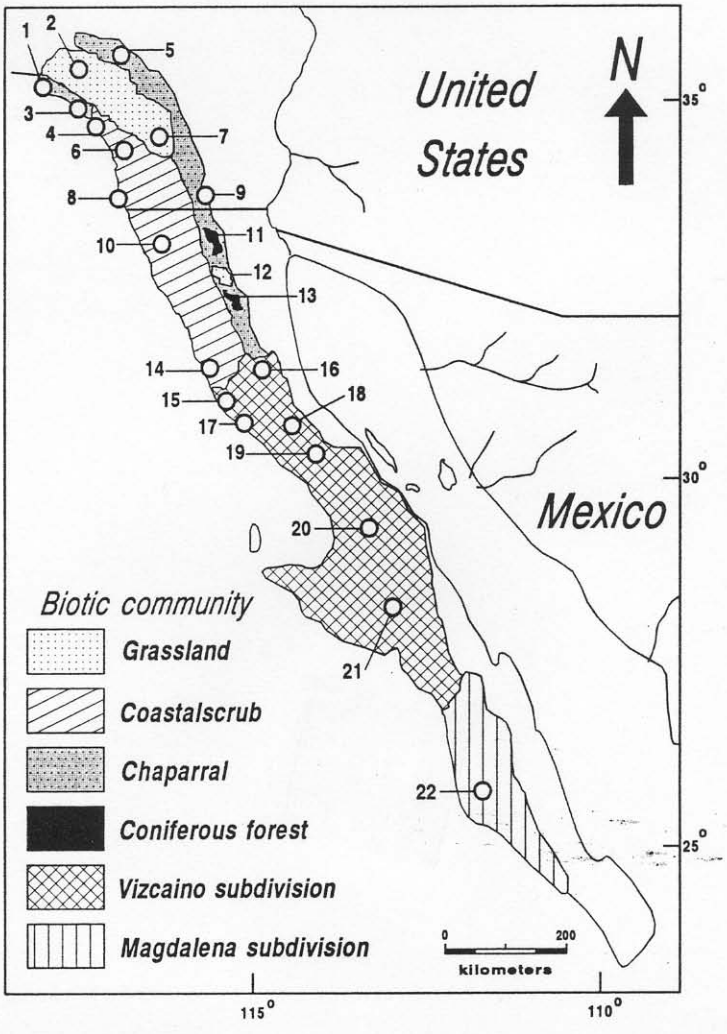

FIG. 1.—Distribution of populations of *Dipodomys simulans* sampled in southern California and Baja California: 1, Soliment (Santa Clara River, Mint Canyon, foothills of Santa Monica Mountains); 2, Los Angeles (foothills of San Gabriel Mountains, San Fernando Valley); 3 Cajon (Riverside, foothills of San Bernardino Mountains); 4, Lake Mathews; 5, Cabazon; 6, San Luis Rey Valley; 7, Warner Springs; 8, San Diego; 9, Jacumba; 10, Ensenada; 11, Sierra Juarez; 12, Valle de Trinidad; 13, San Pedro Martir; 14, San Quintin Plain; 15, El Rosario; 16, San Agustin; 17, Santa Catarina; 18, Laguna Chapala; 19, San Andres (Rosarito, Mission de San Borja); 20, Mezquital (El Arco, San Francisquito Bay); 21, San Ignacio; 22, Magdalena Plain.

(scrub formation), Coastal-scrub (scrub formation), Californian Coastal Grassland (grassland formation), Magdalena Subdivision (desert formation), and Vizcaino Subdivision (Brown and Lowe, 1982). On a geographic scale, these macrohabitats are distributed throughout 9° of latitude. Within most latitudinal bands, distinct elevational gradients in species composition of plants extend inland from the Pacific coast to the central highlands. This array of communities, each with its unique edaphic, climatic, and vegetational characteristics, represents a gradient of macrohabitat heterogeneity on a local scale.

