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RAPID MORPHOLOGICAL CHANGE IN CHANNEL ISLAND DEER MICE

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Abstract.—Deer mice, *Peromyscus maniculatus*, collected over 90 years from three California Channel Islands, were examined for evidence of morphological change. Rapid morphological change has occurred in the endemic subspecies from Santa Barbara (*P. m. elusus*), Anacapa (*P. m. anacapae*), and Santa Cruz Island (*P. m. santacruzae*). Data were divided into two temporal classes, 1897–1941 and 1955–1988. Of the 16 morphological characters measured, between five and 10 measures changed significantly ($P \leq 0.05$) with temporal class in each subspecies, and multivariate test statistics were significant ($P \leq 0.05$) for all three subspecies. For each subspecies, depth of braincase, total length, tail length, and hind foot length became smaller over time, except depth of braincase, which became larger in *P. m. elusus*. The rates of change dramatically exceed those estimated from paleontological records and are even higher than those reported in some experimental selection studies. Temporal change in two characters exceeds differentiation between subspecies. Although changing, each subspecies remained well differentiated, and incorporation of temporal change allowed correct classification of most specimens. Unlike nearly all previous reports of rapid evolution, the changes in these populations were not associated with a founder events or recent introductions. This study demonstrates that rapid phenotypic change can occur in long-established natural populations and temporal stability of morphological characters in such populations, even over short evolutionary time periods, cannot be assumed.

Key words.—California Channel Islands, discriminant function analysis, morphological change, morphometrics, *Peromyscus maniculatus*, temporal variation.

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Natural populations are generally assumed to exhibit morphological stability over short evolutionary time periods (tens to hundreds of years), although there have been reports of rapid morphological change documented over historic times. For example, rapid morphological change in house mice has occurred since their introduction to several British islands within the past 200 years, and has largely been attributed to founder effects (Berry 1964; Berry and Jakobson 1975; Berry et al. 1978). Rapid evolution has also been reported for North American house sparrows introduced haphazardly from Europe (Johnston and Selander 1964) and following experimental introductions, as in *Anolis* lizards to small Caribbean islands (Losos et al. 1997) or guppies (*Poecilia reticulata*) to uninhabited drainages (Reznick et al. 1997). Rapid change has also been reported in response to extreme environmental selection, such as the 1977 drought which favored large beaks in a population of *Geospiza fortis* on Daphne Major Island (Boag and Grant 1981). Thus it is well established that morphological change can occur quickly. In most, if not all cases of reported rapid morphological change, however, a specific causative mechanism seemed apparent, namely a population bottleneck associated with a founder event or clear selection pressures. What generally remains unknown is how often, if ever, rapid phenotypic change occurs in populations when such evolutionary forces are not apparent. Knowledge regarding such “background” patterns of morphological change are important for many reasons, including the interpretation of patterns in the paleontological record and assessment of evolutionary effects of anthropogenic disturbances and global climate change.

We report rapid morphological change in three endemic subspecies of island deer mice, *Peromyscus maniculatus*, occurring on the California Channel Islands of Santa Barbara (*P. m. elusus*), Anacapa (*P. m. anacapae*), and Santa Cruz (*P.*

m. santacruzae) (Fig. 1). Anacapa is actually three tiny islets and mice from all three islets were included. The California Channel Islands have a rather depauperate vertebrate fauna, and deer mice, *Peromyscus maniculatus*, are the only native terrestrial mammal found on all eight islands. Endemic subspecies have been recognized on each island and the subspecies are well differentiated morphologically (Gill 1980). Mitochondrial DNA RFLP analysis (Ashley and Wills 1987) and sequencing of the COII gene (Pergams 1998) indicate that several of the subspecies, including the ones studied here, have unique haplotypes. Analysis of mtDNA also indicates that different island subspecies may have originally derived from separate colonization events from the mainland (Ashley and Wills 1987). Thus the Channel Island subspecies of *P. maniculatus* were likely founded by over water dispersal thousands of years ago and have been isolated from each other and mainland populations since their founding.

The initial impetus of the present study was to classify deer mice recently rediscovered on East Anacapa following an apparent 15 year absence. Comparisons of cranial and external measurements were made on specimens spanning 90 years of collection to conduct discriminant analysis of morphological characters. When mice were divided into temporal time classes, we discovered extensive morphological change had occurred in the three subspecies over this time period.

METHODS

Specimens

A total of 163 mice were measured for this study: 42 *P. m. elusus*, 83 *P. m. anacapae*, and 38 *P. m. santacruzae* skulls and skins from the Santa Barbara Natural History Museum and the Natural History Museum of Los Angeles County. Ten *P. m. anacapae* and two *P. m. santacruzae* were determined to be subadults by pelage color and tooth wear (Layne 1968; Hinesley 1979; Rich et al. 1996) and excluded from analysis.

