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# The Mammals

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In *The Log of the Sea of Cortez,* that memorable treatise of science, adventure, and philosophy, John Steinbeck (1951) made bare mention of mammals. Of course, the main purpose of that effort was to chronicle a trip to the Gulf of California to collect invertebrates in the company of Steinbeck's friend and scientist, Ed Ricketts. The party visited four islands—Tiburón, Coronados, San José, and Espíritu Santo. At anchor off Isla Tiburón, Steinbeck reported a swarm of bats that approached their boat. One bat was collected but, to the best of our knowledge, it was never identified or preserved.

Aside from some descriptions of taxa (e.g., Burt 1932), relatively little was known at the time about mammals from islands in the Sea of Cortés. There is now a reasonably rich history of systematic and biogeographic studies of mammals in and adjacent to the Sea of Cortés (for general reviews, see Orr 1960; Huey 1964; Lawlor 1983; and Hafner and Riddle 1997). Here we summarize much of that information and explore biogeographic patterns that emerge from it, add important recent records of bats, and evaluate new evidence about the origins of insular faunas and the ecological processes and human impacts that affect colonization and persistence of mammals on gulf islands.

## Composition of the Mammalian Fauna

The terrestrial mammalian fauna of islands in the Sea of Cortés (including islands off the Pacific coast of Baja California) comprises 45 species, of which 18 currently are recognized as endemics (but see below), representing 5 orders, 9 families, and 14 genera (app. 12.1). Collectively they share relationships with mainland representatives on both sides of the gulf and are divisible into 28 clades of species or species groups (app. 12.2). Rodents are disproportionately represented, constituting a total of 35 species and 76 of 97 total insular occurrences, and they are the only nonvolant mammals to become established on distant oceanic islands (table 12.1). In addition, except for the few species of lagomorphs, which occur only on landbridge islands, a greater proportion of mainland species of rodents occurs on islands than is the case for other groups of mammals (table 12.1). Overall, large mammals (jackrabbits, carnivores, artiodactyls) are poorly represented. Only larger landbridge islands contain them, and no species is recorded from more than four islands.

*Peromyscus* is the most widely represented genus. Seven mainland species of these seemingly ubiquitous omnivores contribute to island faunas (see app. 12.1). Only *Peromyscus truei*, a species restricted to woodlands and chaparral, does not occur on islands. Pocket mice (*Chaetodipus*), which are largely granivorous, also are well represented. Six mainland species are found on gulf islands (a seventh, *C. fallax*, inhabits Cedros, a Pacific island).

Aside from large landbridge islands (e.g., Tiburón, and the Pacific islands Magdalena and Santa Margarita), it is rare to find more than one species of a genus occupying a given island. Surprisingly, exceptions are on small islands. Willard Island supports *Peromyscus maniculatus* and *P. crinitus*, and San Pedro Nolasco is inhabited by *Peromyscus boylii* and *P. pembertoni* (however, the latter, likely a derivative of *P. merriami*, is probably extinct; see below).

Bats are poorly known from the Sea of Cortés. Twelve species, representing 3 families and 10 genera, are recorded from 29 islands (app. 12.3; Reeder and Norris 1954; Banks 1964a,b,c; Huey 1964; Orr and Banks 1964; Villa-R. 1967; Sanchez-Hernandez 1986; Alvarez-Castañeda and Patton 1999; M. A. Bogan, pers. commun., 1999; M. L. Cody, pers. commun., 1980; T. A. Vaughan, pers. commun., 1980; Alvarez-Castañeda et al., pers. obs.). The most commonly observed species, the fish-eating bat (*Myotis vivesi*), has been reported from 24 islands (and probably occurs on

**Table 12.1** Representation on gulf islands of orders and species of mammals

| | | *Mainland Species Representation on Islands* | | | | | |
|---|---|---|---|---|---|---|---|
| | | All Islands | | Landbridge Islands | | Oceanic Islands | |
| Order of Mammals | No. of Mainland Species[a] | No. | % | No. | % | No. | % |
| Nonvolant | | | | | | | |
| Insectivora | 1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| Lagomorpha | 4 | 3 | 75.0 | 3 | 75.0 | 0 | 0.0 |
| Rodentia | 26 | 19 | 73.1 | 18 | 69.2 | 9 | 34.6 |
| Carnivora | 10 | 3 | 30.0 | 3 | 30.0 | 0 | 0.0 |
| Artiodactyla | 4 | 2 | 50.0 | 2 | 50.0 | 0 | 0.0 |
| Volant | | | | | | | |
| Chiroptera | 47 | 12 | 25.5 | 12 | 25.5 | 7 | 12.8 |

Pacific islands are not included. For nonvolant mammals, only desert-adapted species are considered.
[a] Sonora + Baja California.

virtually all islands); it is the only bat on 17 of 29 islands from which bats are recorded. There are no recognized endemic forms, consistent with the high mobility of bats and proximity of islands to mainland areas.

With few exceptions, insectivorous bats predominate. In addition to the fish-eating bat, two frugivorous species are present: *Leptonycteris curasoae*, which consumes nectar, pollen, and fruit, and derives large quantities of water from nectar (Carpenter 1969); and *Macrotus californicus*, which has a mixed diet of fruit and insects. In general, more species of bats occur on larger, more densely vegetated islands (including eight species on Isla Tiburón, the largest gulf island); no bats are known from Isla Ángel de la Guarda, a large but sparsely vegetated island.

The relatively modest contribution of bat species to insular faunas (table 12.1; app. 12.3) is due mostly to incomplete sampling for these mammals. For example, one night's netting on an easily accessible island (Espíritu Santo) in 1999 (Riddle, Hafner, and Alvarez-Castañeda pers. obs.) yielded four bats of three families and four genera, two of which (*Nyctinomops femorosaccus* and *Lasiurus xanthinus*) were new records for gulf islands. There also has been little effort to collect bats on Pacific islands (only one is recorded; app. 12.3). Increased trapping effort is likely to yield many additional records of bats.

## Origins and Evolution of Insular Faunas

The mammalian faunas of the gulf islands and surrounding mainland areas have been influenced primarily by the evolution of North American regional deserts and geological events associated with the formation and changing shorelines of the Sea of Cortés. In view of the aridity of islands in the gulf and their recent origin, it is not surprising that their mammalian inhabitants are virtually all desert species, each apparently with closely related sister taxa on the closest mainland. However, this straightforward interpretation of the origin of insular mammalian faunas has been complicated somewhat by the recent discoveries of trenchant evolutionary divergences within supposedly circum-gulf species that are concordant with Pliocene and early Pleistocene geological events (Riddle et al. 2000a,b). Thus, as with the herpetofauna of the region (Murphy 1983a,b; Grismer 1994), source populations surrounding gulf islands are more varied than previously recognized. Further, comparison of sequence data from mtDNA of insular populations has provided evidence that the specific source for each island population has not always been from the adjacent mainland (Hafner et al. 2001). Modern mammalian faunas represent a sampling of ancient mainland events in the evolution of North American regional deserts. Earlier views of the gulf and the Baja California peninsula portrayed them largely as peripheral elements in the diversification of regional deserts (e.g., Shreve 1942; Orr 1960; Savage 1960; Wiggins 1960, 1980; Axelrod 1979). However, emerging geological and biogeographic information suggests a greater role for faunas of these areas in the Neogene and Pleistocene assembly of arid-adapted floras and faunas (Murphy 1983a,b; Grismer 1994; Hafner and Riddle 1997; Riddle et al. 2000a,b).

As discussed in chapters 2, 8, and 9, islands in the gulf fall into two categories: old, deep-water oceanic islands and young, shallow-water landbridge islands. This division has important implications for biogeographic analyses of the mammals on the islands. First, it means that well-isolated oceanic islands were colonized by waif dispersal, whereas extant populations on landbridge islands likely originated from fragmentation of widespread mainland populations as the postglacial rises in sea level isolated the islands. The picture is one of two types of faunas: one on oceanic islands made up only of forms that can colonize across water and the other on landbridge islands, consisting chiefly of relictual populations. Expressed in terms of insular biogeographic theory, landbridge islands reach an equilibrium number of species from above, via extinction (they are "oversaturated"), and oceanic islands from below, via dispersal (they are "undersaturated"). The difference in manner of formation of the two types of islands should have important effects on species composition, species diversity, degree of endemism, and amount of morphological variation. Also, the nearly simultaneous (in geological time) separation of landbridge islands from the mainland following the close of the last glacial interval offers an opportunity to reconstruct the full-glacial distribution and species composition of desert refugia surrounding the Sea of Cortés. In effect, landbridge islands serve as genetic and morphological museums of their ancestral founders.

The geologic history of the gulf coincides with the evolution of the North American regional deserts, and insular mammalian faunas consist primarily of desert-adapted species. Among peninsular mammals, and in strong contrast to reptiles, there may be no relicts of more tropical forms in the cape region resulting from initial formation of the gulf approximately 5.5 Ma (Grismer 1994). Instead, relatively mesic-adapted species of mammals occurring today in the cape region probably arrived by dispersal down the higher-elevation spine of the peninsula during pluvial intervals of the Pleistocene, as recently as 10,000 years ago (e.g., *Sorex ornatus*, *Peromyscus truei*) or may have resulted from recent introduction by humans (*Oryzomys couesi*; Nelson 1921; see also Alvarez-Castañeda 1994). Thus, there was little opportunity for dispersal to either landbridge or oceanic islands by other than arid-adapted mammals, particularly from Baja California.

Present-day mammalian faunas of the gulf islands are relatively depauperate subsets of the arid-adapted faunas of the adjacent peninsular and Sonoran regional deserts. Their evolution can reasonably be attributed to events and consequences in geological versus ecological time. Geological events influenced the assembly of the mainland sources for island colonization and resulted in initial isolation of populations on landbridge islands. Subsequent extinction, waif dispersal, and perhaps competition among insular populations then modified the composition of insular faunas.

## Historical Biogeography

### Pertinent Geological Events

Mainland mammalian faunas (of both the peninsular and Sonoran regional deserts) that served as sources for the gulf islands contained species that resulted from ancient, as well as recent, geologic events in the gulf region (Hafner and Riddle 1997; Riddle et al. 2000a,b). These events are of four discrete time periods: Miocene, late Pliocene, early Pleistocene, and late Pleistocene. During the late Miocene to early Pliocene (5.5–4 Ma), the gulf began to form, either due to the separation of Baja California

(Lonsdale 1989; Stock and Hodges 1989) or to subsidence as a result of basin and range extension in North America (Gastil et al. 1983; summarized in Grismer 1994). During the late Pliocene (ca. 3 Ma), northern extensions of the gulf up the Salton Trough formed the San Gorgonio constriction (Boehm 1984; Ingle 1987), and along the course of the Colorado River formed the Boues embayment (Blair 1978; Eberly and Stanley 1978; Buising 1990), effectively isolating the peninsula from continental regions. At the same time, the cape region was isolated from the rest of the peninsula by the Isthmus of La Paz (McCloy 1984). There is circumstantial evidence for a mid-peninsular seaway, across the present-day Viscaíno Desert, in the early Pleistocene, about 1 Ma (Riddle et al. 2000a,b; summarized in Upton and Murphy 1997). Finally, sea levels fluctuated and ecological zones shifted in response to repeated waxing and waning of the late Pleistocene glacial–interglacial climatic cycles, which became markedly longer and more extreme about 700 Ka (Webb and Bartlein 1992). During glacial intervals, sea levels fell, connecting landbridge islands to the adjacent mainland and exposing continental shelves; regional deserts were compressed to the south into isolated refugia (Betancourt et al. 1990), which probably included newly exposed shelves, emergent landbridges, and landbridge islands. Arid-adapted mammals were either restricted to these desert refugia or persisted in pockets of sclerophyllous woodland or marginal grassland habitats. Arid-adapted taxa spread from these refugia during warmer interglacials, providing the opportunity for dispersal into neighboring arid and sclerophyllous regions, and populations on landbridge islands were isolated as ocean levels rose.