To simultaneously assess the statistical significance of between-sex and among-habitat variation, and the interaction between sex and macrohabitat, adjacent populations of kangaroo rats inhabiting different vegetation-macrohabitat

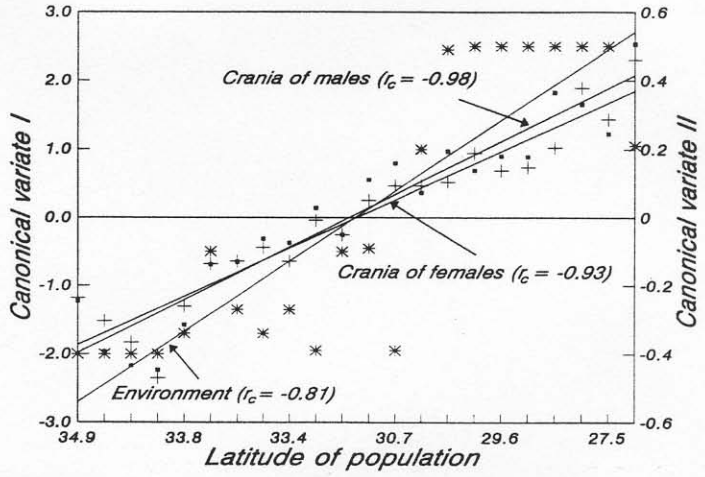

FIG. 2.—Correlations between latitude of sampled population and the first canonical variate of cranial morphology for male and female *Dipodomys simulans* and the first principal component of environmental variation associated with temperature and precipitation.

communities within each latitudinal band were compared by use of a two-way analysis of variance with sex and macrohabitat defining the cells (Price, 1984; Rising, 1987). Four tests were performed on the following pairs or suites of populations representing different macrohabitats: comparison I (populations 2, 3, and 4); comparison II (populations 7, 8, and 9); comparison III (populations 10, 11, and 12); comparison IV (populations 13, 14, and 15). Scores of males and females on the first principal component of external- and cranial-size characters (two separate analyses) were used in the two-way analyses of variance. Comparisons involving more than two macrohabitat types were followed by an a posteriori contrast analysis using the Student-Newman-Keuls multiple-range test (Pimentel and Smith, 1986*b*; Sokal and Rohlf, 1981).

RESULTS

Extent of sexual dimorphism.—A test of the equality of group centroids (MANOVA) showed significant dimorphism in size between sexes of *D. simulans* ($F = 5.4$, *d.f.* = 18,1000, $P < 0.001$). *F*-values produced by the single-classification analysis of variance (ANOVA) showed that males were significantly ($P < 0.05$) larger then females in 61% (11 of 18) of the characters examined (Table 1). Discriminant-function analysis of all characters simultaneously correctly assigned 68% (males) and 52% (females) of the specimens to their respective sex.

Between-sex geographic variation.—Using only external characters, a test of the equality of group centroids was significant for males ($F = 5.5$, *d.f.* = 84,3122, $P < 0.001$) and females ($F = 5.3$, *d.f.* = 84,2810, $P < 0.001$). Similarly, analysis of cranial characters showed significant geographic variation among populations of both sexes (for males $F = 4.9$, *d.f.* = 294,9162, $P < 0.001$; for females $F = 4.9$, *d.f.* = 294,8238, $P < 0.001$). Discriminant-function analysis of external characters correctly classified 19 and 22% of the females and males to their respective populations; using cranial characters the percentages were 32 and 34%. ANOVA revealed significant ($P < 0.05$) heterogeneity among populations of males and females in all morphological characters (Table 1). On the first canonical vector, the distribution of population centroids for both sexes showed a highly significant ($P < 0.001$, *d.f.* = 20) shift in morphology along a north-south latitudinal gradient (Fig. 2). For both sexes, the largest *D. simulans* inhabited the south-

ernmost latitudes, whereas smaller animals characterized populations on northern sites. This pattern was consistent with findings of Best (1981) for selected populations distributed throughout Baja California.