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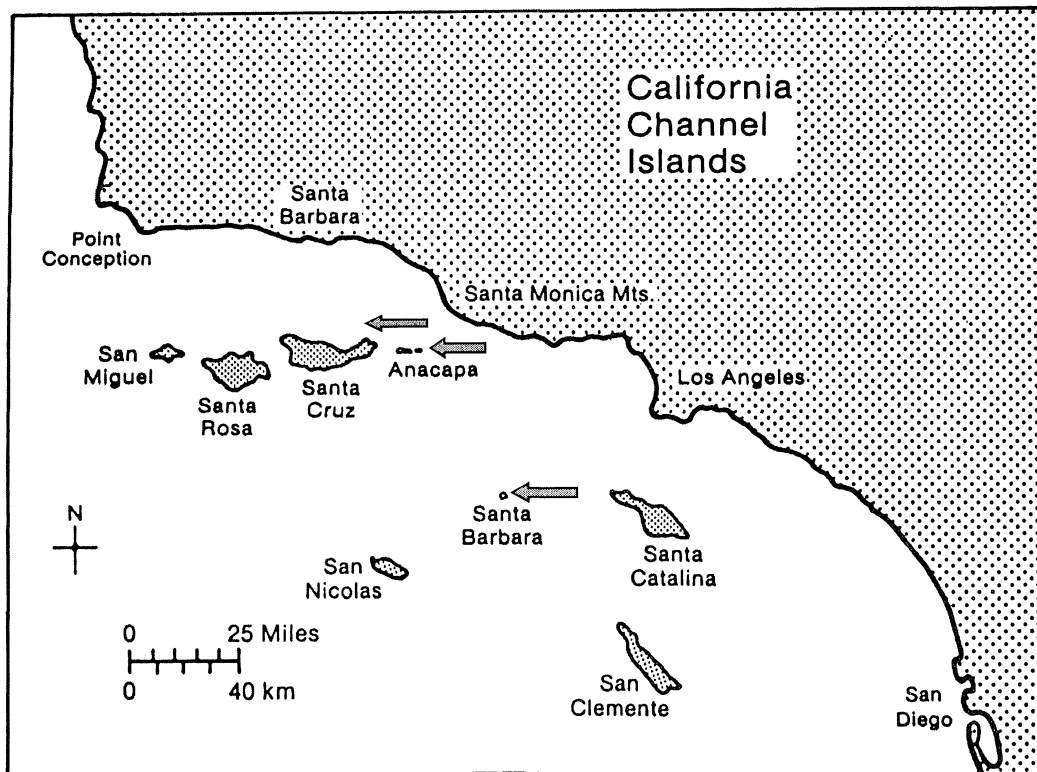


FIG. 1. Map of the California Channel Islands. Arrows indicate islands sampled. *P. m. anacapae* was sampled from Anacapa, *P. m. elusus* was sampled from Santa Barbara, and *P. m. santacruzae* was sampled from Santa Cruz.

The remaining adult specimens and collection years are as follows: *P. m. elusus*: 1897 ($n = 2$), 1919 (3), 1939 (13), 1940 (3), 1955 (1), 1972 (2), 1974 (1), 1978 (14), and 1979 (3); *P. m. anacapae*: 1940 (38), 1978 (35); and *P. m. santacruzae*: 1917 (5), 1938 (3), 1939 (9), 1941 (2), 1967 (13), 1983 (2), 1986 (1), and 1988 (1). The numbers of males and females in each group are as follows (males, females, unknown): *P. m. elusus*: (19, 23, 0); *P. m. anacapae*: (38, 34, 1); and *P. m. santacruzae* (20, 15, 1).

Measurements

Twelve cranial measurements were taken following the methods described in Hooper (1952), Fisler (1965), and Collins and George (1990), unless otherwise indicated: intermeatus width (IW); length of nasals (LN); length of palate plus incisor (LPI, measured as the greatest distance from the anterior edge of the alveoli of the incisors to the mesopterygoid fossa); breadth of rostrum (BR); alimentary tooththrow (AL); length of incisive foramen (LIF); rostral width (RW, the narrowest width of the rostrum and premaxilla dorsally and directly anterior to the infraorbital foramen); zygomatic breadth (ZB); interorbital breadth (IB); depth of braincase (DBC); breadth of braincase (BB); and breadth of zygomatic plate (BZP). All cranial measurements were taken by O.R.W.P. with a digital caliper to the nearest 0.01 mm. The four standard external measurements were originally made by 18 different museum preparers and recorded from museum tags: total length (TOT), tail length (TAIL), hind foot length

(HIND), and ear length (EAR). EAR was not available for six *P. m. elusus* and five *P. m. santacruzae*.

Analysis

SYSTAT version 7.0 (SPSS 1997a) and SYSTAT version 8.0 (SPSS 1998) were used for all statistical analysis, with the exception noted below. We first wanted to be confident that any variation observed was not due to measurement error. Cranial measurement error was estimated by first choosing three mice at random. Each of the 12 cranial variables was then measured 10 times for each mouse ($3 \times 12 \times 10 = 360$ measurements). We then apportioned the variation among measurements and among mice within a subspecies using a nested ANOVA. Lower and upper bounds for the ratio of error among mice over measurement error at the 95% confidence level were then converted to percentages.