## Phylogeographic Variation in Mitochondrial DNA

Recent advances in molecular techniques, particularly the increased facility to sequence large sections of the mitochondrial genome, have provided powerful tools to examine both evolutionary relationships and detailed distributional changes (historical biogeography) of plants and animals. Molecular techniques provide sensitive indicators of relationships among taxa and relative estimates of the timing of divergence events, especially for species with restricted ecological distributions and low vagility ("biogeographic indicator species"; Harris 1985; Sullivan 1988; Hafner 1993). Initial studies of arid-adapted rodents in the gulf region revealed old divisions within and between related taxa of peninsular and Sonoran deserts (Riddle et al. 2000a,b) and supported most of the insular–mainland associations previously recognized while clarifying the relationships of certain problematic insular taxa (Hafner et al. 2001; fig. 12.1).

Old historical (Neogene) divisions between peninsular and Sonoran taxa and among peninsular subgroups thus far revealed by data from mtDNA sequences seem associated with at least three events of the late Neogene: temporary existence of a mid-peninsular seaway across the Viscaíno Desert approximately 1 Ma; northern extensions of the gulf approximately 3 Ma; and simultaneous formation of the Isthmus of La Paz (Riddle et al. 2000a,b,c). A mid-peninsular seaway has long been hypothesized (see Nelson 1921). However, as summarized by Upton and Murphy (1997), evidence to date for the seaway appears largely circumstantial, based on low mid-peninsular elevations, limited stratigraphic data from adjacent regions, and the distribution of marine organisms on either side of the peninsula. According to J. Minch

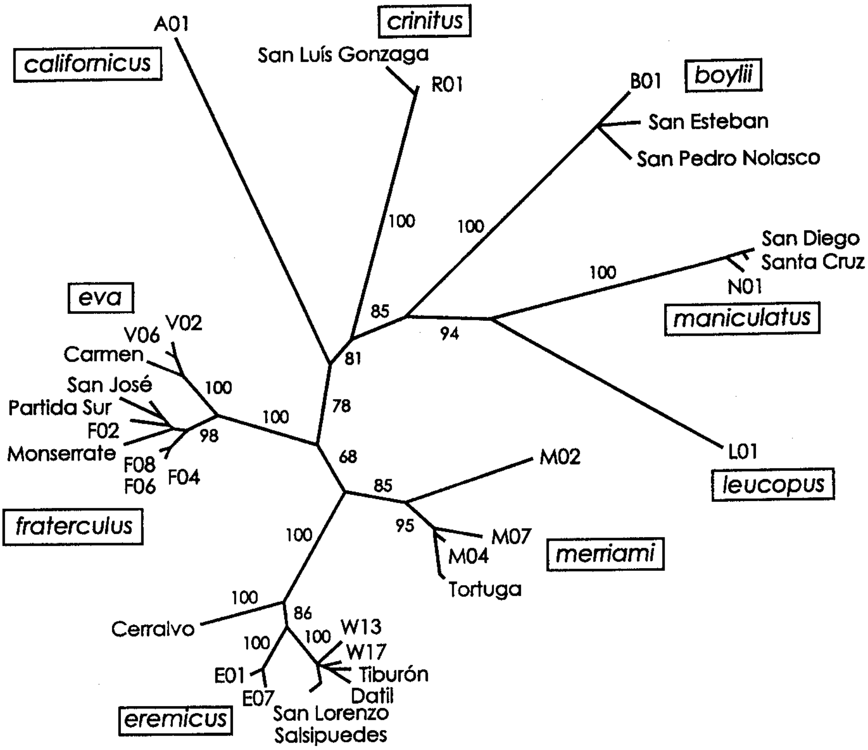

**Figure 12.1** Unrooted neighbor-joining tree (Hafner et al. 2001) comparing 15 insular populations of *Peromyscus* (indicated by island name) to 16 populations of 9 mainland species of *Peromyscus*, based on estimates of sequence divergence among variable haplotypes from a 699 base-pair fragment of the mtDNA COIII gene. Nonparametric bootstrapping values (percent of 500 replications) summarize relative levels of branch support on the neighbor-joining tree. Representative reference sequences are indicated by haplotype number from Riddle et al. (2000a). The clade labeled "*fraterculus*" identifies a new taxon proposed for certain populations of peninsular *Peromyscus* (Riddle et al. 2000a; see text).

(pers. commun., 1997), sedimentary evidence for such a seaway is not likely to be forthcoming because the limestone deposits in the Viscaíno Desert are virtually fossil-free (lacking even foraminiferans) and directly overlay Paleocene deposits.

Upton and Murphy (1997) reported a genetic discontinuity between northern and southern populations of *Uta stansburiana* that is concordant with the existence of such a past seaway, which they estimated (based on a combination of mtDNA phylogeography and dated geologic events) as having been formed about 1 Ma. Five rodent species or species groups (*Peromyscus eremicus*, *Chaetodipus baileyi*, *C. arenarius*, *Dipodomys merriami*, and *Ammospermophilus leucurus*) exhibit signatures of a mid-peninsular seaway (Riddle et al. 2000c). Levels of sequence divergence in these forms are intermediate (1.8–4.1% sequence divergence) to those separating related taxa on opposite sides of the Gulf (8.7–10.5% sequence divergence) and to values of insular versus mainland taxa (~1% sequence divergence; Hafner et al. 2001). Concordant patterns may be expected in another rodent (*Neotoma lepida*; Plantz 1992) and have been reported for a bird (*Toxostoma lecontei*; Zink et al. 1997) and three additional reptiles: *Pituophis melanoleucus* (Rodriquez-Robles and De Jesús-Escobar 2000), *Urosaurus nigricaudus* (Aguirre et al. 1999), and the rock lizards *Petrosaurus mearnsi* and *P. thalassinus* (Aquilars-S. et al. 1988; Grismer 1999).

Most likely, rising sea levels that led to northern extensions of the Sea of Cortés and formation of the Isthmus of La Paz simultaneously separated peninsular from Sonoran desert populations and cape region from other peninsular populations. Subdivision of peninsular and Sonoran populations into separate phylogroups consistent with the northern gulf extensions is present in three rodent groups (*P. eremicus* and *C. baileyi* [Riddle et al. 2000c] and *N. lepida* [Plantz 1992]) and the red-spotted toad (*Bufo punctatus*; Riddle et al. 2000c). Peninsular subdivisions of the former two rodents appear to be cryptic species (*P. fraterculus* [Riddle et al. 2000a] and *C. rudinoris* [Riddle et al. 2000b]). Separation of the cape region from remaining peninsular populations coincident with the Isthmus of La Paz is present in at least *C. arenarius* (Riddle et al. 2000c) and *Urosaurus* (Aguirre et al. 1999), and may be present in *Petrosaurus* (Aquilars-S. et al. 1988; Grismer 1999).

Thus, as a result of northern extensions of the gulf (3 Ma) and a mid-peninsular seaway (1 Ma), there were at least three mammalian faunal sources available to colonize landbridge islands that were last separated from the mainland as recently as several thousand years ago: coastal Sonoran, northern peninsular, and southern peninsular. A potential fourth faunal source (cape region) may have resulted from formation of the Isthmus of La Paz (3 Ma) or initial formation of the gulf (5.5–4 Ma).

## Faunal Relationships

Distributions of mainland species of terrestrial mammals and their island derivatives are shown in appendixes 12.1 and 12.2. For completeness, Pacific island forms are also included. (These do not include two unverified occurrences reported in Dickey [1983]: "two small rodent species" on San Ildefonso and "the white-footed mouse" on Isla Estanque [= Vibora or Pond].) An obvious pattern emerges from these distributions. In general, insular faunas resemble continental faunas of the nearest mainland area. With three suggested exceptions, ancestral forms of eastern gulf islands are represented by extant Sonoran species, and those of western islands by peninsular species (Hafner et al. 2001; app. 12.2). Evidence of cross-gulf colonization is limited to proposed derivatives of Sonoran *Peromyscus* (subgenus *Haplomylomys*) on deep-water oceanic islands that are closer to the peninsular mainland: (1) *Peromyscus dickeyi*, a derivative of *Peromyscus merriami*, a Sonoran species, on Isla Tortuga, and (2) derivatives of Sonoran *Peromyscus eremicus* on the midriff islands at least as far west as Isla Salsipuedes and the San Lorenzos (populations currently labeled *P. interparietalis*), and on Isla Cerralvo (*P. eremicus avius*).

Identification of *Peromyscus eremicus avius* of Isla Cerralvo as a possible derivative of Sonoran *P. eremicus* rather than peninsular *P. eva* or *P. eremicus* (putatively *P. fraterculus*; see above) appears to parallel the distribution of the lizard genus *Sator* in the southern gulf islands (Murphy 1975, 1983b). Murphy (1975) interpreted the distribution of *Sator* as resulting from entrapment of the genus on islands during the initial Miocene formation of the gulf. Indeed, *P. eremicus avius* appears to be a somewhat distant relative of other *P. eremicus*, with a divergence predating separation of Sonoran and Chihuahuan clades of *P. eremicus* (Riddle et al. 2000a). However, mtDNA divergence values indicate a separation of *P. e. avius* subsequent to separation of peninsular (*P. eva* + *P. fraterculus*) and Sonoran (*P. merriami* + *P. eremicus*) species in the subgenus. If correct, a more likely explanation for the origin of *P. eremicus* on Cerralvo is overwater dispersal from mainland Sonora during the Pliocene.

The fact that most populations of mammals on landbridge islands are clearly allied with mainland populations in closest proximity indicates that isolation from mainland populations followed the most recent rise in sea level at the end of the Wisconsin glaciation, in some populations as recently as several thousand years ago (Case 1975; Wilcox 1978). Thus, divergence attained during previous cycles of colonization and isolation may have been obliterated by confluence of landbridge island and mainland populations during the Wisconsin glacial interval. Available data on degree of divergence in mtDNA sequences of landbridge island versus mainland populations of *Peromyscus* (Hafner et al. 2001) are consistent with this interpretation.