Principal-components analysis of environmental variables associated with each site accounted for 99% of the variation on the first axis. The percentage of the variance of each variable contributing to the first component was 100 and 47% for average annual rainfall and average annual temperature, respectively. Examination of factor loadings showed that the first component was highly correlated with average annual rainfall ($r_c = -1.0$) and average annual temperature ($r_c = 0.68$). In the northern part of the range, high positive loadings indicated relatively moist and mild climates compared to southern sites where conditions were warm and arid. Because virtually all variability was contained in the first component, it was justifiable to treat this vector as representing a "real" environmental gradient (Rotenberry, 1978). A plot of population centroids along the first component against latitude showed a significant large-scale gradient associated with variation in precipitation and temperature (Fig. 2). Further, the distribution of population centroids along the first canonical vector of cranial morphology, but not external morphology, was correlated significantly with this climatic gradient for both sexes of *D. simulans* (for males $r_c = 0.791$. $P < 0.001$, *d.f.* = 20; for females $r_c = 0.768$, $P < 0.001$, *d.f.* = 20).

Geographic variation in sexual dimorphism.—Multivariate analyses of variance indicated significant overall dimorphism in size in 23 and 18% of the populations ($n = 22$) using external and cranial characters, respectively (Table 2). Average D^2-values for external characters ranged from 0.38 (Warner Springs) to 1.30 (Los Angeles); the average ± 1*SD* was 0.74 ± 0.22. Average D^2-values for cranial characters ranged from 0.73 (Lake Matthews) to 3.60 (Santa Catarina); the average ±1*SD* was 1.42 ± 0.66. There was no significant correlation ($r_c < 0.10$, $P > 0.05$, *d.f.* = 20) between degree of sexual dimorphism (as measured by D^2-values) in external or cranial characters and latitude of the population. However, although there was no significant association between D_2-values of external morphology and environmental attributes of each site ($r_c = -0.15$, $P > 0.05$, *d.f.* = 22), D^2-values of cranial morphology were correlated significantly with the composite vector (PCI) of temperature and rainfall ($r_c = 0.442$, $P = 0.03$, *d.f.* = 22).

Principal-components analysis (of both sexes simultaneously) accounted for 68% of the variation among populations along the first axis based on external characters and 65% of the variation among populations based on cranial characters (Table 3). Average correlation of external characters with PC1 ranged from −0.492 (San Ignacio) to 0.706 (San Pedro Martir); whereas, among cranial characters the average correlation ranged from 0.330 (Cajon) to 0.701 (San Ignacio). Because all cranial characters were positive and correlated significantly with the first component (average r_c ranged from 0.329 to 0.701), this vector can be interpreted as a measure of size (Patton and Brylski, 1987; Rising, 1987). However, there was no significant correlation ($P > 0.05$, *d.f.* = 20) between the cranial-size index (i.e., difference between factor scores of males and females for each site on PC1) and latitude ($r_c = -0.060$). Moreover, in some populations (Soliment and Magdalena Plain), the cranial-size index was reversed.

Sexual variation among macrohabitats.—Results of the multivariate analysis of variance showed significant variation in external and cranial morphology among *D. simulans* occupying different macrohabitat types. For external morphology, a test of the equality of group centroids was significant for males ($F = 5.5$, *d.f.* = 84,3122; $P < 0.001$) and females ($F = 5.8$, *d.f.* = 20,1000; $P < 0.001$). For cranial morphology, the MANOVA also was significant for males ($F = 4.9$, *d.f.* = 294,9162; $P <$

TABLE 2.—*Results of multivariate analysis of variance (MANOVA) and distance analysis (D^2) between males and females from each population. External and cranial characters were considered different indices of dimorphism between sexes and, therefore, they were analyzed separately. Geographic position of each population is indicated in Fig. 1.*