Though discriminant function analysis is quite robust to skewed or tailed distributions (Afifi and Clark 1996), normality of data was determined by visual inspection of normal probability plots following the method of Afifi and Clark (1996). We plotted 85% ellipses of concentration as group scatterplot matrices, and plots were visually inspected to determine if covariances were approximately equal (SPSS 1997b). To evaluate sexual dimorphism, two-sample *t*-tests were performed on each subspecies, after dropping one specimen of unknown sex from each of the *P. m. anacapae* and *P. m. santacruzae* datasets. Results of *t*-tests were considered

significant at the 95% confidence level. The specimens of unknown sex were included in subsequent analyses.

To determine whether temporal change had occurred, three datasets based on temporal class were created: data from all years 1897–1988 ($n = 140$), 1897–1941 (68), and 1955–1988 (72). Since no mice had been collected between 1941 and 1955, these years served as an obvious, albeit arbitrary, cutoff between “early” and “late” collections. Also, the division between 1941 and 1955 produced approximately equal sample sizes.

One-way MANOVAs, with temporal class as the independent variable (factor) and all 16 measurements as the response variables, were performed on each subspecies and islet. Results from all MANOVAs were considered significant at the 95% confidence level. Complete discriminant analyses were also performed on each temporal class. All discriminant analyses were performed with a tolerance of 0.001.

To compare differentiation between subspecies and relative morphological change over time, we compared the mean squared errors (MSE, or the sum of squares over degrees of freedom) of subspecies and temporal class (Sokal and Rohlf 1997). The variable with the larger MSE was considered to have the greater variance.

We used discriminant function analysis to characterize the direction, degree, and nature of the morphological changes over time. Our discriminant function analysis used the “Weight” function in SYSTAT’s data handling component to assign a weighting of “0” or “1” to individuals and thereby apportion them to temporal class. Individuals collected from 1897–1941 were fully weighted, and individuals collected from 1955–1988 were given zero weight. A complete discriminant function was derived only from individuals from 1897–1941, but applied to individuals from 1955–1988 as well. Centroid coordinates of the late groups were calculated by hand as the means of individual canonical scores. Mahalanobis distances between the centroids of early and late groups were calculated by hand using the distance formula.

We calculated the rate of evolution in darwins with the equation

$$d = |(\ln x_2 - \ln x_1)/\Delta t|$$

(Haldane 1949). The reason for transforming measurements logarithmically is to remove spurious scaling effects. Calculations were made only for those traits found to have significant correlations with temporal class, as evaluated by our MANOVAs of all subspecies and temporal classes. The variables x_1 and x_2 were calculated for *P. m. elusus* and *P. m. santacruzae* by subtracting the mean of all collection years in time class 1897–1941 from the mean of all collection years in time class 1955–1988. The *P. m. anacapa* data was collected in just two years, so the respective means across the time interval of 38 years was used. Δt is the length of the time interval per million years.

RESULTS

On average, cranial measurement errors were estimated to be between 0.74% and 2.44% of the variation among the mice, therefore the average variation between mice was 60-fold higher than the average variation between measurements

of the same mouse. Our measurement errors were similar or less than those reported in other studies (Zink 1983; Patterson and Patton 1990; Yezerinac et al. 1992, Patterson, unpubl. data). Although we could not estimate measurement error for the external characters, we felt confident that external characters could be included in our analysis for two reasons. First, external measures are large relative to cranial measures, and percent measurement error generally will be inversely related to size of a character (Yezerinac et al. 1992). Second, measurement error would increase chances of not finding temporal differences that did exist (Type II error), rather than finding differences that do not exist (Type I error).

Measurements of all characters were determined to be approximately normal in distribution. As a result, and with the exception of calculating darwins, raw data was analyzed and no transformations were needed. We thereby avoided distancing ourselves from the data (Reyment 1972). Covariances were approximately equal. There was no significant sexual dimorphism for any of the 16 measurements of any of the three subspecies, consistent with other studies of *Peromyscus* (e.g., Laerm and Boone 1994; Rich et al. 1996; Sternburg and Feldhamer 1997).

