

COMPARISON OF DISTRIBUTION AND HABITAT CHARACTERISTICS  
BETWEEN AN ENDEMIC AND A WIDE-RANGING CRYPTIC SPECIES  
OF *PEROMYSCUS* ON THE BAJA CALIFORNIA PENINSULA

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**ABSTRACT.**—*Peromyscus eva* and *Peromyscus fraterculus* are 2 morphologically similar species of the *Peromyscus eremicus* group occurring on the Baja California Peninsula. Due to the similarity between these 2 species, their ranges have been greatly confused; consequently, the specific habitat characteristics for each group are not well known. The goal of this study was to assess distribution ranges and characteristics of preferred habitats for *P. eva* and *P. fraterculus* in more detail. We identified taxonomy of individuals by evaluating genetic patterns produced by restriction fragment length polymorphisms (RFLPs). We evaluated the banding pattern generated by *Alu* I and *Bam* HI restriction enzymes in an 850-bp cytochrome *b* fragment. Consistent differences in number and size of fragments allowed for discrimination of individuals to species. The heterogeneity and evenness indexes showed that the microhabitat of *P. fraterculus* contained less-diverse soil types and is more homogeneous than the microhabitat of *P. eva*. In the state of Baja California Sur, *P. eva* occurs exclusively in the flat areas along the Pacific coast from the Vizcaino Desert to the south, including Margarita Island, with one small population in the Loreto area adjacent to Carmen Island. The habitats occupied by *P. eva* were heterogeneous (areas with friable, soft sandy soil and a low percentage of small stones). *Peromyscus fraterculus* occurs mostly in Baja California Norte, with some populations distributed in Baja California Sur, particularly in the western areas of the Vizcaino Desert along the mountain range, in the gulf side of the peninsula south of the city of La Paz, and in a small area on the eastern side of Sierra de Las Cruces. This species was mostly found on hard soil with high medium-size stone content.

*Key words:* rodents, *Peromyscus*, mtDNA, RFLP, Baja California, endemic, Mexico, cryptic.

*Peromyscus eva* and *Peromyscus fraterculus* are 2 species included in the *Peromyscus eremicus* group on the Baja California Peninsula. Accurate information about their microhabitat is lacking although general theoretical distributions of both species have been proposed (Lawlor 1971, Carleton 1973, Hall 1981, Álvarez-Castañeda and Cortés-Calva 1999, 2003, Riddle et al. 2000). It is likely that the close morphological similarity of these species and the geographical limitations of past surveys have prevented a precise delimitation of distribution patterns and habitat associations.

Some characteristics have been suggested to discriminate between individuals of the 2 species. For example, *P. eva* has a longer tail, shorter and more reddish fur, and smaller ears than *P. fraterculus* (Osgood 1909). Also, the zygomatic notch is shallower and generally rounded laterally in *P. eva* but deeper and slightly concave in *P. fraterculus* (Lawlor 1971). The number of vertebrae in the tail also differs: 36 in

*P. eva* and 30–34 in *P. fraterculus* (Lawlor 1971). Differing characteristics of the phallus are key to distinguishing between the 2 species. These include smaller size in *P. eva*, narrower shaft of the baculum in *P. fraterculus*, and a small cartilaginous tip in *P. eva* (Burt 1960). In addition, the base of the penis of *P. eva* is smaller and rounded, and the glans has a small extended tip without lappets (Burt 1960, Lawlor 1971, Álvarez-Castañeda and Cortés-Calva 2003). However, these characteristics are, in most cases, ambiguous and may be missed on voucher specimens. Therefore, it is not surprising that many collection specimens of these taxa are incorrectly identified (Álvarez-Castañeda personal observation).

Since *P. eva* was first described (Thomas 1898), the reported distributions of both species have changed several times (Osgood 1909, Lawlor 1971, 1983, Carleton 1973, Hall 1981, Álvarez-Castañeda and Cortés-Calva 1999, 2003, Riddle et al. 2000, Hafner et al. 2001, Lawlor

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TABLE 1. Geographical information associated with localities used for analysis of *Peromyscus eva* (E) and *Peromyscus fraterculus* (F). Locations are shown in Figure 1.