Population	Sample sizes		External characters			Cranial characters		
	Males	Females	*F*-value	*d.f.*	D^2	*F*-value	*d.f.*	D^2
Soliment	13	16	2.5	4,24	1.253	0.4	14,14	1.205
Los Angeles	10	22	2.5	4,27	1.280	1.9	14,17	2.631
Cajon	13	24	1.1	4,32	0.757	0.5	14,22	1.121
Lake Mathews	80	16	2.1	4,136	0.499	1.2	14,126	0.734
Cabazon	50	47	2.2	4,92	0.614	1.1	14,82	0.856
San Luis Rey Valley	72	45	3.2*	4,112	0.681	1.5	14,102	0.917
Warner Springs	30	22	0.4	4,47	0.377	1.1	14,36	1.219
San Diego	37	32	1.9	4,64	0.679	1.2	14,54	1.108
Jacumba	38	31	2.1	4,64	0.722	0.9	14,54	0.976
Ensenada	24	31	2.9*	4,50	0.948	1.0	14,40	1.145
Sierra Juarez	43	43	1.6	4,81	0.562	1.4	14,71	1.039
Valle de Trinidad	111	123	6.2***	4,229	0.656	3.6***	14,219	0.976
San Quintin Plain	46	41	3.6**	4,82	0.824	1.7	14,72	1.145
San Pedro Martir	25	12	1.2	4,32	0.798	0.8	14,22	1.466
El Rosario	14	15	0.6	4,24	0.608	1.0	14,14	1.920
San Agustin	49	27	1.4	4,71	0.580	3.6***	14,61	1.878
Santa Catarina	12	14	0.7	4,21	0.679	2.3	14,11	3.564
Laguna Chapala	31	28	1.8	4,54	0.719	1.5	14,44	1.315
San Andres	28	17	1.7	4,40	0.833	2.4*	14,30	2.134
Mezquital	44	34	4.0**	4,72	0.933	2.0*	14,63	1.339
San Ignacio	22	22	0.6	4,39	0.485	0.7	14,29	1.167
Magdalena Plain	23	29	1.7	4,47	0.758	1.3	14,37	1.373

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

0.001) and females ($F = 8.9$, *d.f.* = 70,1000; $P < 0.01$). Single classification ANOVAs showed significant ($P < 0.05$) morphologic heterogeneity among macrohabitats in all external characters for both males and females, and in 100 and 93% of the cranial characters for males and females, respectively.

Discriminant-function analysis of external characters correctly classified an average of 40% of males and 36% of females to their respective vegetation types; using cranial characters, 53% of males and 50% of females were classified correctly (Fig. 3). The distribution of macrohabitat centroids along the first canonical discriminate-function of external characters plotted above and below the origin. The largest individuals ploted above the origin and inhabited Valley Grassland and Coastal-scrub macrohabitats (Fig. 4*a*) Conversely, the distribution of macrohabitat centroids along the first canonical vector of cranial characters showed that the largest individuals occurred in the Magdalena Region, followed by the Vizcaino Subdivision, Sierra Montane Conifer Forest, Valley Grassland, Coastal-scrub, and Californian Chaparral (Fig. 4*b*). For each macrohabitat type, 95% confidence intervals surrounding group centroids were much larger for external characters than for cranial characters. Thus, these data, as well as results of the analysis of geographic variation, suggested that cranial morphology probably was a better indicator of variation in size of *D. simulans* than were external characters. This statistical pattern probably resulted from the accumulated error of using data on specimen labels that had been measured by different investigators. At this regional scale, however, the distribution of macrohabitat types

TABLE 3.—*Results of principal-components analyses of males and females from each population. External and cranial characters were considered different indices of dimorphism between sexes; therefore, they were analyzed separately. Geographic position of each population is indicated in Fig. 1. For each population the average correlations (r_c) of external and cranial characters with PCI also are given. Sample sizes for males and females from each population are given in Table 2.*

