



## Microevolution in island rodents

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### Abstract

We perform a meta-analysis on morphological data from four island rodent populations exhibiting microevolution ( $< \approx 100$  years). Data consisting of incidences of skeletal variants, cranial, and external measurements are from house mice (*Mus musculus*) on one Welsh and one Scottish island, black rats (*Rattus rattus*) on two Galapagos islands, and deer mice (*Peromyscus maniculatus*) on three California Channel islands. We report extremely high rates of microevolution for many traits; 60% of all mensural traits measured changed at a rate of 600 *d* or greater (max. 2682 *d*). The proportion of all mensural traits evolving at 600–800 *d* (23%) was idiosyncratic and departed from an expected negative exponential distribution. We argue that selection, rather than founder events, is largely responsible for the substantial shifts in morphology seen among insular rodents. Examining individual traits, there is a trend towards the nose becoming longer and wider, while the skull becomes shallower, shown by both rats and mice on five different islands. We found a significant correlation between island size and degree of skeletal variant evolution and between island distance from the mainland (or nearest island) and degree of cranial and external character evolution. Thus, microevolution of rodents is greater on smaller and more remote islands.

**Abbreviations:** ANOVA – analysis of variance; CA – California; *d* – darwins; *h* – haldanes; GAL – Galapagos; MANOVA – multiple analysis of variance.

### Introduction

Studies of island rodents were among the first recognized examples of microevolution (e.g., Clarke, 1904; Huxley, 1942). It is commonly observed that insular rodents differ from their mainland relatives in a variety of traits, including behavior, demography, genetics, physiology, and morphology (Gliwicz, 1980; Berry, 1986; Adler & Levins, 1994). Study of the human commensals *Rattus rattus*, *R. norvegicus*, *Mus musculus*, and *M. domesticus* have provided important examples of microevolution simply because their arrival to many islands was recent, corresponding to human occupation. Thus a time frame for evolutionary change is established and is often brief, less than 1,000 years in most cases. A comparison with the mainland conspecifics that are presumed to be the source

of island populations allows the nature of microevolutionary change to be characterized and the rates of change to be calculated.

A comprehensive body of work on insular rodent evolution was built by R.J. Berry working at University College, London beginning in the early 1960's. Berry's morphological studies utilized non-metrical minor skeletal variants, originally identified in inbred laboratory strains, to investigate genetical relationships of wild mice. He and his colleagues examined the evolution of these skeletal traits in *Mus musculus* on the British mainland and islands of the North Atlantic (Berry, 1963, 1964), northern island races of *Apodemus sylvaticus* (Berry, 1975), and insular and mainland populations of *Microtus arvalis* (Berry & Rose, 1975). Berry's work was not limited to studies of skeletal variants originally presumed to

be selectively neutral, indeed his studies of physiological adaptations to stressful environments were also an important focus of his work (Berry & Jakobson, 1975; Berry, Jacobsen & Peters, 1978; Berry, Peters & van Aarde, 1978; Berry, Bonner & Peters, 1979). His work went on to incorporate biochemical (allozyme), physiological, demographic, and ecological investigations (e.g., Berry & Tricker, 1969; Berry & Murphy, 1970).

In addition to Berry's work, many others have conducted studies of island rodent evolution. Examples include studies of *Peromyscus* (Gill, 1980; Aquadro & Kilpatrick, 1981; Melton, 1982; Ashley & Wills, 1987; Allard & Greenbaum, 1988; Calhoun & Greenbaum, 1991; Pergams & Ashley, 1999), *Clethrionomys* (Corbet, 1964), *Mus* (Davis, 1983) & *Rattus* (Patton, Yang & Myers, 1975; Yom-Tov, Yom-Tov & Moller, 1999). We recently documented an example of rapid morphological evolution of island mice that differs from previous examples (Pergams & Ashley, 1999, 2000). We examined subspecies of deer mice, *Peromyscus maniculatus*, that occur on the California Channel islands. In our study we used museum collections to measure mice from each island collected over a period of about 90 years. Thus we were not relying on comparison to presumed 'ancestral' state represented by contemporary mainland or source populations, but were rather directly documenting change over time. Channel island deer mice are not recent arrivals, but rather have occupied the islands for tens to hundreds of thousands of years (Ashley & Wills, 1987). Thus the microevolution we observed within the last century was not associated with an introduction or founding event.