Shifts in the distribution of mainland species subsequent to isolation of populations on landbridge islands at the close of the Wisconsin glaciation are indicated by comparing the current distribution of mainland populations with derivatives on landbridge islands. The brush rabbit (*Sylvilagus bachmani*), a chaparral species, may have enjoyed a broader distribution along the Baja California peninsula during the more mesic Wisconsin glaciation, because the nearest mainland relatives of the population on Isla San José (*S. mansuetus*) are located nearly 400 km to the north (Santana) and 200 km to the south (Santa Anita). *Peromyscus eremicus* (putatively *P. fraterculus*; see above) evidently has retreated northward, as indicated by populations on Islas Espíritu Santo and San José and an apparently relict population on the peninsula east of La Paz, at Las Cruces (Lawlor 1971b). Similarly, populations of *Chaetodipus baileyi* and *Peromyscus eremicus* on oceanic islands close to the Baja California peninsula, and of *P. boylii* on oceanic islands on the Sonoran side of the gulf may indicate that source populations formerly occurred along the respective adjacent coasts during the Wisconsin maximum. Reconstruction of former mainland distributions based on oceanic islands is far more tentative, as indicated by the possible long-distance dispersal of *P. eremicus* to Isla Cerralvo and of *P. merriami* to Isla Tortuga (Hafner et al. 2001).

All species of bats thus far recorded from Sea of Cortés islands occur on both the peninsular and the Sonoran-Sinaloan mainlands, but the extent of movement between islands and the mainland, or between Sonoran and peninsular mainlands, is unclear. Genetic (Wilkinson and Fleming 1996) and reproductive (Ceballos et al. 1997) data indicate that large, able fliers such as *Leptonycteris curasoae* regularly migrate across the gulf between the southern Baja California peninsula and Jalisco (see also Rojas-Martinez et al. 1999). Sahley et al. (1993) documented nightly flights of 20–30 km by *L. curasoae* from day roosts on Tiburón to the adjacent Sonoran mainland. Certainly, the presence of *Lasiurus* on oceanic islands, including Hawaii and the Galapagos Islands, attests to the occasional, accidental dispersal of strong, rapidly flying bats, particularly those that regularly undertake long-distance migrations. It is likely that some species of bats dispersed across the gulf (deliberately or accidentally) and became established on the peninsula. For example, four species (*Natalus stramineus*, *Balantiopteryx plicata*, *Pteronotus davyi*, and *Myotis peninsularis*) have disjunct distributions in the cape region (Woloszyn and Woloszyn 1982); their nearest relatives are across the gulf. However, the large degree of variation in flight speeds and endurance found in bats (e.g., Hayward and Davis 1964) would probably lead to varying degrees of isolation among species of insular bats. T. A. Vaughan (pers. commun., 1980) reported that *Antrozous pallidus* from Isla Carmen is smaller than its peninsular counterpart, despite a relatively narrow (6 km) separating seaway. Some species of bats may be reluctant to set out over open water, even if they are capable of flying the distance, and genetic interchange between island and mainland populations may result only from rare, chance dispersal in these species, as with nonvolant small mammals.

### Pleistocene Refugia

Hafner and Riddle (1997) speculated that there may have been three distinct refugia for arid-adapted mammals on the Baja California peninsula during glacial maxima: a California refugium along the northern Pacific coast; a Magdalena refugium along the southern Pacific coast and extending out onto newly exposed continental shelf; and a gulf coast refugium along the southern gulf coast. These remained separate from the continuous Mohavia refugium at the head of the gulf and the Sinaloa refugium along the southern Sonoran and Sinaloan coasts. Initial results from mtDNA analysis of 11 island populations of one group (*Peromyscus* subgenus *Haplomylomys*) provide tentative support for the existence of a separate gulf coast refugium and for northward expansion of the gulf coast, Mohavia, and Magdalena refugia after the end of the Wisconsin glacial interval. Specifically, two populations from islands opposite the southern gulf coast of the peninsula evidently are derivatives of putative *P. fraterculus* (which now occurs to the north) rather than *P. eva*, which occupies the adjacent coast; and all of the midriff-island populations thus far analyzed appear to be derivatives of the Sonoran species, *P. eremicus*.

Analysis of additional island populations of *Haplomylomys* (recorded from 10 other islands surrounding the peninsula), as well as island populations of *P. maniculatus* (12 islands), *Chaetodipus spinatus* (14 islands), and the *Neotoma lepida* species-group (13 islands) should provide informative tests of the hypothesis of separate full-glacial refugia. We expect that relationships among populations of the latter two species, which frequent arid habitats, should conform to the refugium hypothesis, whereas the former, which is widespread in many habitats within its geographic range, should not.

## Ecological Biogeography

### Ecological Characteristics of the Mammalian Fauna

Many ecological factors affect distributions of mammals, including dispersal abilities, habitat quality and diversity, productivity and availability of food sources, natural-history traits, and extent of competition and predation. That colonizing abilities differ among mammals is demonstrated by examination of worldwide patterns of continental and insular distributions of major groups of mammals (Lawlor 1986, 1996). The best colonizers are small, relatively abundant terrestrial species with catholic diets and high population growth rates, and bats. Landbridge islands typically have attenuated continental faunas, whereas faunas on oceanic islands are ecologically incomplete (Simpson 1956; Baker and Genoways 1978; Lawlor 1996). The latter conclusion holds among archipelagoes regardless of differences in the magnitude of isolation by over-water distances or size ranges of islands and relates directly to the manner in which the islands were colonized—either by waif dispersal (oceanic islands) or by fragmentation from mainland faunas (landbridge islands) (Lawlor 1996). These generalizations are supported in gulf island faunas by the fact that only small rodents and bats inhabit oceanic islands, whereas ecologically diverse faunas that include insectivores, lagomorphs, carnivores, and artiodactyls, in addition to rodents and bats, characterize landbridge islands.

The variety of habitats suitable for mammals on gulf islands is limited because of the arid climate and virtual absence of fresh water. Relatively unproductive rocky habitats predominate (see chap. 4). This overall lack of habitat diversity, among other things, suggests that resource coupling is the important determinant of lizard and bird species numbers on gulf islands (Case 1975, 1983, chap. 9, this volume; Case and Cody 1987). For the above reasons, terrestrial mammals preferring situations other than rocky habitats are rare or nonexistent in the Sea of Cortés except on the largest and most diverse islands, which almost invariably are also landbridge islands (e.g., Tiburón, Carmen, San José, Magdalena, Santa Margarita, Espíritu Santo).

The overwhelming majority of mammalian species found on gulf islands are associated with rocky habitats in both mainland and island settings. The species that do not prefer such habitats are broadly adapted (e.g., *Peromyscus maniculatus*), found only on relatively large islands rich in habitat or prey-species diversity (e.g., *Lepus* spp., *Perognathus penicillatus*, *Thomomys bottae*, *Dipodomys merriami*, *Canis latrans*, *Urocyon cinereoargenteus*, *Bassariscus astutus* [see fig. 16.4], *Odocoileus hemionus*), or may have become extinct recently (e.g., *Peromyscus pembertoni* on San Pedro Nolasco).

Diversity, density, and productivity of plant species (see chap. 4) vary considerably on the islands. As discussed below for islands in Bahía de los Ángeles, seasonal and El Niño patterns of rainfall in the Sea of Cortés strongly influence the annual seed production on which many species depend. Consequently, the ability of many species to persist on an island is related directly to seasonal changes in availability of food. Lawlor (1983) argued that the ephemeral nature of seed availability should be much more limiting to granivores such as pocket mice (*Chaetodipus*) than to deer mice (*Peromyscus*), which have a varied diet that also includes terrestrial and marine invertebrates. Two pieces of evidence support this contention. First, one-species islands (those inhabited by only a single species of mammal) are occupied only by *Peromyscus*, never by *Chaetodipus* or, for that matter, by any other mammals. Overall, species of *Peromyscus* and *Chaetodipus* frequent 42 and 25 major islands, respectively (these values become 51 and 28 if occurrences on minor islands [table 12.2] are added). The absence of *Chaetodipus* on such small islands is a significant departure from that expected from the proportion of total mouse populations (consisting of *Peromyscus* and *Chaetodipus*) on gulf islands made up by pocket mice (25/67, or 37.3%; $p <$ .0001, using a test of equality of percentages based upon the arcsine transformation). In other words, the absence of pocket mice from one-species islands is not attributable to an overall paucity of these rodents on gulf islands. Nor is their absence due simply to a lack of sandy habitats on small islands, because the most common species of

**Table 12.2** Characteristics of Bahía de los Ángeles and Bahía de las Ánimas islands inhabited by rodents

| Island | Area ($km^2$) | Distance from Peninsula (km) | *Peromyscus Maniculatus* | *Chaetodipus Baileyi* |
|---|---|---|---|---|
| Blanca | 0.03 | 0.90 | X | |
| Bota | 0.09 | 2.85 | X | |
| Coronadito | 0.10 | 3.09 | X | |
| Flecha | 0.16 | 2.79 | X | |
| Pata | 0.18 | 2.55 | X | X |
| Mitlan | 0.19 | 2.00 | X | X |
| Piojo | 0.57 | 6.30 | X | |
| Cabeza de Caballo[a] | 0.70 | 2.02 | X | |
| Ventana | 1.41 | 3.15 | X | |
| Smith | 9.13 | 2.18 | X | X |

Islands surveyed that lack mice: Bahía de las Ánimas: Las Ánimas Norte, Las Ánimas Sur, Pescador; Bahía de los Ángeles: Gemelos East, Gemelos West, Cerraja, Llave, Jorobado. Island area and isolation from Murphy and Aguirre-Léon (chap. 8, this volume) and Polis et al. (1998).

[a] Rodents were not detected on Cabeza de Caballo until late 2000 and therefore were not included in analyses.

pocket mice (*C. spinatus* and *C. baileyi*) occur in rocky habitats on both islands and the mainland.

Second, congeneric pairs of *Peromyscus* and *Chaetodipus* species occur on five and three islands, respectively. These associations are mostly on large islands (e.g., Tiburón), but *Peromyscus* pairings are known from two small islands (*P. crinitus* and *P. maniculatus* on Willard, and *P. boylii* and *P. pembertoni* on San Pedro Nolasco). Though not significant, this finding is consistent with the especially strong competition for limited seed resources expected among the more highly specialized *Chaetodipus*, especially on small islands.

The structure of insular rodent communities comprising *Peromyscus* and *Chaetodipus* is reminiscent of species assembly patterns described for desert rodent communities in the southwestern United States (Patterson and Brown 1991; Fox and Brown 1993). There, pocket mice and deer mice form hierarchical arrangements in which the more specialized heteromyids frequent fewer locations than their generalized murid counterparts. However, the extent to which this hierarchy of occurrences has been shaped by competition or simply by coexistence of species with distinct dietary adaptations remains an open question.