	External characters			Cranial characters		
	Males	Females		Males	Females	
Population	$\bar{X}$ (±1 *SD*)	$\bar{X}$ (±1 *SD*)	r_c	$\bar{X}$ (±1 *SD*)	$\bar{X}$ (±1 *SD*)	r_c
Soliment	0.000 (0.03)	−0.001 (0.04)	0.674	−0.002 (0.00)	0.002 (0.04)	0.646
Los Angeles	0.008 (0.03)	−0.004 (0.03)	−0.435	0.010 (0.04)	−0.004 (0.03)	0.548
Cajon	0.021 (0.05)	−0.011 (0.05)	0.593	0.011 (0.07)	−0.005 (0.03)	0.330
Lake Mathews	0.008 (0.06)	−0.011 (0.05)	0.475	0.008 (0.03)	−0.010 (0.04)	0.552
Cabazon	0.009 (0.06)	−0.013 (0.06)	0.439	0.008 (0.03)	−0.008 (0.05)	0.467
San Luis Rey Valley	−0.002 (0.04)	0.004 (0.04)	−0.198	0.002 (0.03)	−0.004 (0.03)	0.557
Warner Springs	0.001 (0.06)	−0.002 (0.06)	0.418	0.000 (0.04)	−0.001 (0.03)	0.419
San Diego	−0.001 (0.04)	0.002 (0.03)	−0.287	0.008 (0.03)	−0.009 (0.03)	0.532
Jacumba	−0.009 (0.04)	0.009 (0.06)	0.352	0.004 (0.04)	−0.005 (0.03)	0.585
Ensenada	−0.010 (0.06)	0.009 (0.05)	−0.129	0.011 (0.04)	−0.009 (0.04)	0.544
Sierra Juarez	−0.006 (0.05)	0.004 (0.05)	−0.255	0.009 (0.03)	−0.008 (0.03)	0.452
Valle de Trinidad	−0.004 (0.05)	0.006 (0.05)	−0.250	0.008 (0.04)	−0.008 (0.03)	0.542
San Quintin Plain	−0.005 (0.04)	0.007 (0.03)	−0.270	0.009 (0.03)	−0.010 (0.04)	0.589
San Pedro Martir	0.004 (0.03)	−0.008 (0.03)	0.706	0.000 (0.03)	−0.001 (0.02)	0.571
El Rosario	0.010 (0.05)	−0.008 (0.05)	0.132	0.009 (0.04)	−0.008 (0.03)	0.590
San Agustin	0.001 (0.06)	−0.003 (0.07)	−0.425	0.003 (0.03)	−0.006 (0.04)	0.589
Santa Catarina	0.021 (0.08)	−0.018 (0.08)	0.666	0.002 (0.04)	−0.002 (0.03)	0.388
Laguna Chapala	0.001 (0.04)	0.000 (0.03)	−0.040	0.003 (0.03)	−0.002 (0.03)	0.531
San Andres	−0.001 (0.07)	0.001 (0.08)	0.619	0.003 (0.04)	−0.005 (0.03)	0.385
Mezquital	0.013 (0.07)	−0.015 (0.06)	0.481	0.008 (0.04)	−0.013 (0.03)	0.578
San Ignacio	−0.015 (0.08)	0.015 (0.07)	−0.492	0.003 (0.04)	−0.002 (0.05)	0.701
Magdalena Plain	0.013 (0.06)	−0.011 (0.07)	0.529	−0.004 (0.03)	0.003 (0.03)	0.519