In order to place our findings on microevolution of Channel island deer mice within the framework of other studies, we searched the literature for data sets that would allow direct comparisons of patterns and rates of microevolution of insular rodents. We were interested in uncovering patterns of morphological change associated with evolution on islands through a meta-analysis. For example, do most traits change to the same degree, or do most traits change little with a few evolving rapidly? How do rates of microevolution measured in darwins or haldanes in island rodents compare to those reported for other contemporary examples of microevolution? Are the most rapid rates of change associated with recent founder events? Are rates or types of morphological change correlated with island size or isolation? Among the most rapidly evolving traits, are there consistent pat-

terns across species and islands? We felt the answer to these questions would provide finer resolution of patterns and processes of microevolution among insular rodents than the general trends that have been previously noted in mammals (Foster, 1964; Heaney, 1978; Melton, 1982; Lomolino, 1985).

## Methods

Despite a vast literature on insular rodents, our review yielded only four studies where data from morphological traits of insular rodents could be used to compare rates and patterns of microevolution (Table 1). Because our interest is in contemporary microevolution, only cases where evolution occurred within the approximate life span of a human being were considered (Dobzhansky, 1941, p.12; Hendry & Kinnison, 1999). In many cases the time frame of evolution, while brief on evolutionary time scales (hundreds to thousands of years), was longer than our working definition (e.g., Berry, 1969; Berry & Rose, 1975; Aquadro & Kilpatrick, 1981; Allard & Greenbaum, 1988). The studies used in our meta-analysis were: (1) Berry (1964), a study of *Mus musculus* on the Welsh island of Skokholm; (2) Berry, Jakobson and Peters (1978), a study of *M. musculus* on the Scottish Faroe Islands; (3) Patton, Yang and Myers (1975), a study of *Rattus rattus* on the Galapagos Islands; and (4) Pergams and Ashley (1999), our study of *Peromyscus maniculatus* on the California Channel islands. Two studies, Patton, Yang and Myers (1975) and Berry, Jakobson and Peters (1978), also measured change over much greater time intervals (200–1000 years); these data were not included in our study.

Berry's studies of introduced *Mus* on the small island of Skokholm spanned more than a decade (Berry, 1963, 1964, 1970; Berry & Murphy, 1970; Berry & Peters, 1976); the data from Berry (1964) was appropriate for our meta-analysis of morphological microevolution. Skokholm has an area of just over 100 ha and lies 3 km from the mainland. *Mus* did not occur on Skokholm prior to 1881, and were likely introduced in 1907 (Table 1).

The house mice of the Faroe islands have long been used as an example of extremely rapid evolution because they are very large but undoubtedly arrived to the islands with humans during the last millennium (Huxley, 1942; Matthews, 1952). Indeed, one of the Faroe islands, Hestur, has only had mice since 1939, and thus fit our definition of microevolution. Hestur

Table 1. Summary of data sets used to compare microevolution of island rodents

Paper cit.	Location	Island	Area (ha)	Dist. to near isl., mainland (km)	Species	Diverg. time on island (years)	Sample size from island	Type of traits examined
Berry, 1964	Pembrokeshire, Wales	Skokholm	106	3, 3	<i>Mus musculus</i>	60	332	35 binary skeletal variants
Berry, Jakobsen and Peters, 1978	Faroe islands, Scotland	Hestur	576	1,275	<i>M. musculus</i>	35	48	25 binary skeletal variants, weight, 3 ext. measures, mandible parameters, scapula parameters, hemoglobin conc., 22 allozyme loci
Patton, Yang and Myers, 1975	Galapagos islands, Equador	Baltra	4000	1 <sup>a</sup> ,800	<i>R. rattus</i>	30	17	18 binary skeletal variants, 11 cranial measures, 4 ext. measures, pelage variation, 7 allozyme loci
Patton, Yang and Myers, 1975	Galapagos islands, Equador	Santa Cruz (GAL)	59,000	1 <sup>a</sup> ,800	<i>R. rattus</i>	40	32	18 binary skeletal variants, 11 cranial measures, 4 ext. measures, pelage variation, 7 allozyme loci
Pergams and Ashley, 1999	California Channel island, USA	Anacapa	290	7,20	<i>Peromyscus maniculatus anacapae</i>	38	73	12 cranial measures, 4 ext. measures
Pergams and Ashley, 1999	California Channel islands, USA	Santa Barbara	260	39,61	<i>P. m. elusus</i>	max. 82, mean 44 <sup>b</sup>	42	12 cranial measures, 4 ext. measures
Pergams and Ashley, 1999	California Channel islands, USA	Santa Cruz (CA)	25,000	7, 30	<i>P. m. santacruzae</i>	max. 71, mean 38 <sup>b</sup>	36	12 cranial measures, 4 ext. measures

<sup>a</sup>Baltra and Santa Cruz (GAL) are each app. 20 km from next nearest island Santiago.