Rainfall patterns also determine availability of fresh water. Among rodents, woodrats (*Neotoma*) are the least capable of tolerating dehydration (MacMillen 1964). Woodrats depend heavily on plant tissues for free water. The large seasonal and annual fluctuations in densities of *Neotoma lepida* and related endemics on gulf islands (Lawlor, pers. obs.; T. A. Vaughan, pers. commun., 1980), which match those often seen in mainland settings (Lee 1963; MacMillen 1964; Lieberman and Lieberman 1970), may be due in part to availability of preformed water from plants.

Published natural history information for mammalian populations on gulf islands is confined largely to a few studies of the feeding ecology and behavior of rabbits and woodrats. Jackrabbits (*Lepus californicus*) are common on several islands, where they inhabit a variety of habitats and exploit an expanded diet of cacti and shrubs compared to their mainland counterparts (Hoagland 1992; Cervantes et al. 1996). Woodrats (*Neotoma lepida*) on Danzante are scansorial herbivores with diets restricted largely to ironwood (*Olneya tesota*) leaves (Vaughan and Schwartz 1980), but periodic use is also made of other shrubs and cholla cacti. They occur at low densities on the island, although their biomass exceeds that of the only other species there (a pocket mouse, *Chaetodipus spinatus*), and they occupy unusually large territories for the species. Vaughan and Schwartz (1980) argued that reduced numbers of predators on Danzante produced a mating system based on resource-defense polygyny in these woodrats. In contrast, species of *Peromyscus*, which are not strongly territorial, seemingly exhibit excess density compensation rather than increased territory size on some depauperate islands (Lawlor 1983).

## Case Study: Insular Rodents on Small Islands near Bahía de los Angeles

Stapp has been studying rodent populations in the northern midriff islands, in Bahía de los Ángeles (BLA), with the objective of determining how the availability of foods of terrestrial and marine origin influence insular rodent populations. Compared to other islands in the Sea of Cortés, the landbridge islands in BLA are mostly small (<1 km$^2$ in area; table 12.2) and relatively close to the peninsula. Nevertheless, because rodents are poor overwater dispersers, ecological processes shaping rodent assemblages on BLA islands should largely parallel those affecting rodents throughout the region.

### *Resource Availability and Dietary Breadth*

Like most small islands in the Sea of Cortés, the terrain of BLA islands is very steep and rocky, with little sand except on small, isolated beaches. Island substrate determines the availability of refuges for rodents and also has an important indirect effect on food availability by restricting plant establishment and growth. Perennial shrubs and cacti are present on most islands, but plant cover is relatively low (5–17%) in dry years (Sánchez Piñero and Polis 2000). Terrestrial resources available to rodents on these islands include seeds and leaves of perennial plants (primarily *Opuntia, Pachycereus*, and *Atriplex*), as well as land arthropods (mostly tenebrionid beetles and ground dwelling spiders) and small vertebrates such as lizards (*Uta stansburiana*) and the eggs and nestlings of songbirds.

Foods derived from the ocean also provide important nutrients and energy for island consumers, supporting higher population densities than would be possible based on terrestrial resources alone (Polis and Hurd 1996). Marine resources include invertebrate communities of the rocky intertidal and supralittoral zones, algae and carcasses of marine animals that wash ashore, plus the scavengers and detritivores that are attracted to them. Sea birds are another important conduit of marine-based energy. On nesting-colony islands, sea birds contribute eggs, chicks, and food scraps to island food webs. Guano deposited by sea birds on both roosting and nesting islands fertilizes plant growth, providing nutrients for insular terrestrial communities (Stapp et al. 1999). Marine-based resources may be critical to island populations because terrestrial productivity is seasonally ephemeral and, in most years, relatively low overall, and because inputs from the ocean are less easily depleted than terrestrial resources. In other words, consumers cannot control resource delivery and renewal rates (Polis and Hurd 1996). Consequently, mammals that use marine-based foods may be buffered from extreme year-to-year variability in the availability of terrestrial resources, which in turn may allow them to become more widespread and persistent on islands than species that depend solely on terrestrial foods.

Interspecific differences in the ability of rodents to take advantage of marine-based resources may in part explain patterns of distribution on the Sea of Cortés islands, and perhaps worldwide. Rodents inhabit 10 of the 19 islands in the BLA region, which range in size from 3 ha to 9.1 $km^2$ in area. Like most other small islands in the Sea of Cortés, BLA islands are inhabited chiefly by two types of rodents: omnivores (*Peromyscus*) and granivores (*Chaetodipus*). Deer mice (*Peromyscus maniculatus*) occur on all 10 islands with rodents; pocket mice (*Chaetodipus baileyi*) are restricted to three islands (table 12.2). As in other regions of the gulf, *Chaetodipus* never occurs alone on BLA islands, which Lawlor (1983) attributed to the scarcity of suitable seed resources on most islands, especially small ones. The diversity and availability of seeds may indeed explain the presence of *Chaetodipus* on two small BLA islands (Pata, Mitlan); both islands have extremely high plant species diversity for their size (West, chap. 4, this volume). Although the presence of *Chaetodipus* on Mitlan may also be explained by its close proximity to Smith, the largest island in the area, the presence of *Chaetodipus* on Pata, which is small and relatively isolated, was unexpected; Pata is the smallest gulf island occupied by a granivorous rodent.

Earlier studies of coastal populations have shown that *Peromyscus* feeds on marine invertebrates in intertidal and sandy-beach habitats (McCabe and Cowan 1945; Osborne and Sheppe 1971; Thomas 1971; Herman 1979; Lawlor, pers. obs.). Whereas these past studies have combined behavioral observations with traditional methods for assessing food habits, Stapp et al. (1999) used stable isotope analysis (SIA) to document use of marine resources by *Peromyscus* and other island consumers (e.g., lizards, arthropods). By comparing carbon and nitrogen isotope ratios of consumer tissues to those of potential prey items, SIA provides an estimate of an animal's dietary composition and of its relative trophic position in food webs (Schoeninger and DeNiro 1984; Peterson and Fry 1987). The advantage is that SIA quantifies diets of organisms that are difficult to study with conventional techniques. Furthermore, depending on the tissue analyzed, SIA provides a cumulative record of the relative importance of different food sources through time. Analyses of tail (bone and skin) tissue from *Peromyscus* and *Chaetodipus* provide an integrated index of the contributions of marine and terrestrial-based resources throughout an individual's life, which typically is 1 year or less (Stapp, unpublished data).

SIA results confirm that *Peromyscus* is a dietary generalist and that individuals living close to shore eat marine invertebrates (fig. 12.2). Further inland, the elevated nitrogen isotopic signatures suggest that deer mice apparently consume terrestrial arthropods, other small invertebrates, and in wet years on some islands, seeds (Stapp et al. 1999). In contrast, pocket mice are strictly granivorous both near the shore and inland, consuming a mixture of seeds from plants with C3 and C4/CAM photosynthesis (fig. 12.2).

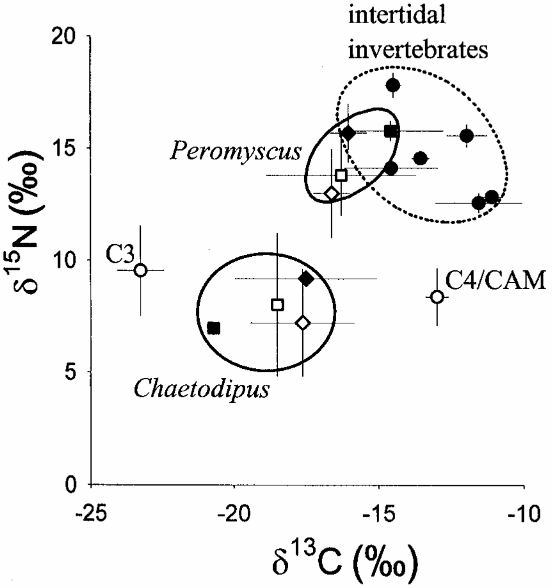

**Figure 12.2** Stable carbon ($^{13}$C) and nitrogen ($^{15}$N) isotopic signatures (mean + SE) of *Peromyscus* and *Chaetodipus* near shore (filled symbols) and in inland areas (>100 m) from shore; open symbols) on Bahía de los Ángeles islands ($n = 1–5$ islands). Squares indicate samples collected in a typical dry year (1997); diamonds are from 1998, an El Niño-Southern Oscillation year. Isotopic signatures of terrestrial C3 and C4/CAM plants and intertidal invertebrates are provided for reference (Stapp et al. 1999).

Subsidies provided by the ocean to island populations of *Peromyscus* influence patterns of abundance of mice on and among islands. During typical dry years, *Peromyscus* tends to be most abundant near shore, especially on islands occupied by both mouse species (fig. 12.3). *Chaetodipus* tends to be more numerous inland, presumably because coastal areas are barren of most perennial, seed-bearing plants. Although competition probably contributes to this pattern (see below), the high-protein foods available near shore may permit relatively high densities of *Peromyscus* in these areas. Moreover, the effects of marine resources on *Peromyscus* populations are evident on an island-wide basis (fig. 12.4). Small islands, which tend to have large shoreline perimeters relative to their areas and, hence, relatively larger fractions of marine inputs, tend to support higher densities of mice than larger islands, at least during normal, dry years (1997, 1999, 2000). High population densities are a common feature of many insular rodent populations (Gliwicz 1980), which has been attributed to lower predator pressure, fewer competitors, or frustrated dispersal (fence effects) on islands. Although all these may contribute to high densities of *Peromyscus* on BLA islands, the disproportionately large input of marine resources to small islands, many of which support roosting and nesting sea-bird colonies, provides another explanation. The success of *P. maniculatus* on small rocky islands in BLA probably reflects both competitive and predatory release, as well as the abundance of marine resources on islands.