| No. | Locality  | Latitude | Longitude | E/F |
|-----|---|----------|-----------|-----|
| 1   | Laguna Juárez                                       | 32.1115  | -115.9271 | F   |
| 2   | 9 km S, 7 km E San Vicente                          | 31.2420  | -116.1179 | F   |
| 3   | 1 km W San Felipe                                   | 31.0203  | -114.8383 | F   |
| 4   | 7 km S, 3 km W Colonet                              | 31.0028  | -116.2191 | F   |
| 5   | 2 km S, 5 km W Rancho Meling                        | 30.9706  | -115.6525 | F   |
| 6   | 10 mi E Rancho Melling                              | 30.9666  | -115.6000 | F   |
| 7   | 5 km N, 7 km E El Rosario                           | 30.0910  | -115.6573 | F   |
| 8   | 23 km N, 21 km W Bahía San Luis Gonzaga             | 29.9545  | -114.5015 | F   |
| 9   | Cataviña  | 29.9000  | -114.9500 | F   |
| 10  | Punta Prieta  | 28.9338  | -114.1590 | F   |
| 11  | 0.5 km N, 2 km W Punta Prieta                       | 28.9209  | -114.1836 | F   |
| 12  | 10 km S, 8 km E Punta Prieta                        | 28.8413  | -114.0726 | F   |
| 13  | 4 km N, 2 km W Nuevo Rosarito                       | 28.6506  | -114.0228 | F   |
| 14  | 40 km N, 40 km E El Arco                            | 28.3940  | -112.9891 | F   |
| 15  | 36 km N, 40 km E El Arco                            | 28.3546  | -112.9860 | F   |
| 16  | El Barril   | 28.2911  | -112.8690 | F   |
| 17  | Calmalí   | 28.1033  | -113.4243 | F   |
| 18  | El Arco   | 28.0086  | -113.3590 | F   |
| 19  | Rancho San Gregorio, 30.2 km N, 11 km W San Ignacio | 27.6726  | -113.0168 | F   |
| 20  | 40 km N, 12 km W San Ignacio                        | 27.6578  | -113.0070 | F   |
| 21  | Rancho Santa Ana, 36 km E Vizcaíno                  | 27.6380  | -113.0245 | F   |
| 22  | San Pedro, 33.6 km N, 17.6 W de San Ignacio         | 27.6009  | -113.0694 | F   |
| 23  | San Francisco de la Sierra                          | 27.5873  | -113.0887 | F   |
| 24  | 1 km S, 1 km W San Francisco de la Sierra           | 27.5581  | -113.0725 | F   |
| 25  | 23 km N, 36 km E San Ignacio                        | 27.5029  | -112.5224 | F   |
| 26  | 2 km S San Ignacio                                  | 27.4666  | -113.4833 | F   |
| 27  | 10 km N, 14 km W Santa Rosalía                      | 27.4026  | -112.4223 | F   |
| 28  | 27 km N, 18.5 km W Bahía Asunción                   | 27.3836  | -114.4671 | E   |
| 29  | San Ignacio   | 27.2919  | -112.8888 | E   |
| 30  | 17 km S San Ignacio                                 | 27.1360  | -112.9068 | F   |
| 31  | 19 km S, 1 km W San Ignacio                         | 27.1190  | -112.9088 | F   |
| 32  | 17 km S, 5 km W San Ignacio                         | 27.1176  | -112.9671 | F   |
| 33  | 23 km S, 15 km E Santa Rosalía                      | 27.1046  | -112.1337 | F   |
| 34  | 27 km N, 3 km E Abreojos                            | 26.9740  | -113.4683 | F   |
| 35  | 14 km N, 16 km E Abreojos                           | 26.9008  | -113.7668 | F   |
| 36  | 16.5 km N, 10.5 km E Punta. Abreojos                | 26.8935  | -113.4683 | F   |
| 37  | 1.5 km S, 45 km W Mulegé                            | 26.8746  | -112.4450 | F   |
| 38  | San Pedro de la Sierra, 6 km S, 4.8 km W Mulegé     | 26.8708  | -112.5115 | F   |
| 39  | 28 km S, 10 km E Mulege                             | 26.8333  | -112.8667 | F   |
| 40  | 18 km S, 5 km E Mulege                              | 26.7167  | -111.9000 | F   |
| 41  | 45 km S, 40 km E Mulege                             | 26.5167  | -111.4500 | F   |
| 42  | 40 km N, 5 km E San Juanico                         | 26.4763  | -112.6856 | F   |
| 43  | 1 km S Cadejé                                       | 26.3560  | -112.5211 | F   |
| 44  | 18.1 km N, 24 km E La Purísima                      | 26.3555  | -111.8515 | F   |
| 45  | 14.2 km N, 19.8 km E La Purísima                    | 26.3203  | -111.8901 | F   |
| 46  | 4 km S, 24 km E San Juanico                         | 26.2021  | -112.3173 | F   |
| 47  | La Purísima   | 26.1926  | -112.0896 | F   |
| 48  | 3 km S, 4 km W La Purísima                          | 26.1761  | -112.0908 | F   |
| 49  | 3 km S, 5 km W La Purísima                          | 26.1735  | -112.1073 | F   |
| 50  | 1 km S San José de Comondú                          | 26.0565  | -111.8038 | E   |
| 51  | 5 km E San José de Comondú                          | 26.0556  | -111.7706 | E   |
| 52  | Isla del Carmen                                     | 25.8250  | -115.2341 | E   |
| 53  | 22 km S, 2 km E Loreto                              | 25.8100  | -111.3092 | E   |
| 54  | 15.7 km N, 21.6 km E Ciudad Insurgentes             | 25.3915  | -111.5586 | E   |
| 55  | San Evaristo, 67 km N San Juan de la Costa          | 24.9089  | -110.7170 | E   |
| 56  | San Pedro de la Presa                               | 24.8691  | -111.0531 | E   |
| 57  | 4 km E, 1 km S Puerto San Carlos                    | 24.7755  | -112.0568 | E   |
| 58  | 3 km S, 4 km E Santa Rita                           | 24.6060  | -111.6916 | E   |
| 59  | Santa Rita  | 24.5870  | -111.4581 | E   |
| 60  | 3 km NW Puerto Cortés, Isla Margarita               | 24.4844  | -111.8358 | E   |
| 61  | Pénjamo, 8 km N, 6 km W El Cién                     | 24.4752  | -112.7503 | E   |
| 62  | 11.4 km N, 16 km E La Paz                           | 24.2343  | -110.1358 | E/F |

TABLE 1. Continued.

| No. | Locality                                 | Latitude | Longitude | E/F |
|-----|--|----------|-----------|-----|
| 63  | Brisamar, 25 km W La Paz                 | 24.1425  | -110.5389 | E   |
| 64  | El Comitán, 17.5 km W La Paz             | 24.1358  | -110.4670 | E   |
| 65  | 5 km S, 28 km W La Paz                   | 24.1032  | -110.5701 | E   |
| 66  | Chametla, 10 km W La Paz                 | 24.1000  | -110.3833 | E   |
| 67  | 4.2 km S, 19.7 km E La Paz               | 24.0591  | -110.1193 | E   |
| 68  | 6.8 km S, 19.7 km E La Paz               | 24.0423  | -110.1093 | E   |
| 69  | 6.3 km S, 0.7 km E Ensenada de Muertos   | 23.9901  | -109.8185 | F   |
| 70  | 6.5 km S, Ensenada de Muertos            | 23.9856  | -109.8255 | F   |
| 71  | El Triunfo                               | 23.8036  | -110.1043 | E   |
| 72  | El Vergel, 12 km NW Santiago             | 23.4995  | -109.8281 | E   |
| 73  | Santa Anita                              | 23.1760  | -109.7178 | E   |
| 74  | Rancho Margaritas, 4 km S, 2 km E Migrño | 23.0050  | -110.0565 | E   |