Results of MANOVAs with temporal class as the grouping factor are given in Table 1. Univariate *F*-statistics and *P*-values show that in mice from Santa Barbara Island (*P. m. elusus*), six measurements (LN, DBC, TOT, TAIL, HIND, and EAR) were significantly correlated with temporal class. For mice from all Anacapa islets pooled together (*P. m. anacapa*), ten measurements (IW, BR, LIF, RW, DBC, BZP, TOT, TAIL, HIND, and EAR) were significantly correlated with temporal class. When Anacapa was divided into islets for analysis, the results remained consistent, though multi-year data was not available for East Anacapa. For mice from Middle Anacapa, three measurements (RW, HIND, and EAR) were significantly correlated with temporal class. For mice from West Anacapa, six measurements (IB, BZP, TOT, TAIL, HIND, and EAR) were significantly correlated with temporal class. For mice from Santa Cruz Island (*P. m. santacruzae*), five measurements (IW, DBC, TOT, TAIL, and HIND) were significantly correlated with temporal class. On all three islands DBC, TOT, TAIL, and HIND showed significant change over time. Direction of change was the same for TOT, TAIL, and HIND, becoming smaller. DBC became smaller on Anacapa and Santa Cruz and larger on Santa Barbara. Comparing MSEs, the temporal change in two characters (TOT and HIND) exceeded differentiation between subspecies. Multivariate test statistics, which carry out a generalization of an ANOVA for cases in which several independent variables have been measured for two or more samples, were significant ($P \leq 0.05$) for each subspecies and islet.

Discriminant functions, cumulative proportions of total dispersion, and Wilk’s lambdas are given in Table 2. Complete discriminant function analysis of data from all years (Fig. 2a) correctly classified 85% (119/140) of individuals, whereas 1897–1941 data alone (Fig. 2b) correctly classified 99% (67/68) and 1955–1988 data alone (Fig. 2c) correctly classified 96% (69/72). All together, 97% (136/140) of individuals were correctly classified by correcting for temporal change. Had we not tested for temporal variation in this data,

TABLE 1. One-way MANOVA results for each subspecies with time class (1897-1941, 1955-1988) as the grouping factor, testing for effects in all measurements. Univariate *F*-statistics and *P*-values are given first, multivariate test statistics are given last. Significant values ($P \leq 0.05$) are underlined. Wilk's lambdas ($P \leq 0.05$) are underlined. Wilk's lambdas = less equal group means).
vary between 0 and 1, and test for the equality of group means (lower Wilk's lambdas = less equal group means).

	<i>P. m. elusius</i>		<i>P. m. anacapa</i> (all)		<i>P. m. anacapa</i> (Middle)		<i>P. m. anacapa</i> (West)		<i>P. m. santacruzae</i>	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
IW	2.654	0.113	14.785	<u>≤0.0005</u>	2.972	0.094	0.776	0.391	10.144	0.003
LN	13.964	0.001	0.225	0.636	2.585	0.117	0.224	0.642	0.527	0.474
LPI	1.584	0.217	1.190	0.279	1.721	0.199	2.044	0.171	0.168	0.685
BR	0.780	0.383	4.468	0.038	2.394	0.131	0.000	0.997	1.1693	0.203
AL	0.130	0.720	1.545	0.218	1.188	0.284	1.140	0.301	1.065	0.311
LJF	0.504	0.483	5.834	0.018	0.182	0.673	2.054	0.170	0.084	0.774
RW	0.720	0.402	4.751	0.033	5.500	0.025	1.782	0.200	0.119	0.733
ZB	2.531	0.121	0.651	0.423	3.134	0.086	1.443	0.246	0.060	0.808
IB	0.231	0.634	1.921	0.170	0.033	0.856	6.116	0.024	0.330	0.570
DBC	13.434	0.001	14.160	<u><0.0005</u>	3.816	0.059	1.858	0.191	7.087	0.013
BB	0.025	0.874	0.220	0.640	0.025	0.876	0.747	0.400	1.948	0.173
BZP	0.031	0.861	6.343	0.014	0.458	0.503	9.640	0.006	2.547	0.121
TOT	37.186	<u>≤0.0005</u>	5.154	0.026	0.028	0.868	5.309	0.034	31.506	<u>≤0.0005</u>
TAIL	56.085	<u>≤0.0005</u>	7.404	0.008	0.263	0.611	14.855	0.001	10.259	0.003
HIND	46.533	<u>≤0.0005</u>	72.865	<u>≤0.0005</u>	37.978	<u>≤0.0005</u>	6.366	0.022	7.754	0.009
EAR	6.883	0.013	18.280	<u>≤0.0005</u>	14.033	0.001	7.388	0.015	2.906	0.099
Multivariate	8.176	<u>≤0.0005</u>	15.596	<u>≤0.0005</u>	4.083	0.003	29.041	0.034	2.945	0.024
Wilk's lambda	0.127		0.183		0.216		0.004		0.229	

TABLE 2. Canonical discriminant functions (standardized by within variance), cumulative proportion of total dispersion (CPTD), and Wilk's lambda. Canonical functions are given standardized by within variance to facilitate comparison. CPTD represent the proportion (max = 1) of variability between groups that the first canonical variable captures. The higher the value, the more between-group variability is being captured. Wilk's lambda tests the equality of group means for the variables. The lower the value (min = 0), the less the group means are equal, the more the function is discriminating.