<sup>b</sup>Museum specimens were assigned two time classes and compared. Max. is the difference between the oldest of the older time class and the newest of the newer time class. Mean is the difference between the mean of the time classes.

has an area of 576 ha and lies 1 km from the nearest island and 275 km from the mainland (Table 1).

Patton, Yang and Myers (1975) studied black rats (*Rattus rattus*) introduced by man to the Galapagos islands. We re-analyzed the morphological data from specimens captured on the islands of Baltra and Santa Cruz 30–40 years after their introduction, the only comparisons that fit our time frame. Baltra has an area of 4000 ha and lies only 1 km from Santa Cruz. Santa Cruz has an area of 59,000 ha. Both lie approximately 800 km from mainland Ecuador (Table 1). James Patton kindly provided original mensural data used in Patton, Yang and Myers (1975).

As mentioned above, we (Pergams & Ashley, 1999) examined museum specimens representing three subspecies of California Channel island deer mice, *Peromyscus maniculatus elusus* (Santa Barbara island), *P. m. anacapae* (Anacapa island) and *P. m. santacruzae* (Santa Cruz island). Santa Barbara is the smallest of the California Islands (260 ha) and the most isolated of the three we studied. Santa Cruz is the largest California Island (25,000 ha) and lies 7 km from Anacapa island (Table 1).

A challenge we faced in comparing data across studies was that a substantive portion of morphological work, including most of R.J. Berry's, involved non-metrical (binary) skeletal traits with discrete character states. We calculated changes in these traits as the difference in percent incidence or frequency of character states between populations. Patton, Yang and Myers (1975) measured both non-metrical cranial characters and mensural traits. Pergams and Ashley (1999) measured only mensural traits. Differences in incidences of binary, presence/absence characters such as skeletal variants are not directly comparable with changes in means of continuous characters such as mensural cranial or external measurements. However, we attempted to present both types of measurements in a way to facilitate comparisons. For each type of data we constructed histograms of trait frequency and amounts of change, using all individual data points in the papers. The histograms for skeletal variant and mensural trait evolution were separately constructed. Wherever possible, we calculated rates of microevolution in darwins and haldanes, but unfortunately, we know of no method of calculating standard rates of microevolution from frequency changes of binary traits, as in most of Berry's work.

We identified the five traits which showed the greatest degree of microevolution. The traits showing greatest microevolution were reported in Patton,

Yang and Myers (1975) through ANOVA and calculation of canonical variate coefficients (vector II), and in Pergams and Ashley (1999) through one-way MANOVA. For Berry (1964) and Berry, Jakobsen and Peters (1978), we identified traits showing the greatest change by calculating percent changes as follows. We used Berry's (1964) genetic distance matrix to determine which mainland population was the most likely source population. This method is conservative, as it calculates evolution from the genetically most similar population. As a result, we compared Skokholm with Caerforiog, and calculated differences in percentage incidences to identify the five with the greatest change. For Berry, Jakobsen and Peters (1978) we compared Hestur mice with those from the closest island, Streymoy. We necessarily made the assumption that the populations defined as the colonizing sources remained constant over the time interval examined.

For Pergams and Ashley (1999), direct calculations of rates of microevolution were possible using the collections dates and measurements of museum specimens collected at known dates. For Berry (1964), Patton, Yang and Myers (1975); and Berry, Jakobsen and Peters (1978) populations were only sampled once. Rates of microevolution were therefore calculated by comparison with a putative source population. For Patton, Yang and Myers (1975) we compared rats from adjoining Baltra and Santa Cruz (GAL) to Santiago, the next nearest island using original data provided by James Patton. For Berry, Jakobsen and Peters (1978) we again used Streymoy mice.

Darwins were calculated with the equation

$$d = |(\ln x_2 - \ln x_1)/(t_2 - t_1)|,$$

where  $\ln x_1$  and  $\ln x_2$  are sample means of  $\ln$  measurements at times  $t_1$  and  $t_2$ , respectively (measured in millions of years). Haldanes were calculated with the equation:

$$h = |[(\ln x_2/s_{\ln x}) - (\ln x_1/s_{\ln x})]/(t_2 - t_1)|,$$

where  $\ln x_1$  and  $\ln x_2$  are sample means of  $\ln$  measurements at times  $t_1$  and  $t_2$  respectively (measured in generations), and  $s_{\ln x}$  is the pooled standard deviation of  $\ln x_1$  and  $\ln x_2$  (Haldane, 1949). Published demographic data was used to estimate generation time for each species (4.4 generations per year for *Mus*, 4.0 for *Peromyscus*, and 3.6 for *Rattus*) (Matthews, 1952; Collins, Storrer & Rindlaub, 1979; Erickson & Halvorsen, 1990, respectively).