et al. 2002). Currently, the proposed range of *P. eva* comprises the middle and southern part of the Baja California Peninsula, including the lowlands and highlands (Osgood 1909, Banks 1967, Lawlor 1971, Woloszyn and Woloszyn 1982). In contrast, *P. fraterculus*, previously known as *P. eremicus fraterculus*, is found from California in the United States to the northern portion of Baja California Sur in Mexico (Riddle et al. 2000). Interestingly, there are 4 localities in which both species have been recorded in sympatry: Calmalli, Aguaje de Santa Ana, San Ignacio, 20 mi W San Ignacio, and Las Cruces (Lawlor 1971). Yet, information on habitat use is insufficient for both species. Surveys along the Baja California Peninsula, with emphasis on those localities at which both species were recorded, suggest differences in habitat use by these species (Lawlor 1971, personal field observation).

Even though some morphological characteristics may help differentiate *P. eva* and *P. fraterculus*, the usefulness of differing morphologies is limited by the availability of relevant structures and by the lack of a series of specimens large enough to make a statistical comparison with adequate power. The goal of this study was to assess distribution ranges and characteristics of preferred habitats for *P. eva* and *P. fraterculus* in more detail. We identified taxonomy of individuals by evaluating genetic patterns produced by restriction fragment length polymorphisms (RFLPs).

## METHODS

### Distribution and Habitat Data

Once specimens were correctly identified, we went back to all localities on the Baja California Peninsula where individuals of the

*P. eremicus* group were collected during the last 10 years by staff of the Mammal Collection of Centro de Investigaciones Biológicas del Noroeste (CIB; Table 1). At the location of capture, we recorded a detailed description of the habitat, including vegetation type, species richness, relative abundance, and proportion of vegetation cover; linear transects (each approximately 20 m per locality) were established and confirmed with several publications on the flora of the Baja California Peninsula (Rzedowski 1978, Wiggins 1980, Roberts 1989, Cody et al. 2002, CONABIO 2008). We determined 4 soil parameters based on criteria found in Cuanalo de la Cerda (1981): (A) friability of soil, reflecting relative resistance to pressure (from 1 – loose, sand that runs between fingers to 6 – clods that are hard to break with the force of a fist); (B) presence of stones (from 0% – total absence of stones to 100% – complete stone cover without soil); (C) size of stones (1 = 0.2–1 cm, 2 = 1–5 cm, 3 = 5–10 cm, 4 = 10–20 cm, 5 = 20–50 cm, 6 = 50–250 cm, and 7 ≥ 250 cm); and (D) ground slope (from 0% – 0° to 100% – 45°).

The distribution pattern of the species was analyzed in relation to zoogeographical provinces (Álvarez et al. 1995) and physiographic regions (Cuanalo et al. 1989) of the Baja California Peninsula. For localities where both species were collected, additional habitat surveys were performed that included detailed notes of the microhabitat in which each species was found. Because the total number of plant species per locality was small, we recorded presence/absence data and used the Jaccard index (Krebs 1999) to determine the association of each plant species to occurrence of *P. fraterculus* and *P. eva*. Also, to compare the association of each mouse species to soil parameters, we used the

TABLE 2. Vegetation structure and composition in the habitats where *Peromyscus fraterculus* and *P. eva* occur. Locality numbers correspond to those listed in Table 1. Cells with an X indicate occurrence of the plant species at the site. The total represents measures of plant species importance.