Periods of unusually high rainfall can have dramatic and long-lasting effects on terrestrial primary and secondary productivity (Noy-Meir 1973; Polis 1991). At Bahía de los Ángeles, El Niño-Southern Oscillation (ENSO) events that occur every 5–8 years bring large amounts of winter precipitation, switching the system from one dominated by marine resources to one driven more by terrestrial productivity (Polis et al. 1997). Average plant cover on BLA islands increases 30–49% (Sánchez Piñero

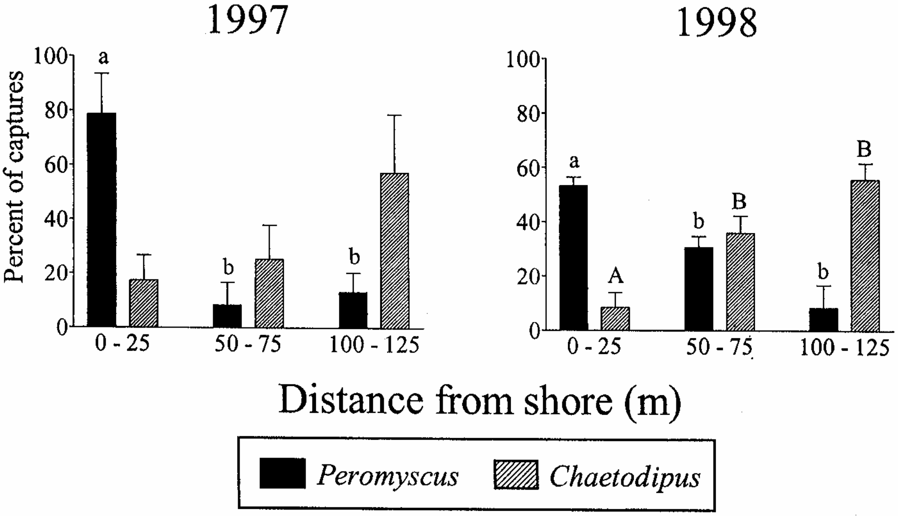

Figure 12.3 Distribution of captures of *Peromyscus* and *Chaetodipus* at different distances from the ocean during a typical dry year (1997) and a wet El Niño Southern Oscillation year (1998). Within a species and year, means with same letter are not statistically different (nested ANOVA, Tukey test, $p < .05$). Values are means (+1 SE; $n = 2$–$3$ islands).

and Polis 2000) and vegetation is dominated by annual plants. This pulse in annual plant growth also supports higher densities of herbivorous insects and their predators (Polis et al. 1997), which serve as prey for deer mice on many islands (fig. 12.2). Unfortunately, there are no accurate estimates of changes in seed production for most plants, but seed output of the dominant perennial on islands (*Atriplex barclayana*) was three times higher in 1998, an intense ENSO year, than in the previous dry year (Stapp et al. 1999). The increase in seed production associated with ENSO events may have wide-reaching effects on island granivores such as pocket mice because some seeds enter soil seed banks that may persist during intervening dry years. Further, *Chaetodipus baileyi*, like other heteromyid rodents, caches large numbers of seeds in extensive burrow systems (Stapp, pers. obs.).

ENSO-related changes in resources have a significant impact on population densities of both species, but the numerical response of *Peromyscus* is much more pronounced. On islands surveyed in both dry (1997) and wet ENSO (1998) years, mean abundance of *Peromyscus* increased by 372% (SE = 91%) immediately following the 1998 ENSO. In contrast, *Chaetodipus* numbers increased only 81% (SE = 58%) from 1997 to 1998 and declined by 33% on Pata, where *Peromyscus* abundance increased sixfold. *Peromyscus* not only increased significantly in abundance but also invaded inland areas of islands during the 1998 ENSO (fig. 12.4). The pulse of terrestrial resources in response to the 1998 ENSO also reduced the relative importance of marine inputs for whole-island abundance, so that population densities were high on all islands, regardless of island perimeter-to-area ratio (fig. 12.4).

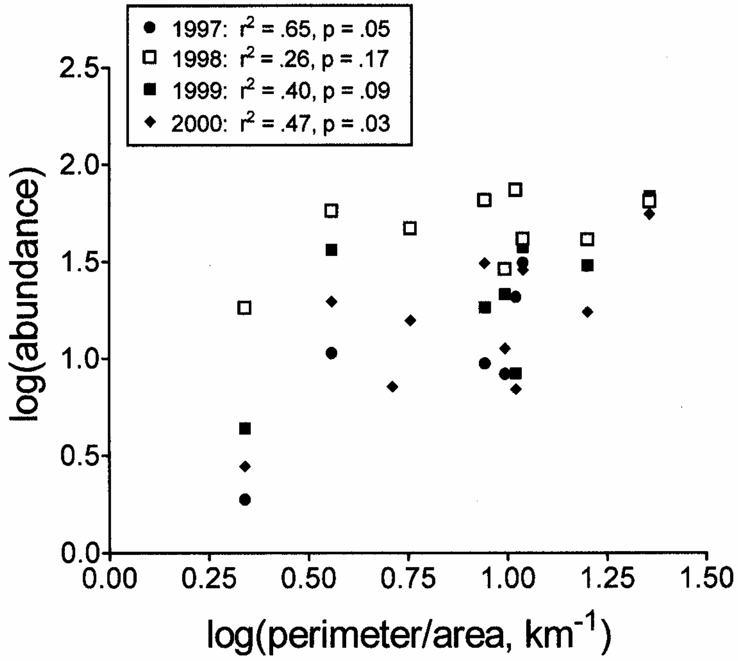

Figure 12.4 Relative abundance of *Peromyscus* during three dry years (1997, 1999, 2000) and an El Niño Southern Oscillation year (1998) on islands as a function of island perimeter-to-area ratio, an index of amount of marine input. Small islands have relatively more shoreline for their size, creating a greater target area for drift of algal wrack and carcasses, and more area for intertidal invertebrate communities. Statistics are regression coefficients.

### *Competition*

Patterns of spatial distribution of *Peromyscus* and *Chaetodipus* on islands where they co-occur suggest distinct habitat preferences that reflect the availability of food resources used by each species. Deer mice tend to be restricted to near shore, whereas pocket mice are more evenly distributed but most common farther inland (fig. 12.3). However, on islands occupied only by *Peromyscus*, there were no significant differences in either 1997 or 1998 in the relative abundance at different distances from shore (Stapp, unpublished data), which suggests that the presence of *Chaetodipus* affects habitat use and local abundance of *Peromyscus*. This hypothesis is consistent with our knowledge of the ecology of these species in other systems: pocket mice (*Chaetodipus*, *Perognathus*) tend to be aggressive and territorial (Jones 1993), whereas *Peromyscus* is behaviorally subordinate to other species in many rodent communities (e.g., Grant 1972; Bowers et al. 1987; Kaufman and Kaufman 1989; Heske et al. 1994; Stapp 1997). We also speculate that, in addition to their seed-caching abilities, the desert-adapted *Chaetodipus* is more efficient than *Peromyscus* at locating and harvesting seeds that are scarce and widely scattered on islands in most years.

Although *Chaetodipus* may have an advantage during arid years typical of the region, *Peromyscus* seems to be more effective at converting the ENSO-related pulse of terrestrial resources into offspring, which subsequently spill over into inland areas inhabited by *Chaetodipus* (fig. 12.3). During these periods of unusually high abundance of *Peromyscus*, we captured individuals of both species simultaneously in the same trap on six occasions. In all cases, deer mice killed and partially consumed pocket mice (by comparison, no mortalities were observed in 32 instances that year of multiple captures involving only a single species). The nature and outcome of competitive interactions between *Chaetodipus* and *Peromyscus* thus appears to switch between wet and dry years. Experimental manipulations of seed resources or population densities are needed to assess the degree of and relative symmetry of competition between island populations of *Peromyscus* and *Chaetodipus*.

### *Dispersal Ability*

The species composition of rodent assemblages on small landbridge islands near BLA is more likely a reflection of differential extinction of species present before island formation than the consequence of regular recolonization over water. To the extent that dispersal may account for compositional differences, characteristics of deer mice appear to make them more effective overwater dispersers than pocket mice. First, the close proximity to and high densities of *Peromyscus* near shore mean that dispersing *Peromyscus* are more likely to head out over water than *Chaetodipus*, which are more closely associated with inland habitats. Second, the generalized diet of *Peromyscus*, which may involve foraging in large algal mats and in marine animal carcasses, may predispose it to dispersal should these rafts be set adrift. Third, human occupancy and visitation of islands may have increased exchange of *Peromyscus* among islands during historic times. During periods of high densities, *Peromyscus* overrun fishing, tourist, and research camps on beaches (Lawlor and Stapp, pers. obs.).

### *Two Different Strategies*

Taken together, these ecological factors offer a mechanistic explanation for the biogeographic distribution of rodents on islands in the Sea of Cortés. *Peromyscus* and *Chaetodipus* appear to have different strategies for coping with the extreme and unpredictable insular environments characteristic of the region, and these strategies reflect differences in diet, life history, competitive ability, and dispersal (table 12.3).

*Peromyscus* is widely distributed among islands because of its ability to persist on islands once established and its capacity to disperse short distances across water. Physical differences among islands, including the availability of suitable refuges and the amount of habitable area, ultimately determine whether an island can support a rodent population. The ability of *Peromyscus* to use a wide variety of food resources, notably the largely unlimited resources available from the ocean, buffers populations against periods of low terrestrial productivity and, ultimately, extinction. *Peromyscus* responds numerically to pulses of terrestrial resources via dramatic increases in reproduction, leading to large temporal variations in population density, but the degree to which these individuals are recruited and contribute to long-term future survival of the population is not clear. On islands with competitors such as *Chaetodipus*, however,

**Table 12.3** Ecological influences on the distribution of *Peromyscus* and *Chaetodipus* among islands in the Sea of Cortés

| Trait | *Peromyscus* | *Chaetodipus* |
|---|---|---|
| Diet | Terrestrial and marine foods | Seeds |
| Distribution of resources among islands | Widespread | Restricted; dependent on plant diversity and abundance |
| Competitive ability | Inferior | Superior |
| Response to ENSO[a] pulse in resources | High reproductive output | Seed caching; modest reproduction |
| Temporal variation in population size | High (CV = 84%)[b] | Low (CV = 48%) |
| Explanation for persistence | Buffered during low terrestrial productivity by ability to use marine-based resources | Seed storage, foraging efficiency, and conservative life history; susceptible to extended drought |
| Dispersal ability and opportunities | Good | Poor |
| Distribution among islands | Widespread | Less common |

[a] El Niño Southern Oscillation.

[b] mean coefficient of variation in relative abundance between 1997 and 1998.

From Stapp (in prep.).

*Peromyscus* may be restricted to areas near the shore by interspecific territoriality and/or the scarcity of preferred terrestrial foods. Similarly, *Peromyscus maniculatus* seems to be unsuccessful in competitor-rich communities on the adjacent mainland (Stapp, unpublished data), underscoring the importance of these islands in maintaining regional species diversity.

In contrast, *Chaetodipus* occurs on a small subset of islands, usually larger islands with a greater variety of plant associations or sandy substrates, or on small islands with unusually high plant diversity. Critical to persistence of *Chaetodipus* is its ability to exploit efficiently the scarce seed resources available during dry years and to monopolize and store large amounts of seeds produced by periodic ENSO rainfall events. Compared to *Peromyscus*, the life-history traits of *Chaetodipus* and other heteromyids are relatively conservative (e.g., long life spans, low reproductive effort; Brown and Harney 1993), which makes them well-adapted for survival under harsh and unpredictable conditions typical of desert islands. Although population densities are probably more stable over time than those of *Peromyscus*, we speculate that insular populations of *Chaetodipus* would be more susceptible to extinction in an extended drought period in which the soil seed bank was not replenished by ENSO winter rainfall. Islands undergoing extinctions would be less likely to be recolonized by *Chaetodipus* because of their limited ability and opportunities for overwater dispersal and because fewer islands have sufficient plant cover or diversity to sustain granivore populations (Lawlor 1983).