	All years, 1897-1988	1897-1941	1955-1988
IW	0.508	0.310	0.411
LN	-0.201	-0.124	-0.198
LPI	0.237	0.180	0.937
BR	-0.371	0.121	-0.509
AL	-0.413	0.309	-0.637
LIF	0.478	0.099	0.549
RW	-0.297	0.036	-0.039
ZB	-0.336	0.309	-0.472
IB	0.274	-0.447	0.120
DBC	-0.392	0.389	-0.136
BB	0.247	-0.215	0.508
BZP	-0.044	-0.390	-0.292
TOT	0.255	-0.260	-0.220
TAIL	-0.616	-0.041	-0.725
HIND	-0.265	0.989	-0.199
EAR	0.320	-1.298	0.158
CPTD	0.842	0.818	0.876
Wilk's lambda	0.150	0.043	0.078

we would have lost the power to classify 12% (17/140) of our sample.

Given the extent of temporal change, we expected the discriminant function giving full weight to individuals from 1897 to 1941 and zero weight to individuals from 1955 to 1988 to be poor at classifying individuals from the later period (see Table 2). This is indeed the case. Only 40% (29/72) of the individuals from 1955 to 1988 are correctly classified.

We compared the relative amounts of movement in morphology over time by calculating the Mahalanobis distances between old and new centroids for each island. *P. m. elusius* and *P. m. anacapa* changed approximately the same amount, whereas *P. m. santacruzae* changed approximately 40% less. In Figure 3, arrows are drawn from the centroids of the 1897-1941 confidence ellipses to the centroids of the groupings of 1955-1988 individuals, illustrating the direction and magnitude of morphological change on the three islands. Late (1955-1988) *P. m. anacapa* appeared to become more like early (1897-1941) *P. m. santacruzae*. We therefore tested this possibility by using one-way MANOVAs, with all measurements as the independent variables. When comparing late *P. m. anacapa* to early *P. m. anacapa*, multivariate test statistics were $F = 15.596$, $P \leq 0.0005$, and Wilk's lambda = 0.183. When comparing late *P. m. anacapa* to early *P. m. santacruzae*, multivariate test statistics were $F = 5.209$, $P \leq 0.0005$, and Wilk's lambda = 0.277. Thus, late *P. m. anacapa* is readily distinguishable from both early *P. m. anacapa* and early *P. m. santacruzae*. Although each subspecies exhibited rapid morphological change, they remain well differentiated, as shown by the high (96%) correct classifi-

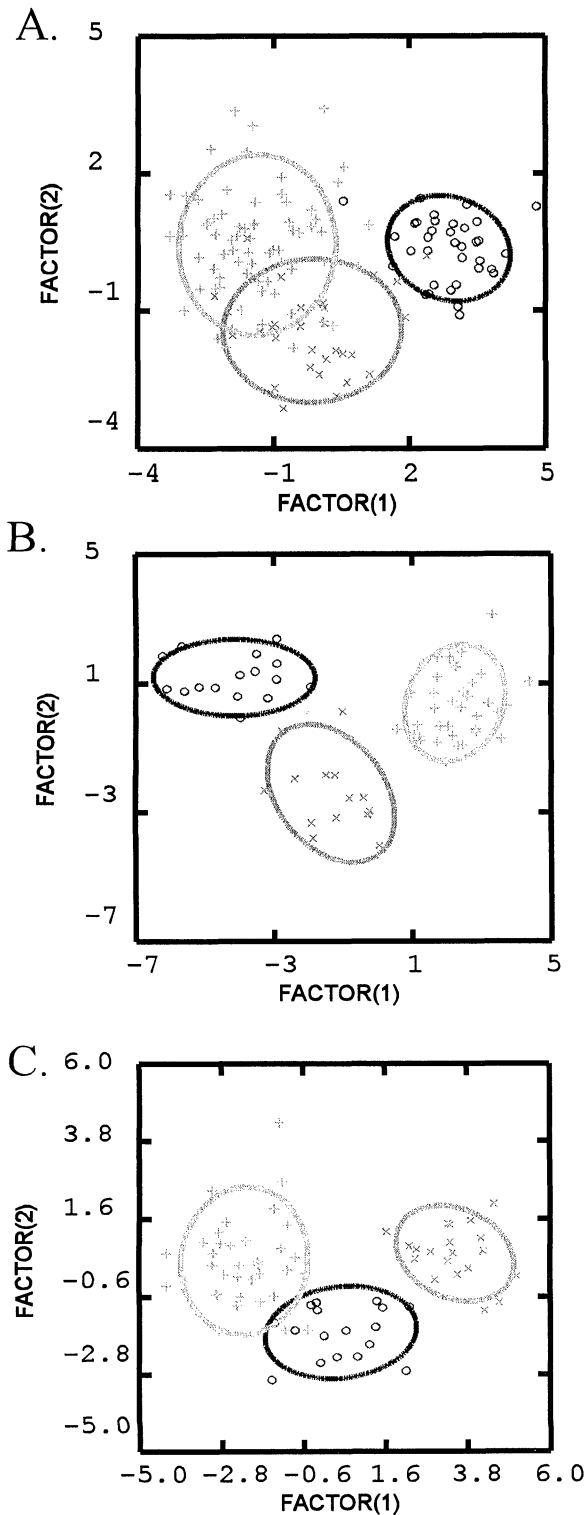


FIG. 2. Canonical scores plots for discriminant function analyses. Ellipses are 85% confidence intervals. (A) All years, 1897-1988; + designates *P. m. anacapae*, o designates *P. m. elusus*, and x designates *P. m. santacruzae*. (B) Early period, 1897-1941; + designates *P. m. anacapae*, o designates *P. m. elusus*, and x designates *P. m. santacruzae*. (C) Late period, 1955-1988; + designates *P. m. anacapae*, x designates *P. m. elusus*, and o designates *P. m. santacruzae*.