| Plant species                    | Peromyscus fraterculus localities |    |    |    |    |    |    |    |    |    |    | Peromyscus eva localities |    |    |    |    |    |    |    |    |    |    | Total | Life form |                      |
|----------------------------------|-----------------------------------|----|----|----|----|----|----|----|----|----|----|---------------------------|----|----|----|----|----|----|----|----|----|----|-------|-----------|----------------------|
|                                  | 23                                | 24 | 27 | 33 | 37 | 40 | 41 | 46 | 47 | 51 | 53 | Total                     | 48 | 49 | 50 | 54 | 57 | 58 | 59 | 61 | 63 | 64 |       |           | Total                |
| <i>Acacia farnesiana</i>         | X                                 |    |    |    |    |    |    |    |    |    |    |                           | X  |    |    |    |    |    |    |    |    |    |       | 6.4       | Shrub                |
| <i>Agave datylio</i>             |                                   |    |    |    |    |    |    |    |    |    |    |                           |    | X  |    |    |    |    |    |    |    |    |       | 3.8       | Succulent            |
| <i>Bursera hindsiana</i>         |                                   |    | X  |    |    |    | X  |    |    |    |    |                           |    |    |    |    |    |    | X  |    |    |    |       | 0.0       | Tree                 |
| <i>Bursera microphylla</i>       |                                   |    |    | X  |    | X  |    |    |    |    |    |                           |    |    |    |    |    |    | X  |    |    |    |       | 1.6       | Tree                 |
| <i>Cercidium microphylla</i>     |                                   |    |    | X  | X  | X  |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.0       | Tree                 |
| <i>Cylindropuntia cholla</i>     |                                   | X  | X  |    | X  | X  |    |    |    |    |    |                           |    |    |    |    |    |    | X  | X  |    |    |       | 7.9       | Succulent            |
| <i>Cylindropuntia clavellina</i> |                                   |    |    |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    | X  | X  |    |    |       | 0.0       | Succulent            |
| <i>Euphorbia californica</i>     |                                   |    |    |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    | X  | X  |    |    |       | 7.0       | Herbaceous perennial |
| <i>Ferocactus peninsulae</i>     |                                   | X  |    |    |    |    |    |    | X  |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.0       | Succulent            |
| <i>Fouquieria digetii</i>        |                                   |    | X  |    | X  | X  |    |    |    |    |    |                           |    |    |    |    |    |    | X  | X  |    |    |       | 7.4       | Shrub                |
| <i>Jatropha cinerea</i>          |                                   | X  |    |    | X  | X  | X  |    |    |    |    |                           |    |    |    |    |    |    | X  | X  |    |    |       | 5.8       | Shrub                |
| <i>Jatropha cuneata</i>          |                                   |    | X  | X  | X  | X  |    |    |    |    |    |                           |    |    |    |    |    |    | X  | X  |    |    |       | 24.3      | Shrub                |
| <i>Krameria grayi</i>            |                                   |    |    |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 2.3       | Herbaceous perennial |
| <i>Krameria paucifolia</i>       |                                   |    |    |    |    | X  |    |    |    |    |    |                           |    |    |    |    |    |    | X  |    |    |    |       | 8.2       | Herbaceous perennial |
| <i>Larrea tridentata</i>         |                                   |    | X  | X  |    | X  |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 8.6       | Shrub                |
| <i>Lycium sp.</i>                |                                   | X  | X  |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.0       | Shrub                |
| <i>Lycium brevipes</i>           |                                   |    |    |    |    |    | X  |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 29.9      | Shrub                |
| <i>Lophocereus schottii</i>      |                                   |    |    |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.0       | Succulent            |
| <i>Mammillaria sp.</i>           |                                   |    |    |    |    |    |    |    |    | X  |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.0       | Succulent            |
| <i>Marina parí</i>               |                                   |    |    |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.0       | Succulent            |
| <i>Melochia tomentosa</i>        |                                   |    | X  |    |    | X  |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.2       | Shrub                |
| <i>Opuntia sp.</i>               |                                   | X  |    |    |    |    |    | X  |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.0       | Succulent            |
| <i>Pachycereus pringlei</i>      |                                   |    |    |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.0       | Succulent            |
| <i>Pedilanthus macrocarpus</i>   |                                   |    |    |    |    | X  |    |    |    |    |    |                           |    |    |    |    |    |    | X  | X  |    |    |       | 0.3       | Shrub                |
| <i>Prosopis articulata</i>       |                                   | X  |    |    |    | X  |    |    |    |    |    |                           |    |    |    |    |    |    | X  | X  |    |    |       | 123.6     | Tree                 |
| <i>Ruellia peninsularis</i>      |                                   |    |    |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.8       | Shrub                |
| <i>Simmondsia chinensis</i>      |                                   |    |    |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.3       | Shrub                |
| <i>Solanum hindsianum</i>        |                                   |    |    |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.0       | Shrub                |
| <i>Stenocereus gunnosus</i>      |                                   |    | X  | X  |    | X  | X  |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 5.8       | Succulent            |
| <i>Stenocereus thurberi</i>      |                                   |    |    |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.9       | Succulent            |
| <i>Vallesia glabra</i>           |                                   |    |    |    |    |    |    |    |    |    |    |                           |    |    |    |    |    |    | X  | X  |    |    |       | 8.9       | Shrub                |
| <i>Viguiera microphylla</i>      |                                   |    |    |    |    |    |    |    |    | X  |    |                           |    |    |    |    |    |    |    |    |    |    |       | 0.0       | Shrub                |

TABLE 3. Habitat characteristics at sites where *Peromyscus fraterculus* or *Peromyscus eva* were collected in the state of Baja California Sur.

| Habitat characteristic    | <i>Peromyscus fraterculus</i>  | <i>Peromyscus eva</i>  |
|---------------------------|--|--|
| Altitude range            | 0–1175 m   | 0–600 m  |
| Slope percentage          | 0–48%  | 0–20%  |
| Soil type                 | stony, pebbles, rocky, sandy   | stony, pebbles, rocky, sandy   |
| Percent vegetation cover  | 30% (10–70)  | 31% (10–70)  |
| Vegetation association    | desert scrub,<br>agricultural areas,<br>tropical deciduous forest                            | desert scrub,<br>agricultural areas,<br>tropical deciduous forest  |
| Physiography              | 29.7% mountains<br>19.1% tablelands<br>14.8% slopes  | 40.6% lowlands<br>18.7% hills<br>18.6% mountains   |
| Associated mammal species | <i>Neotoma lepida</i> ,<br><i>Ammospermophilus leucurus</i> ,<br><i>Chaetodipus spinatus</i> | <i>Neotoma lepida</i> , <i>Ammospermophilus leucurus</i> , <i>Chaetodipus arenarius</i> ,<br><i>Dipodomys merriami</i> , <i>Dipodomys similans</i> |

heterogeneity  $D =$  Simpson's index (Krebs 1999) and performed a Mann-Whitney  $U$  test at a 95% confidence level using STATISTICA ver. 6.0 (Starsoft, Inc., Tulsa, Oklahoma).

#### Genetic Identification of Specimens

To distinguish between specimens of *P. eva* and *P. fraterculus*, we developed a genetic test based on PCR amplification of an 850-bp of the cytochrome  $b$  gene, followed by digestion with 2 restriction enzymes. The first step involved selecting those restriction enzymes that could produce diagnostic digestion profiles for each species. To do this, 30 individuals from localities known to be exclusive for each species were sequenced (i.e., Carmen Island where only *P. eva* occurs and northern Baja California where *P. fraterculus* occurs). Then, the aligned sequences were examined for potential diagnostic restriction sites. We used Sequencer ver. 4.8 software (Gen Code Co., Ann Arbor, MI) to determine the enzymes that could generate distinct fragment patterns and to distinguish between specimens of *P. eva* and *P. fraterculus*.