## Diversity Patterns

Mammals are the least conspicuous and diverse vertebrates frequenting Sea of Cortés islands. Assemblages on oceanic islands are most impoverished, containing no more than three species of nonvolant mammals. Although one landbridge island supports 14 species (Tiburón), others have 7 or fewer (although Magdalena, a Pacific island, contains 9; apps. 12.1, 12.2).

### *Species–Area Relationships*

The power model of the relationship between species number and island size takes the typical form $\log(S) = c + z(\log A)$, where $\log(S)$ is log species number, $A$ is island area, $c$ is a constant, and $z$ is the slope of the line described by the equation. In the equilibrium model of island biogeography (MacArthur and Wilson 1963, 1967), high $z$-values (e.g., $>0.40$) are associated with well-isolated archipelagos in which rates of colonization are low and rates of extinction are high and vary inversely with island size. Low $z$-values (e.g., $<0.20$) are characteristic of interconnected faunas in which immigration rates more than offset effects of extinction, as in the case of nonisolated samples on continents. Intermediate, or equilibrial, $z$-values (0.20–0.35) typify insular situations in which rates of colonization and extinction are equal or nearly so.

For a variety of reasons, interpretations of the species–area relation must be made with caution (see, e.g., Rosenzweig 1995). Both $c$ and $z$ depend on the taxa and types of islands being examined (Preston 1962; MacArthur and Wilson 1967; Brown 1978), and in a power model $c$ and $z$ are not wholly independent (Lomolino 1989). Moreover, a variety of factors can interact to produce identical $z$-values, so by itself a single species–area curve cannot discriminate among biogeographic hypotheses.

The $z$-values for mammals from all islands, including those along the Pacific coast off Baja California, and for islands confined to the Sea of Cortés, are 0.265 ($n = 34$) and 0.242 ($n = 26$), respectively; both values resemble those typical of equilibrial faunas. In contrast, dividing major islands into shallow-water landbridge and deep-water oceanic islands reveals markedly different values. The $z$-value for landbridge islands (0.365; $n = 24$; 0.310 if only gulf landbridge islands are plotted) conforms to established values for such fragmented insular faunas, but the value for oceanic islands (0.119; $n = 14$) departs from theoretical prediction (fig. 12.5).

The distinction between $z$-values for the two types of islands is a departure from that predicted by equilibrium theory. However, it is consistent with qualitative differences among species–area curves for mammalian faunas on oceanic and landbridge islands worldwide that Lawlor (1986, 1996) attributed to the legacy of events shaping the assembly of mammalian faunas on islands (waif dispersal vs. extinction, respectively). In all cases in which intra-archipelago comparisons can been made, $z$-values are steeper for landbridge islands than for oceanic islands.

Previous analyses using stepwise multiple regression (Lawlor 1983) revealed that island area was the best predictor of species richness in the Sea of Cortés; isolation was not significantly correlated with diversity. In contrast, no single variable contributed overwhelmingly to explanations of variation in species numbers on oceanic islands, although measures of both island area and isolation were significantly correlated with richness.

Incorporation of species numbers from the small BLA islands (table 12.2) into species–area analyses of landbridge-island faunas reveals a prominent small-area effect (fig. 12.6). Species richness is relatively stable (one to three species) and independent of area for roughly four orders of magnitude of the smallest islands. MacArthur

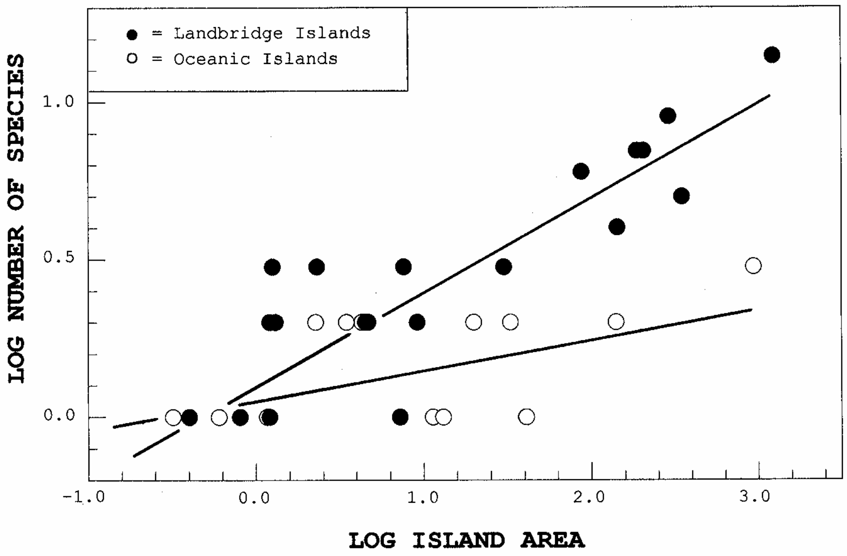

Figure 12.5 Log-log plot of species–area relations for terrestrial mammals occurring on major landbridge and oceanic islands (*n* = 20 and 14, respectively) along the peninsular Pacific coast and in the Sea of Cortés. Species numbers are provided in appendix 12.2.

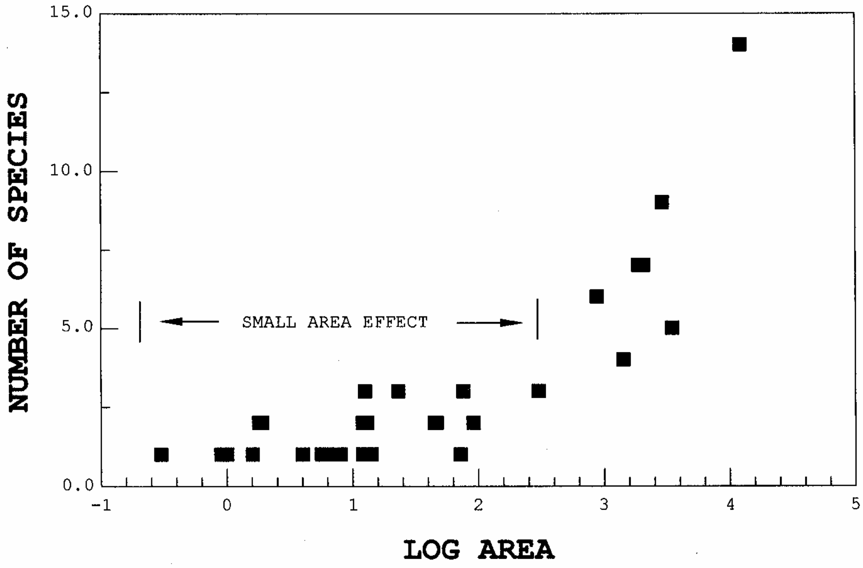

Figure 12.6 Semi-log plot of species–area relations for terrestrial mammals occurring on major and minor landbridge islands along the peninsular Pacific coast and in the Sea of Cortés (*n* = 29). Note the prominent small-island effect. Species numbers are provided in appendix 12.2.

and Wilson (1967) attributed this pattern to population instability on very small islands. In his species-based, heirarchical model of island biogeography, Lomolino (2000) argued that the effect may be characteristic of a more general sigmoidal relationship between species and area in archipelagos containing a wide range of island sizes. The only mammals frequenting resource-limited small islands in the gulf are rodents of the genera *Peromyscus*, *Chaetodipus*, and *Neotoma*.

### *Species Assemblages*

For the historical-legacy model to be sustained, compositional differences between assemblages on oceanic and landbridge islands also must be consistent with it. Three predictions of the model are relevant here. First, terrestrial mammals on oceanic islands should be confined to a much narrower range of taxonomic and ecological groupings of mainland fauna than for landbridge islands (Lawlor 1996). This prediction is confirmed from the facts that oceanic islands contain only rodents, whereas landbridge islands are occupied by a much wider range of taxa with a greater diversity of ecological roles.

Second, occurrence frequencies (the number of available islands occupied by each species) and average incidence per species of such occurrences should be lower on oceanic than on landbridge islands. This prediction follows because mammals have poor dispersal capabilities over water, so species on deep-water islands should have relatively low probabilities of invading all islands.

These expectations are confirmed. Oceanic-island faunas are characterized by a highly disproportionate number of species that occupy only one island (10 of 14 total species, or 71%); the maximum number of islands inhabited by any given species is 4 (1 species). In contrast, on landbridge islands, incidences range from 10 species occupying only a single island (42% of 24 species) to one species present on 11 islands. Average incidences (the average fraction of total landbridge and oceanic islands inhabited by each species) are 15.2 and 11.1, respectively (Lawlor 1996).

Third, faunas on different-sized landbridge islands should constitute a graded series of nested subsets, whereas those on oceanic islands should be characterized by unordered assemblages of species. This, too, is the case, although the narrow range of variation of species numbers on oceanic islands (one to three) does not provide a robust test. As reported by other authors using the matrix of species occurrences provided by Lawlor (1983), only terrestrial mammalian faunas on landbridge islands are significantly nested (Patterson and Atmar 1986; Patterson 1987, 1990; Wright and Reeves 1992; Wright et al. 1998). This distinction is sustained, regardless of which landbridge islands are targeted, using the updated species matrix (app. 12.2) and Atmar and Patterson's (1993, 1995) nestedness temperature calculator (fig. 12.7).

### *Equilibrium or Historical Legacy?*

Compared to lizards and birds (reviewed in Case 1983; Case and Cody 1983, 1987), diversity patterns in mammals are much less dynamic, reflecting what appears to be a much greater impact of historical influences on species numbers and assemblages. Insular isolation has marked effects both on invasion likelihood and extinction rates of terrestrial mammals, especially for those on small islands. Contemporary ecological

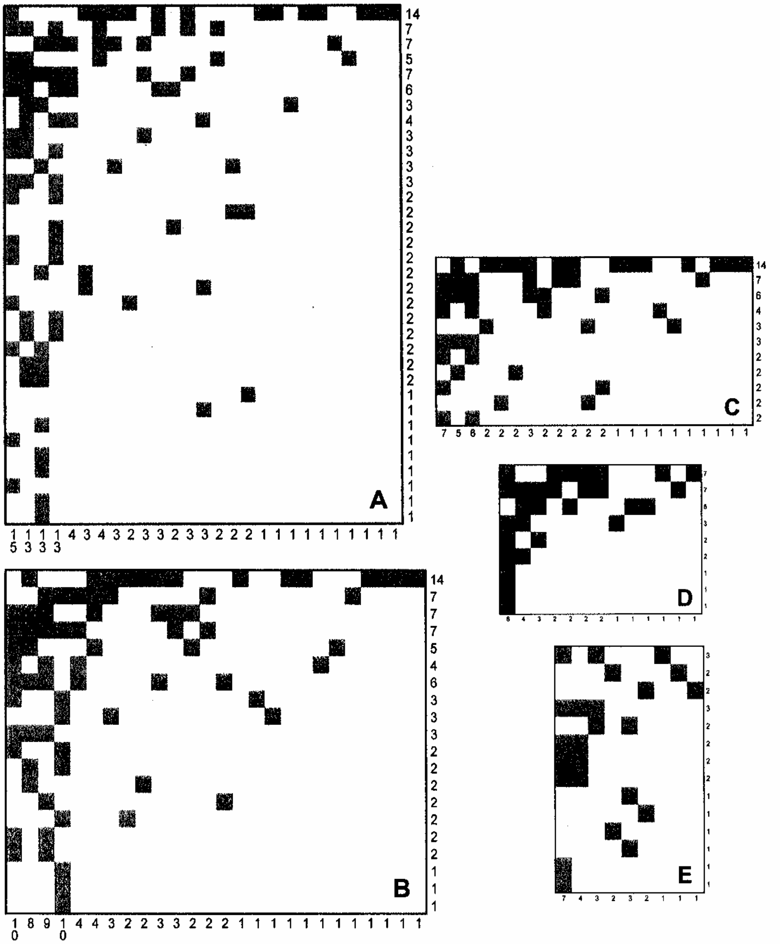

**Figure 12.7** Nested species arrangements of clades (species or species groups; app. 12.2) from major islands in the Sea of Cortés determined by use of Atmar and Patterson's (1993, 1995) nestedness temperature calculator. Data are ordered by number of species per island (from most to fewest; *y*-axis) and number of insular occurrences per species (from most to fewest; *x*-axis). Individual plots are (A) all islands (including both Sea of Cortés and Pacific islands); (B) all landbridge islands; (C) landbridge islands in Sea of Cortés only; (D) Pacific landbridge islands only; (E) oceanic (deep-water) islands only. Except for oceanic islands (E), all sets are significantly ordered.

effects, while not insignificant, have evidently shaped biogeographic patterns of insular faunas to a lesser extent in terrestrial mammals than in other vertebrates.