For each island, the five traits showing the greatest change were identified and used for correlation analysis (Table 2). Of these, 29 rates were expressed in

Table 2. Comparison of results synthesized in this paper

Island	Pop. compared	Type of trait	Five traits with greatest change	Percent change	<i>d</i>	<i>h</i>		
Skokholm	Caerforiog	Skeletal vars.	Dyssymphysis of Th.I	+80.7	n/a	n/a		
			Dyssymphysis of Th.X	+50.5	n/a	n/a		
			Interfrontal present	+50.3	n/a	n/a		
			Parted frontals	+31.6	n/a	n/a		
			Foramen ovale single	-31.1	n/a	n/a		
Hestur	Streymoy	Skeletal vars.	Parted frontals	-51.4	n/a	n/a		
			Preoptic sutures present	+46.9	n/a	n/a		
			Alae patinae present	-26.2	n/a	n/a		
			Proc. spin of Th.I absent	+21.7	n/a	n/a		
			For. sphen. med. present	+14.6	n/a	n/a		
			Weight & measures <sup>a</sup>	Weight	+16.3	2105	n/a <sup>b</sup>	
				Head + body length	+7.8	1397	n/a <sup>b</sup>	
		Hind foot length		+5.1	1277	n/a <sup>b</sup>		
		Baltra	Santiago	Skeletal vars. <sup>c</sup>	Tail length	+1.8	108	n/a <sup>b</sup>
					Foramen palatinum majus double	-45.2	n/a	n/a
Acc. maxillary foramen	-22.4				n/a	n/a		
Frontal foramen double	-10.3				n/a	n/a		
Foramen hypoglossi double	+8.6				n/a	n/a		
Preorbital foramen double	-5.4				n/a	n/a		
ANOVA by Patton et al.	Cranial & ext. measures				Length of nasals	+1.2	389	0.001
			Zygomatic breadth	-2.5	849	0.003		
			Rostral width	-4.4	1508	0.005		
			Cranial depth	-4.1	1377	0.005		
			Basilar length	+1.2	386	0.001		
			Frontal foramen double	-30.4	n/a	n/a		
Santa Cruz (GAL)	Santiago		Skeletal vars. <sup>c</sup>	Foramen palatinum majus double	-24.3	n/a	n/a	
		Foramen hypoglossi double		+8.1	n/a	n/a		
		Acc. maxillary foramen		-5.0	n/a	n/a		
		Preorbital foramen double		-0.7	n/a	n/a		
		ANOVA by Patton et al.		Cranial & ext. measures	Length of nasals	+1.4	337	0.001
					Zygomatic breadth	+1.0	236	0.001
					Rostral width	-2.2	557	0.002
	Depth of brain case		-2.0		495	0.002		
	Basilar length		+2.8		700	0.002		
	Intermeatus width		-6.4		1,730	0.003		
	Anacapa	Anacapa <sup>d</sup>	Cranial & ext. measures	Hind foot length	-6.2	1,695	0.004	
				Ear length	+5.3	1,351	0.006	
				Tail length	-3.6	952	0.003	
Depth of brain case				-2.6	702	0.004		

Table 2. (continued)

Island	Pop. compared	Type of trait	Five traits with greatest change	Percent change	<i>d</i>	<i>h</i>
Santa Barbara	Santa Barbara <sup>d</sup>	Cranial & ext. Measures	Tail length	-9.9	2,376	0.006
			Hind foot length	-8.3	1,971	0.008
			Total length	-7.6	1,789	0.006
			Ear length	-5.3	1,231	0.004
			Length of nasals	+4.1	916	0.003
Santa Cruz (CA)	Santa Cruz (CA) <sup>d</sup>	Cranial & Ext. measures	Intermeatus width	-9.7	2,682	0.008
			Tail length	-8.9	2,442	0.006
			Hind foot length	-6.0	1,642	0.007
			Total length	-5.3	1,430	0.005
			Ear length	+4.5	1,152	0.004

'Pop. compared' refers to the population used for calculating percent changes and the traits showing the greatest change, for Berry (1964) and Berry, Jakobsen and Peters (1978).

<sup>a</sup>Only these four ext. and weight measures were taken.

<sup>b</sup>No standard deviations were given so haldanes could not be calculated.

<sup>c</sup>Eighteen skeletal variants were examined, but only incidence values for these five, those with the greatest variation, were given.

<sup>d</sup>Museum specimens from the same location were divided into two time classes, 1897-1941 and 1955-1988, and compared.

darwins and 25 rates were expressed in haldanes. The data were first examined for normality of distribution through inspection of normal probability plots (Afifi & Clark, 1996) and Lilliefors test (SPSS, Inc. 2000b). A Spearman rank-order correlation analysis was then performed. Both analyses used SYSTAT v. 9 (SPSS Inc. 2000a).