DNA was extracted from liver tissues preserved in 95% ethanol using a DNeasy kit (QIAGEN Inc., Valencia, CA). The first 850 bp of cytochrome  $b$  (*cyt-b*) gene was amplified with primer pairs MVZ05/MVZ16 (primer sequences given in Smith 1998). Amplification reactions included the following: 12.5  $\mu$ L (10 ng) template, 4.4  $\mu$ L ddH<sub>2</sub>O, 2.5  $\mu$ L of each primer pair (10 nM concentration), 0.474  $\mu$ L (0.4 nM) dNTPs, 0.5  $\mu$ L (3 mM) MgCl<sub>2</sub>, 0.125  $\mu$ L Taq polymerase, and 1X Taq buffer to a final volume of 25  $\mu$ L. Amplification conditions consisted of

3 minutes of initial denaturation at 94 °C followed by 37 cycles of denaturation at 94 °C for 45 seconds, 1 minute of annealing at 50 °C, and 1 minute of extension at 72 °C.

The second step involved the digestion and analysis of PCR products with the *Alu* I and *Bam* HI restriction enzymes. Voucher specimens are deposited in Centro de Investigaciones Biológicas del Noroeste (CIB) according to recommendations established by the American Society of Mammalogists Animal Care and Use Committee (1998).

## RESULTS

### Microhabitat Use among Species and Spatial Variation

Vegetation at the localities where both species were collected was not different and had a low value for the Jaccard index ( $S_j = 0.419$ ). In the contact zone between species, neither species was associated with particular types of vegetation; the structure and composition of the vegetation were not different (Table 2). The dominant vegetation was desert scrub with shrub forms and mesquite trees (*Prosopis* sp.), which were common. In general, the distribution of the 2 *Peromyscus* species was not related to a particular type of vegetation or cover. *Peromyscus eva* and *P. fraterculus* were found in scrub, desert scrubland, and agricultural areas; additionally, *P. eva* was found in the subtropical deciduous forest.

With respect to microhabitat features, the most marked distinction between *P. eva* and *P. fraterculus* was in their soil preferences. The species-specific association was different for all

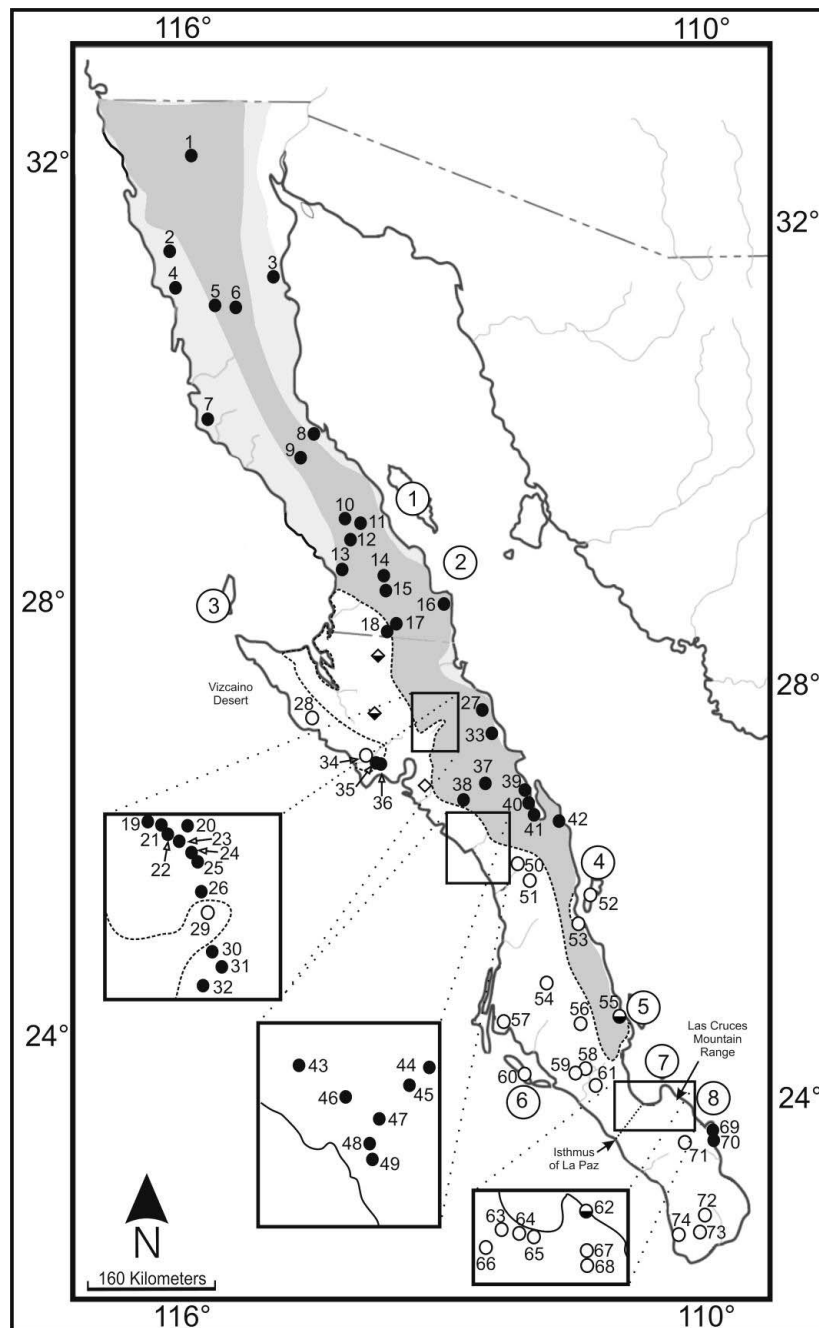


Fig. 1. Map of sampled sites. Localities within a circle correspond to sites sampled for the RFLP analysis. Solid circles represent specimens assigned to *Peromyscus fraterculus*; open circles correspond to *P. eva*; half-solid circles represent sites where both species occur. Open rhombuses correspond to sites of *P. eva*; half-solid rhombuses represent sites where both species may occur together, according to the morphological study of Lawlor (1971), and that were not sampled for the RFLP analysis. Site numbers correspond to those listed in Table 1. Islands (represented by numbers within circles) where species of the *eremicus* complex occur (Hafner et al. 2001) are (1) Ángel de la Guarda Archipelago (Ángel de la Guarda, Mejía, Granito); (2) Salsipuedes Archipelago (San Lorenzo, Animas, Salsipuedes); (3) Cedros; (4) Carmen; (5) San José; (6) Margarita; (7) Espíritu Santo; and (8) Cerralvo. Light gray is the distribution area of *P. fraterculus* and dark gray is the mountain ranges.