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

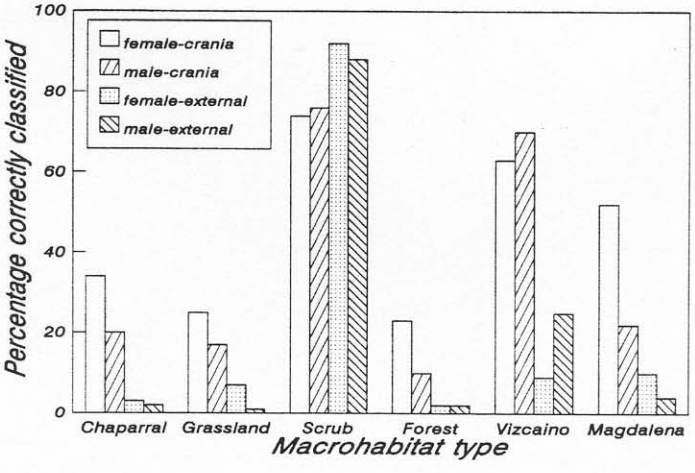

FIG. 3.—Percentage of male and female *Dipodomys simulans* correctly classified to habitat type by use of canonical analysis of discriminance (MDA BIOΣTAT II—Pimentel and Smith, 1986*b*).

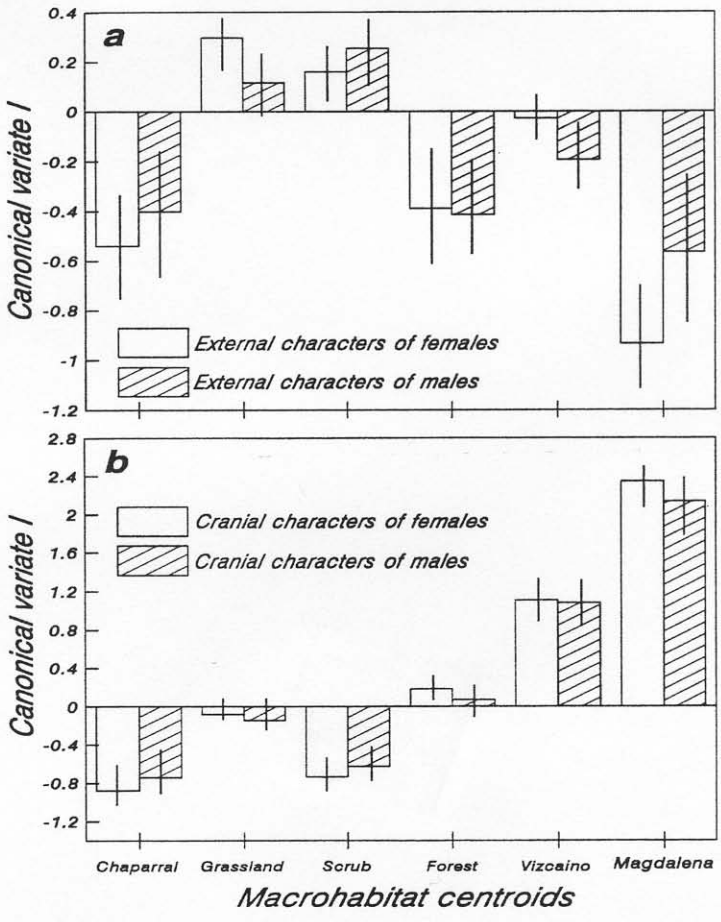

FIG. 4.—Distribution of centroids along the first canonical variate of morphology among different macrohabitat types. Males are indicated by stippling, females by shading.

probably is not divorced from the environmental effects associated with latitude. For example, the distribution of size variation in cranial morphology of both males and females in each macrohabitat type, suggests a clinal pattern of variation concordant with earlier assessments of variation over geographic distance, and without reference to particular plant communities.