Despite the large amount of data reported in each study, there were relatively few variables in common across the studies. We chose five variables for Spearman rank-order correlation analyses, each having at least four data points. The variables were: (1) change in darwins of mensural traits; (2) differences in percent incidences of skeletal variants; (3) island size; (4) distance to the *a priori* defined source population (except in Pergams & Ashley, 1999) and; (5) divergence time as factors. We calculated correlations between (1) change in mensural traits and the rest of the variables, and (2) change in skeletal traits and the rest of the variables, or seven correlations altogether. Change in mensural traits and skeletal variants were the means of the traits in Table 2 (those with the greatest change). Probabilities based on resulting rank-based correlation coefficients (Spearman's *rho*) were calculated from statistical tables (Rohlf & Sokal, 1981) and results were considered to be significant at the 95% level.

## Results

### *Skeletal variants*

For the non-metrical characters, a histogram of differences in percent incidence of all skeletal variants (Figure 1a) shows that the majority of traits changed very little, but approximately 40% of traits changed 10% or more in incidence. A few traits changed drastically, one over 80% in incidence (dyssymphysis of the first thoracic vertebrae in Skokholm *Mus*). For the five skeletal variants that changed the most (Table 2), change in island *Mus* (range of 14.6-80.7%, mean of 42.1%) was greater than for *Rattus* (range of 0.7-45.2%, mean of 16.0%), despite fairly similar time frames.

### *Cranial and external measurements (mensural traits)*

The histogram of rates of change of all mensural traits (Figure 1b) showed that while many traits changed very little, a substantial portion of traits experienced rapid evolution. More than 60% of the traits changed at a rate of 600 *d* or greater. There were a high frequency of cases ( $\approx 23\%$ ) with a 600-800 *d* rate of change, indeed, more than any of the other 13 frequency cat-

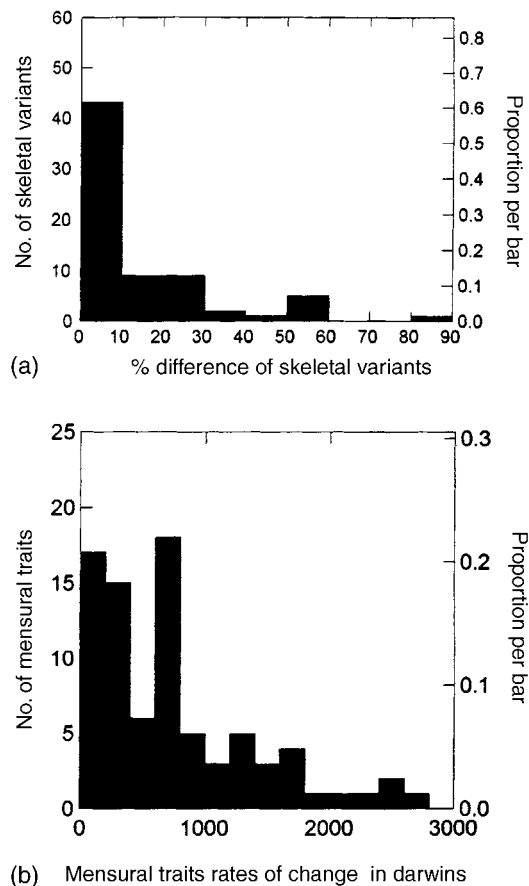


Figure 1. (a) Histogram showing number of skeletal variants at differing percent differences of change for all studies; (b) Histogram showing number of mensural traits at differing rates of change in darwins for all studies.

egories. These traits are listed in Table 4 by island, species, and rate of change in darwins.

Visual inspection of normal probability plots (Afifi & Clark, 1996) as well as Lilliefors tests (SPSS, Inc. 2000b) showed change in mensural traits (both when calculated in darwins and haldanes) and change in skeletal variants to be normally distributed (2-tail Lilliefors  $P$ : change in mensural traits = 1.00, change in skeletal variants = 1.00). However, both methods found island size, distance, and divergence time to be non-normally distributed (2-tail Lilliefors  $P$ : island size = 0.005, distance = 0.001, and divergence time = 0.269), so we used a Spearman rank-order correlation analysis. We could not obtain standard deviations to calculate haldanes for some mensural traits (those from Berry, Jakobsen & Peters, 1978), but we also performed a Spearman rank-order correlation analysis on the reduced haldane data set.