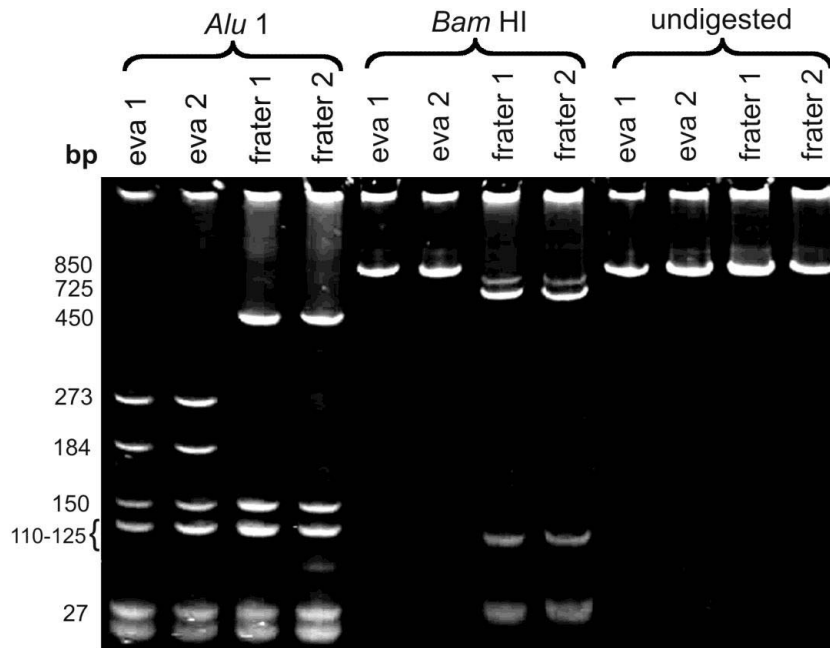


Fig. 2. *Alu* I and *Bam* HI digestion patterns of an 850-bp cytochrome *b* fragment: Lanes 1–2 (samples of *Peromyscus eva*) and Lanes 3–4 (samples of *P. fraterculus*) were produced by *Alu* I; Lanes 5–6 (samples of *P. eva*) and Lanes 7–8 (samples of *P. fraterculus*) were produced by *Bam* HI; Lanes 9–12 are undigested PCR products.

soil characteristics analyzed: substratum ( $P = 0.003$ ), percentage of stoniness ( $P = 0.002$ ), hardness ( $P = 0.023$ ), and consistency ( $P = 0.016$ ). *Peromyscus eva* was associated with friable soils ( $\bar{x} = 1.9$ ) with low percentage of stones (1%–5%) that were mostly small in size ( $\bar{x} = 1.9$ ; range 1–5 cm). *Peromyscus fraterculus* was mostly found on a medium to hard soil ( $\bar{x} = 5.0$ ) with a very high percentage of stones (50%) that were mostly medium in size ( $\bar{x} = 3$  cm; range 5–10 cm). Simpson's heterogeneity index showed that the habitats occupied by *P. eva* were heterogeneous ( $D = 0.74$ ;  $E_{1/D} = 0.76$ ), whereas those occupied by *P. fraterculus* were more homogeneous ( $D = 0.66$ ;  $E_{1/D} = 0.98$ ).

In areas where both species occur (middle and southern part of the Baja California Peninsula), *P. fraterculus* is mostly present in moderately high mountain ranges with steep slopes (29.7%) but was also found on tablelands (19.1%) and sloped areas (14.8%). In contrast, *P. eva* mostly preferred lowlands (40.6%) but was also present in hills (18.7%) and in mountain ranges (18.6%; Table 3). The association of *P. eva* with mountainous areas occurs only in the southern

part of the Isthmus of La Paz, where *P. fraterculus* is practically absent (see Fig. 1).

#### Genetic Comparison

The RFLP analysis showed that the use of *Alu* I (TCGA) and *Bam* HI (CCCGGG) were adequate to differentiate the 2 species. The product of the PCR was digested separately with the *Alu* I and *Bam* HI enzymes. The digestion of the PCR product with *Alu* I produced 2 diagnostic fragments in *P. eva* (184 and 273 bp) and one in *P. fraterculus* (450 bp). *Bam* HI did not digest the PCR product in *P. eva* but did generate one diagnostic fragment in *P. fraterculus* (725 bp; Fig. 2). Therefore, specimens of these species could be genetically differentiated and correctly identified. Of 206 specimens from 74 localities, 111 specimens from 40 localities could be assigned to *P. eva* and 95 specimens from 36 localities to *P. fraterculus* (Appendix). *Peromyscus fraterculus* is widespread in the Baja California Norte (northern half of the Baja California Peninsula); however, its range extends toward Baja California Sur through the midlands and highlands of the Sierra de La Giganta, and it can be found from sea level to 1175 m.

*Peromyscus eva* is distributed exclusively in Baja California Sur on lowlands below 600 m.

#### DISCUSSION

Even though *P. fraterculus* and *P. eva* have both been found in the southern part of the Baja California Peninsula, their morphological resemblance has made it difficult to accurately delimit their distribution (Osgood 1909, Lawlor 1971, Hall 1981, Álvarez-Castañeda and Cortés-Calva 1999, 2003, Riddle et al. 2000, Hafner et al. 2001). In addition, data on the specific microhabitat preferences for each species has not been available. The genetic test that we performed differentiated reliably between individuals belonging to each species, which allowed us to infer a more accurate pattern of distribution and habitat preference. Our results showed that *P. fraterculus* is found in mountains in the Baja California Peninsula from the northern part of Baja California Norte to the southeastern part of Baja California Sur.

