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Peromyscus levipes (Rodentia: Cricetidae)

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Abstract: *Peromyscus levipes* Merriam, 1898, commonly called the nimbled-footed deermouse, is 1 of 56 species of *Peromyscus*. It is often confused with other members of the *boylii* group; therefore, researchers may need to rely on craniometric and karyotypic data to make a positive identification. *P. levipes* is found in Mexico on both sides of the Sierra Madre Oriental from central Nuevo Leon and western Tamaulipas to central Veracruz and into the northern slopes of the Transversal Neo volcanic area from Queretaro through Morelos. It has a preference for rocky areas in mixed forest associations, cloud forest, tall sacaton grass, and mixed grasses. DOI: 10.1644/824.1.

Key words: *boylii* species group, cricetid, Mexico, nimble-footed deermose, rodent

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Peromyscus levipes Merriam, 1898
Nimble-footed Deermouse

Peromyscus levipes Merriam, 1898:123. Type locality "M[oun]t. Malinche, Tlaxcala, Mexico, 8400 ft."
Peromyscus boylei levipes: Osgood, 1909:153. Name combination (with unjustified emendation of *Hesperomys boylii* Baird, 1855:335).
Peromyscus boylii levipes: Hall and Kelson, 1959:635. Name combination.
Peromyscus boylii ambiguus Álvarez, 1961:118. Type locality "Monterrey, Nuevo León," Mexico.

CONTEXT AND CONTENT. Order Rodentia, suborder Myomorpha, superfamily Muroidea, family Cricetidae, subfamily Neotominae, tribe Reithrodontomyini, genus *Peromyscus* (Musser and Carleton 2005), subgenus *Peromyscus*. *P. levipes* is a member of the *boylii* species group (Carleton 1989; Musser and Carleton 2005). Two subspecies are recognized (Castro-Campillo et al. 1999; Houseal et al. 1987; Schmidly et al. 1988; Tiemann-Boege et al. 2000):

P. l. ambiguus Álvarez, 1961:118. See above.
P. l. levipes Merriam, 1898:123. See above.

DIAGNOSIS

Peromyscus levipes (Fig. 1) may be confused with other members of the *boylii* species group that are sympatric (*P. beatae* and *P. boylii*). When compared to *P. boylii rowleyi*, *P. levipes* can be distinguished by overall larger size, darker color, and more cinnamon dorsum. The following characteristics of *P. levipes* usually distinguish it from *P. boylii rowleyi* (Schmidly et al. 1988): ratio of greatest anterior width of nasal bone to posterior width is <1.9; ratio of greatest posterior width of nasal bone to length of nasal bone is <0.17; maxillofrontal suture is a continuous line

Fig. 1.—Adult male *Peromyscus levipes* from 7.9 km SW San Salvador el Seco (19°04′33.6″N and 97°41′11.1″W), Puebla, Mexico. Photograph by Noé González-Ruiz.

without bending; lateral border of parietal is more angular; nasolacrimal canal is situated less than halfway along infraorbital plate; mesostyle of right M2 is absent; and ectolophid of m1 is present. Length (in mm) of molar toothrow in *P. levipes* is 4.2–4.8 compared to 3.6–4.2 in *P. boylii* (Schmidly et al. 1988).

Peromyscus levipes is slightly smaller than *P. beatae* and has lighter coloration, particularly in dorsal band (Schmidly et al. 1988). The following characteristics of *P. levipes* usually distinguish it from *P. beatae* (Schmidly et al. 1988): posterior extensions of premaxillae extend beyond the posterior border of nasals; lateral border of parietal is less rounded; nasolacrimal canal is not located midway along infraorbital plate; anterior ethmoid foramen is less frequently located at edge of 1st cavity from ventral border of ethmoid region; and alisphenoid has a smaller angle, making sphenoidal fissure more difficult to see (Schmidly et al. 1988). Fundamental number (FN) of *P. beatae* is 48–54 compared to 56–60 in *P. levipes* (Houseal et al. 1987; Schmidly et al. 1988).

Peromyscus levipes also may be confused with sympatric specimens of *P. pectoralis*, but it can be distinguished by its relatively short tail, larger skull, more swollen lacrimal region, and longer maxillary toothrow (>4.2 mm in *P. levipes* and <4.0 mm in *P. pectoralis*—Schmidly 1974). *P. levipes* cannot be distinguished morphologically from allopatric *P. schmidlyi*, but the 2 species differ genetically in mitochondrial cytochrome-*b* gene sequence (3.25%) and FN (56–60 in *P. levipes* and 54–56 in *P. schmidlyi*—Bradley et al. 2004).

GENERAL CHARACTERS

Upper body parts of *Peromyscus levipes* vary from rich ochraceous buff to tawny; dusky hairs present. Sides of body are tawny with lateral line not sharply marked. Dorsum with dusky hair that sometimes forms a diffuse blackish stripe. Orbital ring is blackish and slightly more pronounced toward a grizzled area between eyes and base of ears. Ears are dusky, scarcely edged with white, and have a tuft of soft blackish slate hairs at anterior base. Underparts of body are white, occasionally creamy white, with a pectoral spot sometimes present; pelage at tarsal joint is white. Tail is distinctly bicolored (dusky brown above and white below) and penicillate at tip (Castro-Campillo et al. 1999; Osgood 1909; Schmidly et al. 1988). One specimen had a monocolored tail (Hooper 1947).

Skull (Fig. 2) is short and broad with relatively large auditory bullae and molar teeth; supraorbital border is not sharply angled (Osgood 1909). Braincase is rounded, and zygomatic arches are nearly parallel. Supraorbital border is not sharply angled and seldom develops a shelf; intraorbital notch is slightly or scarcely evident (Álvarez 1961; Osgood 1909).