For mensural traits (cranial, external, weight) that evolved most rapidly, all species exhibited remarkably high rates of microevolution. Overall, the rates of evolution ranged from 108 to 2682  $d$ , arithmetic mean of 1230  $d$ , geometric mean of 987  $d$  (Table 2). The rates by species ranged from 236 to 1508, arithmetic mean of 683 in *Rattus*; 108 to 2105, mean of 1222 in *Mus*; and 702 to 2682, mean of 1604 in *Peromyscus*. The highest rates of microevolution were therefore in *Peromyscus*, *Mus* was intermediate, and *Rattus* had the lowest rates of change. By island, mice on Santa Barbara had the most rapid evolution (mean of 1657  $d$ ), followed by the other California Channel islands, whereas rats on Santa Cruz (GAL) had the lowest rates (mean of 465  $d$ ).

Among *Mus* examined by Berry (1964) (Berry, Jakobsen & Peters, 1978), weight and all external measures (4/4) grew bigger. Among *Peromyscus* examined by Pergams and Ashley (1999) external measurements generally grew smaller (9/11). The exception was ear length, which grew larger in two islands and smaller in one. No external measures were among the five with the greatest change in the *Rattus* examined by Patton, Yang and Myers (1975); these five were all cranial measures.

Two cranial measurements, length of nasals and depth of brain case, were among the most rapidly evolving in both Galapagos *Rattus* and Channel island *Peromyscus*. In all cases (four islands, two species), length of nasals grew greater and depth of brain case grew smaller. Depth of brain case was significant but sixth in rank in Santa Barbara (Pergams & Ashley, 1999). Interestingly, another of the most rapidly evolving traits in Galapagos *Rattus* shows the same trend in Channel island *Peromyscus*; rostral width grows larger in Santa Cruz (CA), Baltra, and Anacapa, though in Anacapa it is ninth in rank. Thus the nose became longer and wider while the skull became shallower in rats and mice on five different islands.

### Correlations

Our Spearman correlation analysis identified three pairs of variables significantly correlated at the 95% level (Table 3). The same correlations were significant when calculated in haldanes. There was a +100% ( $P=0.01$ ) correlation between change in mensural traits and change in skeletal variants. Whenever the rate of evolution of mensural traits increased, the difference in percent incidence of skeletal variants increased. These two ways of measuring evolutionary

Table 3. Spearman rank-order correlation coefficients and associated probabilities

	Cranial/external	Skeletal variants
Skeletal variants	<b>1.000 (0.01)</b>	
Island size	-0.429 (0.25)	<b>-1.000 (&lt; 0.005)</b>
Distance	<b>0.833 (0.04)</b>	0.775 (0.18)
Divergence time	0.261 (0.33)	0.400 (0.51)

Results significant at the 95% probability level are in bold.

Table 4. Mensural traits comprising an idiosyncratic 600–800 *d* range from papers analyzed in this study and represented in Figure 1(b)

Island	Species	Trait	Darwins
Santa Barbara	<i>Peromyscus maniculatus elusus</i>	Intermeatus width	757
Santa Barbara	<i>Peromyscus maniculatus elusus</i>	Depth of braincase	619
Anacapa	<i>Peromyscus maniculatus anacapae</i>	Length of incisive foramen	688
Anacapa	<i>Peromyscus maniculatus anacapae</i>	Nasal width	603
Anacapa	<i>Peromyscus maniculatus anacapae</i>	Depth of braincase	702
Anacapa	<i>Peromyscus maniculatus anacapae</i>	Breadth of zygomatic plate	685
Anacapa	<i>Peromyscus maniculatus anacapae</i>	Total length	620
Santa Cruz (CA)	<i>Peromyscus maniculatus santacruzae</i>	Breadth of rostrum	660
Santa Cruz (CA)	<i>Peromyscus maniculatus santacruzae</i>	Depth of braincase	793
Santa Cruz (CA)	<i>Peromyscus maniculatus santacruzae</i>	Breadth of zygomatic plate	677
Baltra	<i>Rattus rattus</i>	Ear length	720
Baltra	<i>Rattus rattus</i>	Diastema	624
Baltra	<i>Rattus rattus</i>	Length of molar tooth row	630
Santa Cruz (GAL)	<i>Rattus rattus</i>	Ear length	609
Santa Cruz (GAL)	<i>Rattus rattus</i>	Basilar length	700
Santa Cruz (GAL)	<i>Rattus rattus</i>	Rostral length	725
Santa Cruz (GAL)	<i>Rattus rattus</i>	Length of molar tooth row	732
Santa Cruz (GAL)	<i>Rattus rattus</i>	Width of molar tooth row	711

This range was about 23% of the total sample of mensural traits and diverged from the expected negative exponential distribution described in Kinnison and Hendry (this volume, Figure 1(a)).

change are apparently closely linked. There was a -100% ( $P < 0.0005$ ) correlation between island size and change in skeletal variants. Changes in skeletal variants were invariably higher on smaller islands. There was a +83% ( $P = 0.04$ ) correlation between change in mensural traits and distance, that is the rate of evolution of mensural traits increased significantly with distance of the island from the nearest island or mainland.