This overall interpretation is supported by combined evidence derived from both species-richness patterns and analysis of species assemblages in mammals from islands in the Sea of Cortés. It is further supported by worldwide patterns. For instance, low *z*-values characterize oceanic faunas regardless of archipelago age and relative isolation (Lawlor 1996), suggesting that subsaturation is pervasive.

## Extinctions and Introductions

Although colonizing abilities may explain the initial appearance of a species on an island, they do not account fully for the persistence of a species after its arrival. For example, landbridge islands in the gulf probably had a more or less complete continental fauna of desert-adapted species when formed. Extinctions have since pared down each fauna to its present composition. As previously discussed, faunas on these islands have collapsed since separation from the mainland and, as expected, relaxation has been most pronounced for faunas on small islands. Using estimated extinction rates, Case and Cody (1987) confirmed this effect and demonstrated that mammals became extinct faster than reptiles on landbridge islands in the Sea of Cortés.

It is also clear that extinctions have not been random among taxa. Relatively small omnivorous, granivorous, and herbivorous species predominate on all gulf islands. Hence, in addition to being good colonists, these species are also more resistant to extinction once established, as exemplified by rodents on BLA islands. Of course, the ultimate reason for this is their ability to sustain relatively large population sizes, as predicted for such species by MacArthur and Wilson (1967).

Extinctions of mammalian populations on islands in the Sea of Cortés have not been limited to prehistoric or ecological influences, however. Surveys conducted by Alvarez-Castañeda, together with Centro de Investigaciones Biologicas del Noroeste (CIBNOR) and others, have identified eight taxa of mammals that evidently have disappeared recently (app. 12.1) and several others that are vulnerable (e.g., *Neotoma lepida* on Danzante and San Francisco) or in imminent danger of extinction (*Dipodomys merriami insularis* and *Neotoma albigula varia* on San José and Turner, respectively) (Schultz et al. 1970; Lawlor 1983; Mellink 1992a,b; Smith et al. 1993; Alvarez-Castañeda 1994, 1997a; Alvarez-Castañeda and Cortés-Calva 1996, 1999, in press; Bogan 1997; Cortés-Calva et al. 2001a,b). Of course, many taxa on islands in the Sea of Cortés are vulnerable to extinction because they have distributions restricted to one or a few islands, limited population sizes on islands of relatively small size, or both. Yet most modern extinctions are uniquely attributable to human activities involving habitat disturbances or introductions of non-native species. The latter include predators (chiefly domestic cats, *Felis cattus*) and non-native rodent competitors (rats, *Rattus rattus*; and house mice, *Mus domesticus*), in addition to other domestic species (table 12.4).

Four extinctions involve species endemic to single islands; the remaining ones are local extirpations of otherwise more widespread species (app. 12.1). Domestic cats, which have well-known negative impacts in island settings (Owen 1977; Konecny 1987a,b; Van Rensburg and Bester 1988), and introduced rodents are implicated in four and three disappearances, respectively. Human activities such as guano mining (e.g., Granito, San Roque), poison-control efforts to eradicate introduced rats (e.g., San Roque), establishment of fishing camps (e.g., Granito), and tourist visitations (e.g., Danzante, Espíritu Santo) doubtless have had impacts as well. The remaining island, San Pedro Nolasco, is one of five islands (and one of only two small ones; see above) containing two species of *Peromyscus* (*P. pembertoni* and *P. boylii*). Although it will never be known for certain, the apparent disappearance of *P. pembertoni* from San Pedro Nolasco may be the result of competitive interactions with the other *Peromyscus* species.

**Table 12.4** Introduced domestic mammals recorded from islands in the Sea of Cortés

| | *Introduced Mammals* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Island | Cats | Rodents | Goats | Rabbits | Cattle | Horses | Dogs | Native Mammals | Extinct Mammals |
| Sea of Cortés | | | | | | | | | |
| Willard | | | | | | | Coyote? | 2 | |
| Mejía | | X | | | | | | 2 | 1 |
| Granito | | X | | | | | | 1 | 1 |
| Angel de la Guarda | X | | | | | | | 3 | |
| San Pedro Nolasco | X | | | | | | | 2 | 1 |
| Tiburón | | | | | | | Coyote | 14 | |
| San Marcos | X | X | X | | | X | X | 2 | |
| Coronado | X | | | | | | | 3 | |
| Carmen | X | | X | | | | | 4 | |
| Monserrat | X | | | | | | | 2 | 1 |
| Catalina | X | | | | | | | 1 | |
| Santa Cruz | X | | | | | | | 1 | |
| San José | X | | X | | X | X | X | 7 | |
| San Francisco | | | X | | | | | 2 | |
| Espíritu Santo | X | | X | | | | | 6 | |
| Cerralvo | X | | X | | | | | 2 | |
| Pacific Ocean | | | | | | | | | |
| San Martín | X | | | | | | | 3 | 1 |
| San Gerónimo | X | | | | | | | 1 | 1 |
| Cedros | X | | | | | | X | 5 | |
| Natividad | X | | | | | | | 1 | |
| Asunción | X | | | | | | | 1 | |
| Magdalena | | | | | | | Coyote | 9 | |
| Santa Margarita | X | X | | | | | X | 7 | |

For sources of data, see text. Islands are arranged from north to south in each category. Note that domestic species are absent on those islands inhabited by coyotes.

Another replacement may have occurred on Santa Catalina. In 1995, Alvarez-Castañeda failed to locate the native species, *Peromyscus slevini*, a *maniculatus*-like form (Burt 1932; see app. 12.2). Instead, he found an *eremicus*-like mouse previously unknown from the island (Hafner et al. 2001). The status of these species is undergoing further exploration (Carleton and Lawlor in prep.).

Predictably, small islands demonstrate disproportionate numbers of extinctions compared to large ones. In fact, in all cases in which potentially competing species (*Mus, Rattus*) have been introduced to very small islands (those <3.0 km$^2$), the single native species has been extirpated. Because only *Peromyscus* occupies single-species islands, members of this genus are most heavily affected (islas Granito, Mejía, San Roque). Introduced species are reported from no small single-species islands on which *Peromyscus* persists (San Diego, Santa Catalina).

On slightly larger islands (3–10 km$^2$) containing woodrats (*Neotoma*) and one or two other rodent species, woodrats characteristically disappear first (Todos Santos, San Martín, Turner, Coronado). This is consistent with their greater susceptibility to predation from domestic cats or to competition from introduced *Rattus* with more generalized diets. By contrast, woodrats are common on Espíritu Santo, despite the presence of introduced cats and native ring-tails (*Bassariscus astutus*) (Alvarez-Castañeda et al. submitted). Could interactions with established predators preadapt insular woodrats for coexistence with domestic cats?

It is impossible to establish with certainty that extinctions have occurred, but in each of the above instances intensive effort has been expended without success to establish the presence of populations. In some instances, many surveys involving thousands of trap-nights have been undertaken by different investigators over many seasons and years (decades in a few cases). For example, the last known collection of *Peromyscus pembertoni* (San Pedro Nolasco) was made by W. H. Burt in 1931, and attempts to locate this species, involving more than 7000 trap-nights and several investigators, have failed to find it (Lawlor 1983). Moreover, most disappearances are reported for small islands, on which thorough sampling has been conducted in every habitat and at all locations.

Intentional or inadvertent introductions by humans are common on gulf islands (table 12.4). Domestic cats are especially widespread. It is interesting that cats are absent on three islands on which coyotes are present (table 12.4), an observation consistent with the absence of these mesopredators in the face of large carnivores elsewhere (e.g., Crooks and Soulé 1999).

Introductions are implicated in two occurrences of antelope ground squirrels (*Ammospermophilus* spp.) on Sea of Cortés islands (Espíritu Santo and San Marcos). These highly visible squirrels were first reported from San Marcos in 1987 (J. Reichman, pers. commun., 1989), despite several earlier visits by biologists. They are kept as pets by people in Santa Rosalía and Loreto, on the peninsular coast (Hafner, pers. obs.; Wright 1965). Isla San Marcos is only 5 km from the mainland and, with fresh water provided by brackish wells, was once the site of a small tannery (Slevin 1923). It is currently the site of a gypsum mine that supports mine workers and their families on the island, and squirrels are especially numerous in the canyon immediately north of the mine. If ground squirrels were introduced as escaped pets on San Marcos, the same might be true of the population on Espíritu Santo. Only 6 km from La Paz, this island supported several hundred Indians during aboriginal times, was the site of experimental pearl farming operations in the early 1900s, and is routinely visited by fishermen from the peninsular mainland (Dickey 1983).

## Patterns of Variation

### Population Variation

In general, Sea of Cortés mammals exhibit only modest degrees of differentiation from related mainland species. The numbers of endemic species and subspecies (see above and app. 12.1) are relatively low but are high compared to those of lizard faunas on the same islands (Case and Cody 1983; Murphy 1983b, Grismer 1994; chaps. 8, 9, this volume). Predictably, the most divergence among terrestrial mammals has taken place on oceanic islands, presumably because of their greater isolation.

Among gulf mammals, variation in members of the genus *Peromyscus* has been studied most intensively (Banks, 1967; Lawlor 1971a,b, 1983; Avise et al. 1974; Gill 1981; Riddle et al. 2000a; Hafner et al. 2001) and to a lesser degree in *Chaetodipus* (Gill 1981; Riddle et al. 2000b). In contrast to landbridge island forms, populations on oceanic islands are characterized by relatively large deviations in body size (see below), peculiar characteristics of the skull and phallus, and unique chromosomal and biochemical (mtDNA and allozyme) attributes.