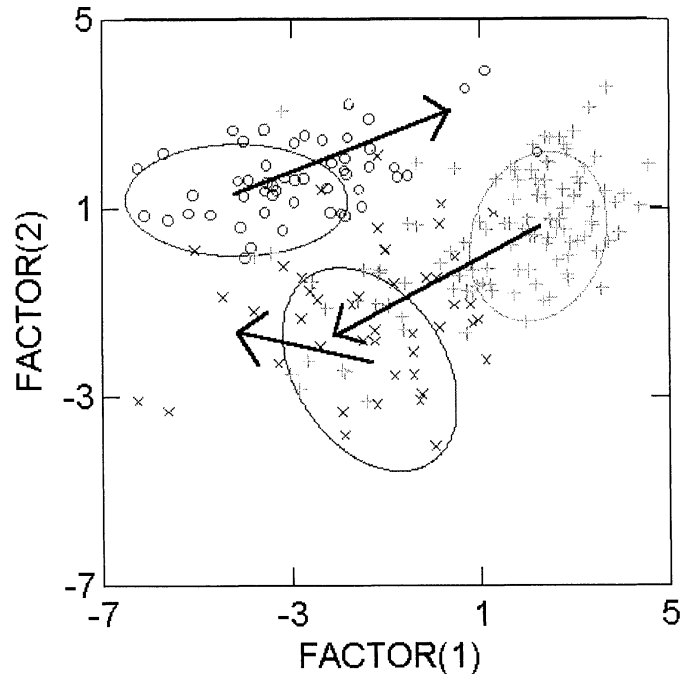


FIG. 3. Canonical scores plot for discriminant function analysis of all years, 1897-1988, but with discriminant function defined only by years 1897-1941. Ellipses are 85% confidence intervals for data from the early period; + designates *P. m. anacapae*, o designates *P. m. elusus*, and x designates *P. m. santacruzae*. Arrows show the relative movement of morphological change of each subspecies. Each arrow begins at the centroid of the early period of a subspecies and ends at the centroid of the late period of the same subspecies.

cation rate of the 1955-1988 group using the discriminant function from this period only.

To determine the characters that changed between the two time periods, we examined the weightings of the canonical discriminant coefficients in Table 2. The 1897-1941 dataset has two variables with a value ≥ 0.900 : HIND and EAR. The 1955-1988 dataset has one variable with a value ≥ 0.900 : LPI. Therefore between the early period and the later period HIND and EAR lost importance and LPI gained importance as discriminating variables.

Results of our calculations of rate of evolution are presented in Table 3. We only calculated rates for those characters with significant temporal variation, as determined by the MANOVAs of all subspecies and temporal classes. The *P. m. anacapae* data were collected in two years, with an interval of 38 years. For the other two subspecies, rates of evolution had to be based on two, large temporal classes, the means of which were 44 years for *P. m. elusus* and 38 years for *P. m. santacruzae*. Rates of change were of the same order of magnitude in all subspecies. The percentage change of traits over these time periods ranged from 1.77% to 9.93%, and the rate of evolutionary change ranged from 461 to 2682 darwins.

DISCUSSION

Collections of island deer mice in the first half of this century provided an opportunity to examine temporal variation in morphological characters. We found that all three

TABLE 3. Calculations of amount and rate of evolutionary change.