## Discussion

Our goal was to explore patterns of microevolution of insular populations of rodents over very short evolutionary times. We conducted a meta-analysis combining morphological data from seven islands and

three species (Table 1). We were interested in finding consistencies across data sets, traits, and rates of microevolution that could provide detailed resolution of insular rodent evolution. We hoped to identify other patterns in fine-scale morphological change in insular rodents though our meta-analysis.

When a large number of traits are measured, as in our meta-analysis, what is the distribution of change? Do most traits change an 'average' amount, or do most traits change very little, with a few changing to a greater degree? For skeletal variants (Figure 1a), there was a negative exponential distribution, but still 40% of the traits changed in incidence 10% or more. For mensural traits, an even larger proportion of the traits showed rapid evolution of 600 *d* or more (60%). Clearly microevolution, especially in cranial and external traits, is not limited to a small number of traits.



Rodents apparently respond to evolutionary forces on islands with substantial adjustments of their morphology, and do so quickly. The peak we observed at 600–800 *d* ( $\approx 23\%$  of the total) in mensural trait evolution warrants further investigation (Figure 1b). The traits are from five islands, two species, and two studies. This peak contrasts with the distribution found by Kinnison and Hendry (this volume, Figure 1a), where no departure from a negative exponential distribution was noted.

Gingerich (1983) reviews and documents rates of morphological evolution in a study of the effects of temporal scaling on evolutionary rates. He calculated a geometric mean value of 0.08 *d* for fossil vertebrates and 3.7 *d* for post-Pleistocene mammals, with a maximum of 32 *d*. In our data set the five traits with the greatest rates of evolution ranged from 108 to 2682 *d*, with a geometric mean of 987 *d*. This is two orders of magnitude greater than the mean Gingerich reports for post-Pleistocene mammals and exceeds the mean he reports for colonization/ introductions (370 *d*). There are, however, acknowledged limitations in comparing rates calculated across different temporal scales (Gingerich, 1983; Hendry & Kinnison, 1999). The evolutionary rates we calculated were very similar to the mean values reported from a database describing microevolution on contemporary time scales (Kinnison & Hendry, 2001).

Temporal variation of phenotypic characters can be explained by four mechanisms: (1) non-genetic, environmental effects; (2) gene flow from morphologically different source populations; (3) genetic drift; and (4) response to natural selection. For true microevolution to occur, observed phenotypic change must have a genetic basis, at least in part. Although we cannot rule out the possibility that some of the morphological differences represent phenotypic plasticity expressed in a novel environment, we feel that the magnitude of the changes indicates an evolutionary response. Furthermore, the types of phenotypic traits measured in the studies we compared (skeletal variants, cranial characters, and body dimensions) are generally assumed to have an underlying genetic component with moderate to high heritabilities (e.g., Berry, 1963; Leamy, 1974).

Gene flow from morphologically distinct source populations could also result in observed phenotypic changes. However, this seems an unlikely explanation; the islands included in this study are relatively remote, and with the possible exception of Baltra, Galapagos, these islands experience limited boat traffic and introduction of rodents stowaways in numbers needed

to bring about rapid change seems unlikely. It is also difficult to envision a movement pattern (source and destination) to explain the trajectory of the observed changes.

Genetic drift, particularly founder events, certainly warrant consideration as an explanation for microevolution in island rodents. The *Rattus* and *Mus* data in our meta-analysis represent recent colonists that presumably evolved in response to their initial introduction and likely experienced some founder effect. The Channel island *Peromyscus* are not recent arrivals and the changes we observed were unrelated to their initial introduction, yet they exhibited higher rates of evolution than either *Rattus* or *Mus*. Given the finding that long established populations of island *Peromyscus* exhibited the highest rates of change, the role of founding events in driving insular rodent evolution may need to be reconsidered. Through much of his career, Berry emphasized the processes associated with founder events as driving the differentiation of island populations (Berry & Peters, 1976; Berry, Jakobsen & Peters, 1978). For example, he states, "... mouse evolution *has* taken place on the Faroes, albeit by way of vagaries of sampling..." (Berry, Jakobsen & Peters, 1978; author's emphasis). Indeed he chose to investigate binary skeletal variants which he originally assumed to be selectively neutral polymorphisms (Berry, 1963). Even the evolution of these characters, however, seems to be influenced by selection and not solely by random processes. By monitoring Skokholm mice for 10 years, he detected cyclical variation in the frequencies of skeletal variants that suggested stabilizing selection during summer months (Berry & Jakobson, 1975). Observation of progressive change during this period also led Berry to favor 'long-term genetical adjustment' of skeletal variants in response to selection (Berry & Peters, 1976).