In Baja California Sur, *P. fraterculus* is restricted to the La Giganta Range from north of La Paz northward and to the mountain ranges and lowlands in the western part of the Vizcaino Desert. Lawlor (1971) indicated that *P. fraterculus* extends some distance southward along the east and west coasts of the peninsula. These areas are geographically connected, and no vicariance events have been reported. These mountain systems are the coolest regions in Baja California Sur. Within the Isthmus of La Paz, *P. fraterculus* is present only in a small mountain range on the gulf side, of which Espiritu Santo Island is an extension. Populations of *P. fraterculus* found on the islands of Animas, Cedros, Cerralvo, Espiritu Santo, Guardia, Mejia, Montserrat, Salsipuedes, San José, and San Lorenzo seem to have their counterpart on the peninsula. Almost all the islands, with the exception of Montserrat, are land bridges (Hafner et al. 2001); therefore, their physiography is similar to that of the peninsula, with mountains, steep slopes, and scarce flat areas (<30% of the island surface).

*Peromyscus eva* is found exclusively in Baja California Sur and is mostly restricted to lowlands and warm areas, including the central lowlands of the Vizcaino Desert and the southern and southwestern parts of the peninsula. The range of the species was restricted to the Cape faunal district, in the sense described by

Nelson (1921) and Lawlor (1971); although *P. eva* can be found within mountain ranges, its habitats are characterized by smooth hills with stony and sandy soil and relatively few rocks (Cortés-Calva and Álvarez-Castañeda 1997, Cortés-Calva 2004). This species is present only on 2 islands, Carmen Island on the gulf side, from which there were previous records, and Margarita Island on the Pacific side, where the species was believed to be *P. fraterculus* (Hall 1981, Álvarez-Castañeda and Cortés-Calva 1999). Even though Carmen Island has a central mountain range, a flat area in the southwestern part of the island appears to be a suitable habitat for *P. eva*. Interestingly, although this species was recorded on the peninsula, we were not able to collect specimens on the side adjacent to Carmen Island. In this locality (the Giganta range), we only found *P. fraterculus*. Nevertheless, we collected *P. eva* further south, near Loreto at the gulf side. The distribution of *P. eva* populations at Carmen Island and near Loreto may be explained by the Huatamote Canyon, which the main highway traverses from Ciudad Insurgentes to Loreto. This canyon could have been a corridor between the Pacific coastal plain, where *P. eva* also occurs, and the gulf coastal plain near Loreto. On Magdalena Island, the presence of *P. eva* is congruent with the distribution of populations on the peninsula adjacent to the island. These areas share very similar habitat.

Even though *P. fraterculus* and *P. eva* have, in general, a nonoverlapping distribution, we found a few localities where both species existed together, which was also observed by Lawlor (1971). However, Lawlor recorded *P. fraterculus* (sensu *P. eremicus*) in areas near Bahía Concepción (#39–#41) and Las Cruces (#69 and #70) with soft, sandy soils and low stone content. The range of the 2 species overlaps more than 500 km along the west side of the La Giganta Range. Although specimens of *P. fraterculus* and *P. eva* were collected at the same sites, they were not strictly sympatric, since each species was restricted to a distinct microhabitat. Analyses of soil characteristics showed that *P. eva* occupies areas with friable and soft sandy soil with a low percentage or an absence of small stones. In contrast, *P. fraterculus* was mostly found on hard soil with high content of medium-size stones. The heterogeneity and evenness indexes showed that the microhabitat of *P. eva* contained more diverse soil types and



is more heterogeneous than the microhabitat of *P. fraterculus*.

The microhabitat for *P. fraterculus* is limited to soil characteristics; this species is not found in the southern portion of the Isthmus of La Paz, except around Las Cruces, where soil conditions are suitable. The ecological behavior of *P. eva* was as a generalist.

Many mouse species in the Cricetidae family reduce competition by partitioning vertical space (Vickery 1981), although preference for a specific soil type has not been well documented. Because *P. eva* and *P. fraterculus* were never collected in the same microhabitat, it may be true that these species avoid competition preferring distinct soils.

Vegetation preferences were not significantly different among localities where both species were collected. Nevertheless, *Prosopis articulata* and *Jatropha cuneata* were associated with both species. *Peromyscus fraterculus* habitats contained the distinct shrub forms *Larrea tridentata* and *Fouquieria diguetii*; *P. eva* was most frequently associated with *Lycium brevipes* and *Vallesia glabra* (Table 2).

All the sympatric localities were found in transition zones between flat areas and steep mountains or canyons. *Peromyscus eva* was collected primarily in the flatter areas and *P. fraterculus* was typically associated with mountains or canyons. The overlapping area between the 2 species seems to be very limited because of the preference of *P. eva* for lowlands with stony or sandy soils and the preference of *P. fraterculus* for areas with rocky soils and steep slopes. Both species were found in the foothills along the Pacific side of the peninsula in a narrow band stretching more than 300 km. The southernmost locality where both species were recorded in sympatry is Las Cruces Range (#69 and #70), south of La Paz. Interestingly, this site is also the southernmost record for *P. fraterculus*.

Lawlor (1971), in his revision of the *eva-fraterculus* complex, recorded *P. eva* at El Potrero, a site in the middle of the La Giganta Range. Although we made several attempts to collect *Peromyscus* in this locality, we were unsuccessful. Since El Potrero is a deep canyon that cuts through the central part of the range to the western coastal plains of the peninsula, there is some possibility that the orientation of the canyon explains the record of *P. eva* from Lawlor (1971).

Based on our results and observations, we demonstrated that the correct identification of individuals belonging to either *P. eva* or *P. fraterculus* was critical for delimiting areas of distribution and preference for particular microhabitats. Most of the geographic range of each species is unique, although there are areas of sympatry. At sympatric sites, microhabitat conditions are different for each species. Hopefully the information on geographic ranges and microhabitats will help in discriminating between these 2 phenotypically similar species in the field.