Hafner (1981) quantified the occurrence of upper premolars ($P^3$) in antelope ground squirrels (*Ammospermophilus*), the size and occurrence of which are extremely variable in the rodent family Sciuridae. The tooth is reduced and occasionally absent in all *Ammospermophilus*, its absence varying in frequency from 2% to 15%. In *A. insularis* from Espíritu Santo, fully 55% of specimens lacked one or both of the premolars. Howell (1938) considered this to be one of the major distinctive features of this insular endemic species.

Interisland morphological variation among terrestrial mammals is demonstrated in both body size and pelage coloration. As in mammals elsewhere, pelage color typically matches the color of the surrounding background. Dark substrates on volcanic islands promote melanism in several island populations. Examples include the black jackrabbit (*Lepus insularis*) on Espirítu Santo, occasional melanistic individuals of rock squirrels (*Spermophilus variegatus*) on Tiburón, a gray morph in pocket mice (*Chaetodipus spinatus*) on Mejía, and relatively dark populations of *Peromyscus guardia* and *Peromyscus pseudocrinitus* on Mejía and Coronado, respectively (Burt 1932; Banks 1967; Lawlor 1971a; Gill 1981).

Although important for assessing the impact of genetic bottlenecks and amounts of gene flow among insular populations, intra-island variation in gulf mammals has been little explored. Patterns of allozymic, morphometric, and discrete character variation in *Peromyscus* seem most consistent with the hypothesis that genetic bottlenecks, either recently or historically, have led to reduced intrapopulation variability (Lawlor 1983). Using two measures of morphological variation (coefficients of variation and epigenetic character variation), Lawlor (1983) found that populations on oceanic islands and small landbridge islands were less variable than those on large landbridge islands and the mainland, and that intrapopulation variation was least in morphologically more divergent oceanic-island populations. Additionally, unique chromosomal, allozymic, and morphological traits are found only in populations on oceanic and small landbridge islands (Lawlor 1971a; Avise et al. 1974). Overall, Lawlor (1983) found no support for hypotheses based on indices of habitat complexity, competition, or resource availability. That marked reductions in population size occur periodically on small islands is verified by measured density changes of rodents on islands in Bahía de los Ángeles and the disproportionate number of disappearances of small-island populations recorded in the Sea of Cortés (see above).

## Variation in Body Size

Body size varies in regular ways among insular mammals. When assessed across taxa on a worldwide basis, gigantism prevails in rodents, whereas dwarfism predominates in carnivores and in the herbivorous lagomorphs, artiodactyls, and elephants, although there are exceptions. Generally, small species exhibit gigantism and large ones exhibit dwarfism. Van Valen (1973a) coined the "island rule" to recognize the common occurrence of this phenomenon. Hypotheses to explain insular size variation center on an interplay among competition, predation, and resource limitation (e.g., Foster 1963; Van Valen 1973a,b; Case 1978, 1979; Heaney 1978; Lawlor 1982; Angerbjorn 1985, 1986; Lomolino 1985; Smith 1992), although other explanations have been posited (Foster 1965; Wassersug et al. 1979; Melton 1982; Lomolino 1985). These relationships vary among species and locations (summarized in Dayan and Simberloff 1997).

Body-size (as indexed by body length) shifts in mammals on islands in the Sea of Cortés are not wholly consistent with other studies (fig. 12.8). Lagomorphs tend to be larger, not smaller, on gulf islands (*contra* Hoagland 1992). Within rodents, departures from mainland relatives tend toward larger sizes and are striking in some populations of *Peromyscus* and *Neotoma*; a maximum body length increase of 27.5% is achieved in woodrats (*Neotoma bunkeri*) on Coronado (Smith 1992). In contrast, smaller sizes obtain in insular *Chaetodipus*, with a maximum decrease of 12.7% in *Chaetodipus spinatus* on San Marcos (Lawlor 1982). Data for multiple congeneric species occurring on the same island suggest that, whatever the selective factors for determining body size, they may operate consistently in closely related species that share similar diets. For example, all three species of seed-eating pocket mice occurring on Tiburón (*Chaetodipus baileyi*, *C. intermedius*, and *C. penicillatus*) show similar decreases in body length (Lawlor 1982).

Lawlor (1982) proposed that body-size differences in small mammals from gulf islands evolved in response to differing levels of competition and available resources in low-productivity environments. Assuming that predators and overall food sources are reduced on islands, there should be different consequences for species competing for particulate foods (granivores) than for those with generalist diets or that feed on vegetative matter (omnivores, folivores). Insular conditions should induce dwarfism in specialists because they exploit a resource that is distributed discontinuously in space and time, but such conditions should favor gigantism in generalist species, whose food supply is more homogeneously distributed and perhaps enhanced in competitor-poor environments.

Among genera of rodents, the order of specialist to generalist was expected to be *Chaetodipus-Peromyscus-Neotoma*. Supporting data for this pattern stem mostly from

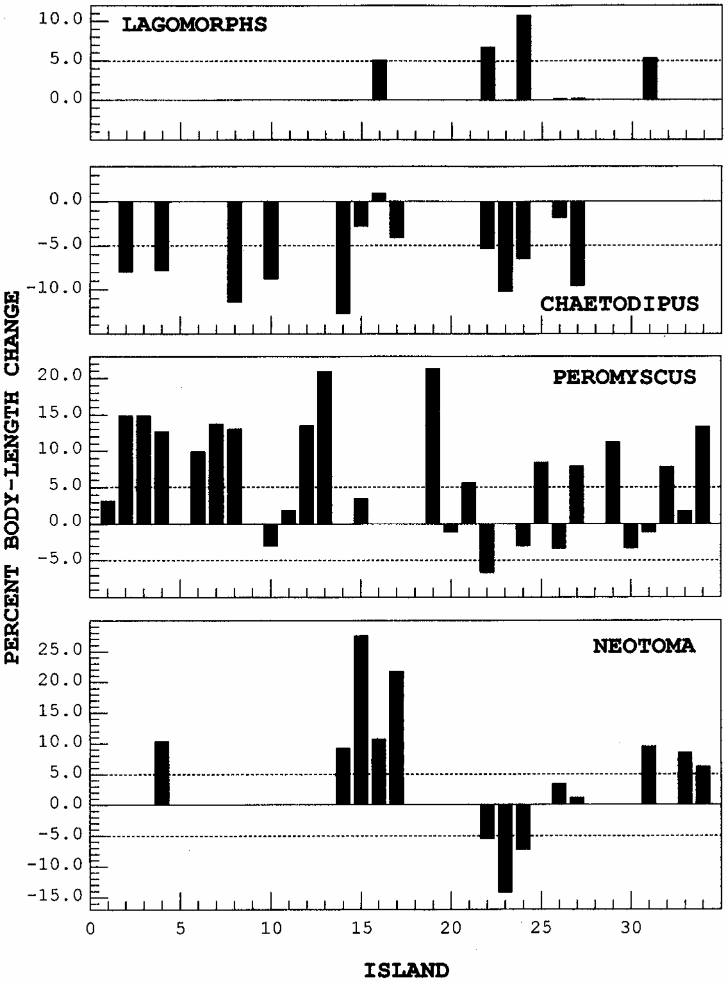

Figure 12.8 Changes in body length for rodents and lagomorphs occurring on Pacific and Sea of Cortés islands. Islands (number designations on $x$-axis) are identified in appendix 12.1. Data are summarized from Lawlor (1982) and Smith (1992).

three predictions (Lawlor 1982). First, among widespread species of similar body sizes and diets, seed specialists (*Chaetodipus*) should inhabit fewer islands than omnivores (*Peromyscus*), and this effect should be most pronounced on very small islands (islands on which seed depletion should be most severe). As reported above, pocket mice frequent many fewer islands than deer mice, a difference due entirely to the absence of pocket mice on small, one-species islands, on which only *Peromyscus* occur. Contrary to the suggestion of Angerbjorn (1985), this pattern is not explicable simply by the presence of fewer potential mainland species of *Chaetodipus* available to colonize islands compared to *Peromyscus* (six and seven, respectively).

Second, there should be fewer congeneric associations of pocket mice than deer mice. Congeneric pairings of *Peromyscus* and *Chaetodipus* occur on five and three islands, respectively; those of pocket mice are limited to only large landbridge islands.

Third, effects of increasing intensity of competition, as indexed by the extent of overlapping food habits and number of potential competitors that they encounter, should produce more marked effects in granivores (*Chaetodipus*) than in generalists (*Peromyscus, Neotoma*). Simply put, dwarfism should be induced in *Chaetodipus* in the presence of fewer potential competitors than in *Peromyscus*, which in turn should exhibit reduced body size in the face of fewer competitors than *Neotoma*. Alternatively, gigantism should be rare or nonexistent in pocket mice and relatively more common in deer mice and woodrats in the presence of competing species. In fact, dwarfism in pocket mice occurs in the presence of as few as one species, and there are no demonstrable examples of gigantism. In contrast, aside from one exception in each, gigantism prevails in *Peromyscus* and *Neotoma* in all significant departures from mainland body sizes (Lawlor 1982; Smith 1992).

Although these data generally support the central hypothesis, the hypothesis requires modification. Smith (1992) confirmed that body size does increase in insular *Neotoma*. She also demonstrated a significant relationship between body size and reduction of predation pressure but no relation with presence of other rodent species, and, citing data from Vaughan and Schwartz (1980), argued persuasively that woodrats on gulf islands are probably specialists (on leaves and twigs) rather than generalists. Despite this correction, the size patterns in *Neotoma* remain in agreement with the hypothesis because their strictly herbivorous diet still predicts large body sizes for insular populations.

Patterns of morphologic variation in the Sea of Cortés agree with Lomolino's (1985) general explanation of insular body-size changes. In a review of worldwide trends in mammals, he proposed that factors promoting gigantism (e.g., competitive release, physiological advantages) should decrease with larger body sizes, whereas those influencing dwarfism (e.g., resource limitation) should increase with larger body sizes. If true, the combined effects of selective forces should produce a tendency for insular body size to decrease with increasing body sizes of species on the mainland. In the Sea of Cortés, pocket mice are an apparent exception to the suggested patterns (i.e., despite their small size overall, they become smaller, not larger, on islands), but their reduced body size is explained by the limited quantities and ephemeral qualities of seed resources on gulf islands.

## Conclusions

The biogeographical distribution of rodents on islands in the Sea of Cortés reflects a combination of evolutionary and ecological processes acting over both short and long time scales. In combination, the patterns of distributions, species richness, and variation and differentiation represent a historical legacy of colonization differences among populations on landbridge and oceanic islands. Populations on landbridge islands are largely relict derivatives of previously cosmopolitan populations, whereas those on oceanic islands are evidently descendants of the chance characteristics of a small number of overwater dispersers (the "sweepstakes" winners of Simpson [1940]).

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