Sexual dimorphism among macrohabitats.—The two-way analyses of variance showed that at a local level, *D. simulans* living in different macrohabitats at about the same latitude also exhibited significant size dimorphism in overall dimensions of the cranium (50% of comparisons), but not in overall dimensions of external characteristics (Table 4). Although dimorphism in size was significant in only 50% of the two-way analyses of variance, males were larger than females in all comparisons involving cranial morphology. Further, in 75% of comparisons involving cranial characters, large-sized kangaroo rats occurred in Sierra Montane Conifer Forest or Californian Chaparral, whereas small-sized *D. simulans* occurred in Coastal-scrub, California Grassland, or Vizcaino vegetative communities (Table 4).

The two-way interactions between sex and macrohabitat were significant in 75% of the comparisons involving overall cranial morphology, yet inconsistencies existed. For example, although a significant inter-

TABLE 4.—*Summary of the two-way analysis of variance testing for effects of sex and macrohabitat for samples of male and female kangaroo rats (*Dipodomys simulans*). Statistically homogeneous subsets derived from the Student-Newman-Keuls multiple-range test following the analysis of variance. Variation in averages (read small to large from left to right) of habitat. Data used were scores for specimens on the first principal component of external and cranial characters.*

			External characters				Cranial characters		
Comparison	*d.f.*	*F*-ratio	Multiple-range test			*F*-ratio	Multiple-range test		
Comparison I			Grassland	Coastal-scrub	Chaparral		Grassland	Coastal-scrub	Chaparral
Sex	1	2.5 ns				5.2***			
Habitat	2	0.9 ns				4.0***			
Interaction	2	2.2 ns				3.3*			
Error	204								
Comparison II			Coastal-scrub	Grassland	Chaparral		Coastal-scrub	Grassland	Chaparral
Sex	1	0.0 ns				0.0 ns			
Habitat	2	0.8 ns				2.0 ns			
Interaction	2	0.6 ns				4.3*			
Error	184								
Comparison III			Grassland	Coastal-scrub	Forest		Grassland	Coastal-scrub	Forest
Sex	1	0.9 ns				0.1 ns			
Habitat	1	0.5 ns				6.2**			
Interaction	2	1.9 ns				9.8***			
Error	369								
Comparison IV			Vizcaino	Coastal-scrub	Forest		Vizcaino	Coastal-scrub	Forest
Sex	1	1.6 ns				6.1***			
Habitat	1	1.7 ns				3.0*			
Interaction	2	0.9 ns				2.3 ns			
Error	147								

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ns = $P > 0.05$.

action was indicated in three of the comparisons (Table 4), there was no significant sexual dimorphism (comparison II and III) or habitat separation (comparison II) in two of these. Only the first comparison involving cranial characters showed significant size dimorphism associated with sex and macrohabitat, coupled with a significant interaction between sex and macrohabitat.

Discussion

Geographic patterns of variation.—Smith and Patton (1980, 1984) hypothesized that differences in nutritional quality of available food resources can directly affect variation in external size among populations of *T. bottae*. Studies by Patton and Brylski (1987) supported this hypothesis by demonstrating significant shifts in external-size characteristics between *T. bottae* sampled from areas of natural vegetation and those obtained from alfalfa fields. Moreover, these authors showed that dimorphism was highly correlated with average size of adult males in the population, but not with size of females. Because males do not breed the first year, they continue to grow, but females do not. Thus, factors that influence external size, such as quality of habitat, also may influence levels of sexual dimorphism (Daly and Patton, 1986; Patton and Brylski, 1987).