We found that the described range of *P. eva* has increased. Analyses of the habitats showed that the range of the 2 species includes large areas with very low human impact. However, the populations of the 2 species could be under pressure in upcoming years from tourist developments in the Baja California Peninsula.

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APPENDIX.—List of the 206 specimens included in the RFLP analysis by species and locality. Number of specimens analyzed, museum voucher numbers, and individuals that were sequenced at each locality are indicated within parentheses. All specimens are in the collection of Centro de Investigaciones Biológicas del Noroeste (CIB).

*Peromyscus eva* (111): 2 km S San Ignacio (2: 7437, 7439); 10 km N, 14 km W Santa Rosalía (4: 2726–2729); 17 km S San Ignacio (1: 9224); 19 km S, 1 km W San Ignacio (4: 9225, 9227–9228); 17 km S, 5 km W San Ignacio (2: 8061, 8062); 23 km S, 15 km E Santa Rosalía (3: 9231–9232); 14 km N, 16 km E Abreojos (1: 7443); San Pedro de la Sierra, 6 km S, 4.8 km W Mulegé (6: 8395–8400); 1.5 km S, 45 km W Mulegé (1: 8390); 16.5 km N, 10.5 km E Punta Abreojos (6: 9723–9728); 40 km N, 5 km E San Juanico (5: 9733, 9734, 9736, 9737, 9739); 1 km S Cadejé (4: 8064–8067); 14.2 km N, 19.8 km E La Purísima (5: 10037–10040, 10042); 4 km S, 24 km E San Juanico (2: 9730, 9731); La Purísima (2: 7440, 9741); 3 km S, 4 km W La Purísima (4: 9742, 9744, 9747, 9750); 3 km S, 5 km W La Purísima (2: 9752, 9757); 1 km S, San José de Comondú (1: 9762); 5 km E, San José de Comondú (2: 9771, 9772); Isla del Carmen (3: 567, 568, 569); 15.7 km N, 21.6 km E Ciudad Insurgentes (1: 10034); 3 km S, 4 km E Santa Rita (1: 8068); San Evaristo, 67 km N San Juan de la Costa (9: 8855–8863); San Pedro de la Presa (1: 585, 586); 4 km E, 1 km S Puerto San Carlos (1: 7442); Santa Rita (1: 7444); 3 km NW Puerto Cortés, Isla Margarita (1: 6080); Pénjamo, 8 km N, 6 km W El Cién (1: 7448); Brisamar, 25 km W, La Paz (1: 588); El Comitán, 17.5 km W La Paz (1: 595); 5 km S, 28 km W La Paz (1: 7454); Chametla, 10 km W La Paz (1: 596); El Triunfo (3: 1212, 7465, 7466); El Vergel, 12 km NW Santiago (3: 8415, 8416, 8420); Santa Anita (3: 8869–8871); Rancho Margaritas, 4 km S, 2 km E Migrño (1: 8868); 18.1 km N, 24 km E La Purísima (1:

10031); 11.4 km N, 16 km E La Paz (5: 12515–12519); 4.2 km S, 19.7 km E La Paz (9: 12520–12528); 6.8 km S, 19.7 km E La Paz (3: 12529–12531).

*Peromyscus fraterculus* (95): Laguna Juárez (1: 3257); 9 km S, 7 km E San Vicente (2: 7406, 7407); 1 km W San Felipe (5: 3269–3272, 3274); 7 km S, 3 km W Colonet (5: 7415–7418, 7420); 2 km S, 5 km W Rancho Meling (1: 7404); 10 mi E Rancho Meling (3: 3267, 3288, 3289); 5 km N, 7 km E El Rosario (5: 7424, 7426, 7427, 7436, 7441); 23 km N, 21 km W Bahía San Luis Gonzaga (1: 3275); Cataviña (2: 2680, 2682); Punta Prieta (4: 9214, 9215, 9217, 9218); 0.5 km N, 2 km W Punta Prieta (2: 2694, 2696); 10 km S, 8 km E Punta Prieta (3: 9220, 9221, 9223); 4 km N, 2 km W Nuevo Rosarito (5: 2705–2709); 36 km N, 40 km E El Arco (3: 9197, 9198, 9201); El Barril (1: 3606); Calmallí (1: 9211); 40 km N, 40 km E El Arco (5: 9188, 9189, 9191–9193); El Arco (1: 9212); Rancho San Gregorio, 30.2 km N, 11 km W San Ignacio (3: 8837, 8838, 8839); 40 km N, 12 km W San Ignacio (1: 8825); Rancho Santa Ana, 36 km E Vizcaíno (4: 3316–3318, 3328); San Pedro, 33.6 km N, 17.6 W de San Ignacio (1: 8836); San Francisco de la Sierra (3: 3308, 3309, 3310); 1 km S, 1 km W San Francisco de la Sierra (3: 8841, 8842, 8843); 23 km N, 36 km E San Ignacio (4: 8846–8849); 27 km N, 18.5 km W Bahía Asunción (3: 9698–9700); San Ignacio (1: 8853); 27 km N, 3 km E Abreojos (3: 8850–8852); 1.5 km S, 45 km W Mulegé (2: 8392, 8394); El Requesón, 28 km S, 10 km E Mulegé (3: 12509–12511); El Coyote, 18 km S, 5 km E Mulegé (5: 12504–12508); Punta Pulpito, 45 km S, 40 km E Mulegé (2: 12512–12513); Puerto Escondido, 22 km S, 2 km E Loreto (1: 12514); 11.4 km N, 16 km E La Paz (2: 12517, 12519); 6.3 km S, 0.7 km E Ensenada de Muertos (2: 12535, 12536); 6.5 km S, Ensenada de Muertos (2: 12532–12534).