			Response (R)	% change	Rate (darwins)
Santa Barbara					
	Means of time periods				
	1932.29	1976.29			
Significant trait	Means (SE)	Means (SE)			
LN	9.72 (0.10)	10.12 (0.04)	0.40	4.11%	916
DBC	7.38 (0.05)	7.59 (0.03)	0.20	2.76%	619
TOT	173.62 (1.68)	160.48 (1.78)	-13.14	-7.57%	1789
TAIL	76.29 (0.94)	68.71 (0.66)	-7.57	-9.93%	2376
HIND	21.21 (0.16)	19.45 (0.18)	-1.76	-8.31%	1971
EAR	18.50 (0.20)	17.53 (0.29)	-0.98	-5.27%	1231
Anacapa					
	Years collected				
	1940.00	1978.00			
Significant trait	Means (SE)	Means (SE)			
IW	2.23 (0.02)	2.09 (0.03)	-0.14	-6.36%	1730
BR	4.47 (0.03)	4.55 (0.03)	0.08	1.77%	461
DBC	7.86 (0.04)	7.65 (0.04)	-0.21	-2.63%	702
LIF	5.31 (0.03)	5.17 (0.05)	-0.14	-2.58%	688
RW	3.15 (0.03)	3.22 (0.02)	0.07	2.32%	603
BZP	2.24 (0.02)	2.30 (0.02)	0.06	2.64%	685
TOT	179.26 (1.15)	175.09 (1.46)	-4.18	-2.33%	620
TAIL	84.13 (0.76)	81.14 (0.80)	-2.99	-3.55%	952
HIND	21.61 (0.11)	20.26 (0.11)	-1.35	-6.24%	1695
EAR	16.42 (0.11)	17.29 (0.17)	0.87	5.27%	1351
Santa Cruz					
	Means of time periods				
	1933.26	1971.24			
Significant trait	Means (SE)	Means (SE)			
IW	2.24 (0.05)	2.02 (0.03)	-0.22	-9.68%	2682
DBC	7.92 (0.06)	7.69 (0.05)	-0.24	-2.97%	792
TOT	176.32 (3.11)	167.00 (1.09)	-9.32	-5.28%	1430
TAIL	84.29 (1.52)	76.82 (1.34)	-7.47	-8.86%	2442
HIND	21.47 (0.14)	20.18 (0.35)	-1.30	-6.04%	1642
EAR	17.29 (0.19)	18.06 (0.38)	0.77	4.47%	1152

island subspecies examined here, *P. m. elusus*, *P. m. santacruzae*, and *P. m. anacapae*, exhibited significant temporal change in several characters. Multivariate test statistics were significant ($P \leq 0.05$) for each subspecies and islet. Although the changing suites of characters were different in each subspecies, some clear trends emerged. Three of the external body measurements (TOT, TAIL, and HIND) and one of the cranial measurements (DBC) exhibited temporal variation in all three subspecies. The trend was for the mice to decrease in these characters over time, with DBC for *P. m. elusus* being the only exception to this trend. For all three subspecies, two or more cranial characters also show significant temporal variation, although at least one of the characters that changed differed among subspecies. The rates at which many characters changed were surprisingly high (Table 3), with rates ranging from 461 to 2682 darwins. Gingerich (1983) calculated a geometric mean value of 0.08 darwins for fossil vertebrates and 3.7 darwins for post-Pleistocene mammals. The maximum value he reports for post-Pleistocene mammals was 32 darwins, more than an order of magnitude lower than any of our values. Our geometric mean value, 1139 darwins, exceeds the Gingerich (1983) geometric mean rate of 370 darwins for colonizations/introductions but falls within the range he reports for colonizations.

Despite parallel trends in several characters, Figure 3 illustrates that each subspecies is following an independent morphological trajectory. Although it appears that *P. m. anacapae* evolved to be similar to early *P. m. santacruzae*, this is not corroborated by a MANOVA, and overall the mice are not converging on a certain phenotype but are remaining well differentiated.

Several of our results show the importance of testing temporal samples for morphological change, and incorporating such information into discriminant function analysis, systematics, and classification if it is found. First, the change in two characters (TOT and HIND) exceeded the level of differentiation between subspecies, suggesting that these characters would be useful only for comparing specimens within a given time period. Second, discriminant function analysis of data from the early years allowed correct classification of only 40% of the samples from the later years. This suggests that the common practice of classification of modern specimens based on comparisons with much older museum type specimens should be done cautiously. Finally, incorporating the data on temporal variation increased correct classification from 85% to 97%. This latter result cautions against simply pooling morphological data from samples collected over many years for systematic studies.

The type of comparison we employed, using museum specimens to examine short-term evolution change, has been a relatively rare and perhaps underutilized approach. Zink (1983) conducted a study similar to ours in which he compared measurements of fox sparrows to those collected at the same sites 50 years previously. Although some traits did exhibit temporal variation, there were no clear temporal trends for particular characters or particular populations over time. His results also differed from ours in that many characters had measurement errors that approached or exceeded temporal differences, limiting the power of resolving temporal and spatial patterns. In our study, average measurement error of cranial characters was only 0.74% to 2.44% of the variation among individuals; none of our traits had excessive measurement error. We therefore are confident that the temporal patterns observed are real and not methodological artifacts.

Clearly the populations of mice have undergone rapid phenotypic change during this century. Rapid morphological and genetic evolution of island rodents has been reported before, particularly *Mus domesticus* introduced in historic times to several British Islands (Berry 1964, 1986; Berry and Jakobson 1975; Berry et al. 1978). These rapid changes in island house mice have largely been attributed to founder events, an explanation that cannot hold for Channel Island deer mice that have been established on the islands for thousands of years. Our study was not designed to identify the underlying mechanism, and we can only offer a posteriori hypotheses. There are several aspects of the habitat, biology, and history of the deer mice that may be relevant to the observed changes and help to assess the relative likelihood of alternative explanations. Four possible explanations for temporal variation of phenotypic characters are: (1) nongenetic, environmental effects; (2) gene flow from morphologically different source populations; (3) stochastic evolutionary change through genetic drift; or (4) response to natural selection.