Genetic drift can also occur during population bottlenecks, and thus stochastic microevolution on the California Channel islands as well as the other islands in this study could result. There is indeed evidence that deer mice on Santa Barbara and Anacapa experience cyclical population changes (Drost & Fellers, 1991; Pergams, Lacy & Ashley, 2000). However, deer mice on these islands reach extremely high densities (probably due to a lack of competitors and predators), and extrapolation of census data suggests that population sizes remain in the thousands even during 'crashes' (Pergams & Ashley, 1999; Pergams, Lacy & Ashley, 2000). Also arguing against extremely small population bottlenecks are allozyme studies that indicate at

least moderate levels of variation are maintained in the rodent populations in our meta-analysis (Patton, Yang, & Myers, 1975; Berry & Peterson, 1976; Berry, Jakobsen & Peters, 1978; Gill, 1980).

Perhaps the strongest argument against genetic drift or other stochastic processes is the observation that several of the same morphological characters are changing and often changes are in the same direction. There were striking trends seen in mensural trait evolution; a strong tendency for the nose to become longer and wider, while the skull becomes shallower. This pattern was shown by both *Rattus* and *Peromyscus* on five different islands. Interestingly, such changes in facial shape may in fact be a commonality of rodent evolution on both micro and macro scales. In a study of neotropical savanna mice (*Zygodontomys*), variability across localities and species was found to be greatest in measures of the facial skeleton such as rostral width and zygomatic breadth (Voss, Marcus & Escalante, 1990). Although the adaptive implications of such a restructuring of facial shape in rodents is unknown, the pattern is worthy of further investigation. It may be objected that many traits may change simply because they are correlated with overall body size. However, the tendency for the nose to become longer and wider, while the skull becomes shallower cannot be strictly the result of size differences and allometry, because some of the rodents experiencing this trend were getting smaller overall (Channel islands) and some were getting larger (Galapagos). Also, in the Channel islands five cranial traits showed a significant increase and five showed a significant decrease (Pergams & Ashley, 1999), even though mice were growing smaller overall, contradicting size allometry on even a local basis.

There is a body of literature of mammalian evolution on islands, mostly dealing with gross body size rather than the finer scale morphological features we investigated. In a study of tri-colored squirrels in Malaysia, Indonesia, and Thailand, Heaney (1978) shows an inverse correlation of body size with island area up to an island area of about 100 km<sup>2</sup>, above which body size increases. Heaney suggests that on small islands food limitation is the most important factor, while on larger islands predation and interspecific competition become more important. Our findings of an inverse correlation between island area and amount of change in skeletal variants extends Heaney's hypothesis, indicating greater evolution on small islands for a number of traits. The single island larger than 100 km<sup>2</sup> (10,000 ha) for which skeletal

variant data exists (Santa Cruz (GAL)) has the lowest mean difference (13.7) of any island.

Lomolino (1985) showed that trends in body size associated with islands were tied to the animals' absolute size rather than their taxonomic order. Larger mammals tend to become smaller on islands and smaller mammals tend to become larger. Our three species would fall into Lomolino's category of small mammals. In *Mus*, weight and all external measurements increased dramatically, clearly fitting Lomolino's prediction. Although we observed that *Peromyscus* on the Channel islands became significantly smaller during the past 90 years, they remained among the largest subspecies of *P. maniculatus*, still fitting the predicted pattern. For *Rattus*, changes in external measurements were not among the five traits showing highest rates of evolution and did not show a strong trend towards larger body size, contradicting Lomolino's predicted patterns.

Heaney (1978) also discusses the evolution of body size in relationship to distance of an island from the mainland, with body size increasing to a greater degree on more isolated islands. We can extend this argument to rates of change for mensural traits in general because greater evolutionary rates were correlated with island isolation. Increased distance from the mainland or other islands may promote local island adaptations by lowering the frequency of 'contamination' by nonadaptive genes via immigration.

Our results suggest that island rodents consistently exhibit very rapid rates of microevolution, and much of the change may be adaptive. What factors may underlie rapid responses to island environments in mice and rats? Genetic variation within populations is a prerequisite for adaptive responses, and it might seem that population bottlenecks associated with founder events and small population sizes on islands might seriously erode genetic variation. Multiple founders, repeated colonizations and/or rapid expansion following invasions may serve to retain substantial variability, sufficient to allow island populations to respond to selection. Furthermore, rapid adaptive response may happen more readily in isolated populations. The homogenizing effect of gene flow over larger spatial scales is removed, leaving island populations free to track local environmental conditions.

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