A similar shift in size-related characteristics occurs in *D. simulans*, because parallel patterns of size variation at both regional and local geographic scales were suggested by our data. For example, geographic variation in size among populations of both sexes showed a clinal pattern of variation that was significantly correlated with latitude; small individuals predominated in the northern latitudes and large individuals characterized southern sites. Analysis of climatic attributes, indicate that northern areas are more equable (Harris, 1987) than southern sites because of more moist and mild climatic regimes to the north. Whereas southern sites presumably are subject to substantial variation in availability of food due to an unpredictable precipitation regime. Thus, on a regional scale, the prediction that the largest-sized *D. simulans* should be found in more equable northern parts of the species' range is not supported by our results. This pattern of size distribution is contrary to Bergmann's rule, that geographically variable species of homeotherms are represented by relatively larger races in colder parts of their ranges than in warmer parts (James, 1970; Kendeigh, 1969; Lasiewski and Dawson, 1967). Instead, strong geographic variation in external size exhibited by *D. simulans*, may indicate that temporal variation in availability of food resources could be an important factor leading to geographic variation in size (Boyce, 1978, 1979, 1988); however, this more "proximate-level" ecological hypothesis, as well as the inherent sociobiological implications, such as sexual selection, have not been examined. Because patterns of geographic variation in size are now defined, investigations of social behavior and use of resources by *D. simulans* clearly warrant future study. In addition, the thermoregulatory implication of this ecomorphologic pattern is that populations of homeotherms from cooler climates tend to have larger external size, hence smaller surface-to-volume ratios than related populations living in warmer climates (Brown and Gibson, 1983). Given the resolution of our data, to propose a mechanism that causes *D. simulans* to be large in the southern parts of its range and small in the north is to engage in considerable speculation. Nevertheless, physiologically a number of factors favor large external size in warm and arid climates as opposed to cooler and wetter areas, including higher thermal inertia, lower rates of mass-specific heat production, and smaller surface area for absorbing heat by radiation and convection (Lindstedt and Boyce, 1985; Owen, 1989).

The magnitude of dimorphism, measured by the generalized distance or principal-components analyses of size-related characteristics, did not exhibit a significant cor-

relation with latitude or climatic variation. Lack of a coordinated response to an environmental factor in a significant and potentially interpretable way implies that the extent of dimorphism in kangaroo rats may be largely random, or uninteresting noise (Gauch, 1982) associated with temporally uneven sampling periods. For many species of mammals, including pocket gophers (Geomyidae), insufficient detail is available regarding the geographic extent of sexual dimorphism in size and the pattern of relationship to habitat heterogeneity (Patton and Brylski, 1987). In populations of savanna sparrows (*Passerculus sandwichensis*), lack of significant geographic variation in extent of dimorphism was attributed to conservatism in evolution of size dimorphism in polygenic structures such as external size and shape of bill (Lande, 1980; Rising, 1987).

Local patterns of variation.—At a local level, variation in external and cranial size characteristics of *D. simulans* indeed may be associated with the structural complexity of adjacent macrohabitats. Animals living in presumably more structurally diverse plant communities (coniferous forest and chaparral vegetation) within the same latitudinal zone appear to exhibit an increase in overall cranial-size characteristics compared to animals living in macrohabitats that are presumably less structurally diverse. Sexual dimorphism in size also is well developed in *D. simulans* and large animals of both sexes generally occupy these macrohabitats, yet there was no conspicuous interaction between dimorphism and type of macrohabitat. Instead, large individuals of both sexes tended to occupy relatively more heterogeneous vegetation communities, whereas smaller individuals of either sex generally occupied less heterogeneous areas. Because productivity of habitats presumably affects the sexes equally, there appears to be insufficient evidence of an interaction between sex and "productivity" as indexed by overall size in external or cranial characters. In *D. simulans*, these results, therefore, do not provide strong evidence to substantiate the hypothesis (Bowers and Smith, 1979) that the magnitude of dimorphism among populations living in different macrohabitats is a reflection of the degree of habitat partitioning between sexes, or that nutritional quality of the habitat is a major factor affecting sexual dimorphism in size (Smith and Patton, 1980, 1984).

Acknowledgments

We thank M. S. Boyce, D. J. Hafner, and R. A. Smartt for providing suggestions that improved the manuscript. This is a contribution from the Alabama Agricultural Experiment Station.

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Submitted 28 April 1995. Accepted 26 September 1996.

Associate Editor was Karen McBee.