In order for evolutionary change to have occurred (by either stochastic or directional forces), at least some of the phenotypic variance observed must have a genetic basis. Certainly an underlying genetic foundation for the type of phenotypic traits we measured (cranial characters and body dimensions) are assumed in taxonomic and systematic studies. Heritability estimates in rodents for the types of traits we measured can be characterized as moderate to high (e.g., Leamy 1974) and thus would respond to selective forces should they exist. We feel that nongenetic environmental factors such as nutrition or maternal effects are an unlikely explanation for all of the morphological changes observed; changes appear so great that some genetic component must be involved.

Smith and Patton (1984) argued that gene flow accounted for a large temporal change in one of several populations of pocket gophers for which museum specimens were compared. Several factors argue against gene flow in the case presented here. First, the deer mice inhabit oceanic islands separated by at least several kilometers from other islands or from the nearest mainland point. Santa Barbara, for example, lies 63 km from the nearest mainland point and 39 km from the nearest island. Although rare colonizations obviously occurred (because all islands have deer mice), the islands show

reduced levels of mtDNA diversity, suggesting small numbers of founders and low historical gene flow (Ashley and Wills 1987, Pergams 1998). Our mtDNA studies, RFLPs and COII sequencing, used mice collected from 1983 to 1985 and 1996 to 1997. Two of the subspecies (*P. m. anacapae* and *P. m. elusus*) had unique, endemic haplotypes, suggesting genetic isolation. Certainly the islands do experience limited boat traffic and occasional stowaways may move between islands, but not in the numbers needed to bring about rapid change of metric characters. Finally, it is difficult to envision a movement scenario (source and destination) to explain the trajectory of the changes indicated in Figure 3.

A third causative factor that merits consideration is genetic drift. Santa Cruz is the largest of the Channel Islands (249 sq km), thus population sizes may be extremely large. On the other hand, two of the islands, Santa Barbara (2.6 sq km) and Anacapa (2.9 sq km, all Anacapa islets together) are quite small, but on these islands mice are often extremely abundant (> 300/ha on Santa Barbara), probably due to a relative lack of competitors and predators (Drost and Fellers 1991). Drost and Fellers (1991) reported that deer mice on Santa Barbara experience cyclic population crashes associated with climatic factors, analogous to cyclic microtines, and census data (Schwemm 1995; Austin 1996a,b, pers. comm.) suggests the same may be true for Anacapa. Genetic drift may occur during population bottlenecks, but extrapolation of census data (Drost and Fellers 1991; Schwemm 1995; Austin 1996a,b; Austin pers. comm.) suggests that population sizes on the Anacapa islets and Santa Barbara probably remain in the hundreds to thousands even during crashes, and rebound quickly to tens of thousands. Also arguing against severe population bottlenecks is the maintenance of moderate amounts of allozyme variability in these three island populations (Gill 1980). A final argument against genetic drift is the observation that several of the same morphological characters are changing, and in most cases, changes are in the same direction. Even if certain characters exhibited higher levels of evolutionary plasticity, genetic drift would not be expected to direct changes in such characters in a uniform direction.

Concordant changes in suites of characters provide evidence for natural selection for new morphological types. Selection forces may involve changes in the abiotic environment or changes in biotic interactions, including predators, competitors (introduced animals) and resources (introduction of exotic plants and decline of native flora). Abiotically, the islands have probably been more stable than most contemporary ecosystems, with little human development or habitat loss. Biotic changes have been numerous, however. Santa Barbara had feral goats by 1840 (Remington 1971), and sheep were introduced to all three islands between the early 1830s and the late 1860s (Brumbaugh 1980, Doran 1980, Federal Register 1997). European rabbits were introduced to Santa Barbara, and there were reports of feral pigs on Santa Cruz (Remington 1971, Federal Register 1997). Black rats (*Rattus rattus*) were accidentally introduced to Anacapa in the second half of the nineteenth century (Collins et al. 1979, Doran 1980). With the exceptions of rats on Anacapa and pigs and a few sheep on Santa Cruz, the exotic faunas were eliminated by the 1950s (Brumbaugh 1980, Johnson 1980, Minnich

1980, Federal Register 1997). Rats may have a dramatic effect on Anacapa mice because they are abundant and are both competitors and predators of deer mice (Collins et al. 1979), but they have not been reported on Santa Barbara or Santa Cruz Island. The introduction of exotic grasses for fodder, along with overgrazing, caused the extirpation of some native plants (Banks 1966). Examination of stomach contents of Anacapa and Santa Barbara deer mice showed that they were eating a mixture of native and exotic plants (Collins et al. 1979, Philbrick 1980, Federal Register 1997, CalFlora 1998), thus dietary changes have occurred.

None of the biotic changes clearly stands out as a likely causal explanation for rapid morphological change or clearly correspond to the time frame of our study. The island deer mouse populations are likely responding to differing combinations of stochastic and environmental factors that have resulted in rapid phenotypic change.

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