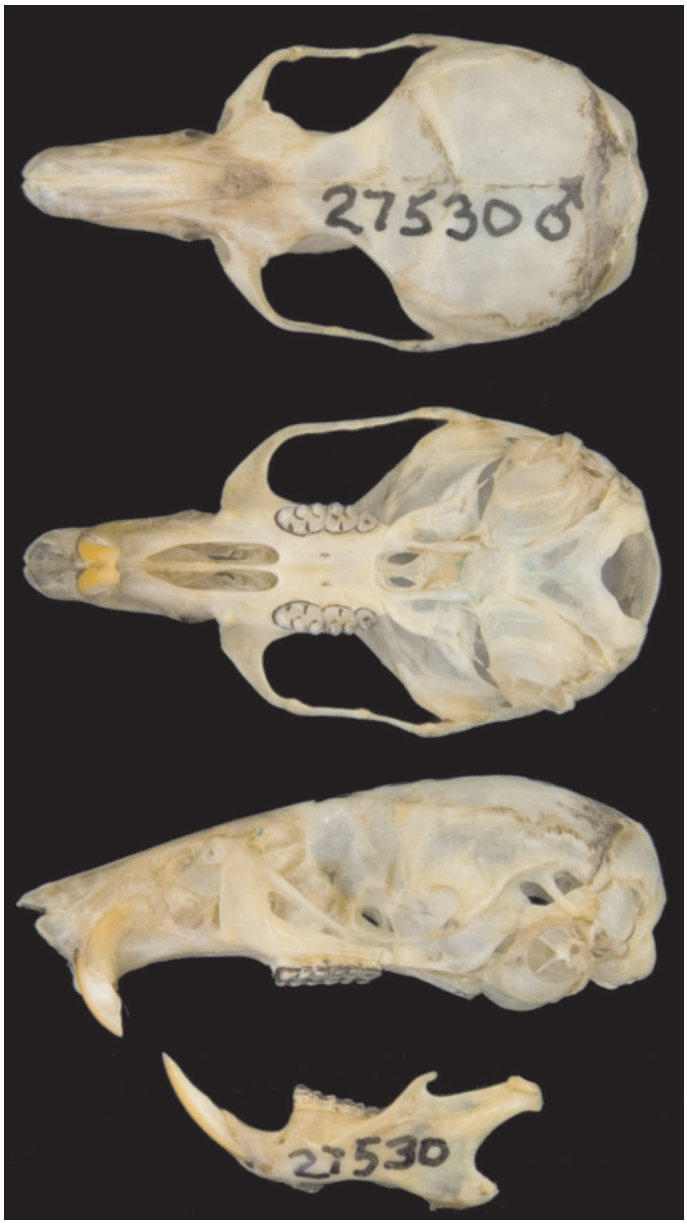

Fig. 2.—Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult female *Peromyscus levipes* from Mexico (Escuela Nacional de Ciencias Biológicas, 27530). Greatest length of cranium is 27.2 mm. Photograph by Horacio Cabrera Santiago.

Mean and range (in parentheses) of external and cranial measurements (in mm) from 37 topotypes of *P. levipes* (Schmidly et al. 1988) were: total length, 205.1 (180–220); length of tail, 103.5 (91–115); length of hind foot, 23.0 (22–24); length of ear, 20.3 (19–22); length of skull, 28.3 (26.6–30); length of rostrum, 11.6 (10.8–12.7); length of nasal, 10.4 (9.2–11); postpalatal length, 9.5 (8.4–10.6); zygomatic breadth, 14.2 (13.4–15); breadth of braincase, 12.8 (12.2–13.4); mastoid breadth, 12.0 (11.4–12.8); least interorbital width, 4.4 (4.1–4.7); length of molar toothrow, 4.4 (4.2–4.8);

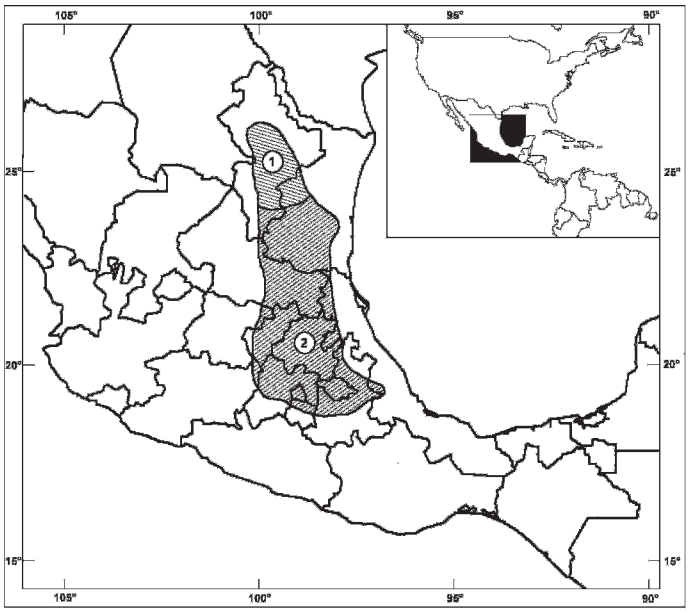

Fig. 3.—Geographic distribution of *Peromyscus levipes*. Subspecies are 1, *P. l. ambiguus* and 2, *P. l. levipes*. Map modified from Carleton (1989).

length of auditory bulla, 5.4 (4.7–5.8); depth of braincase, 10 (9.5–10.5); length of mesopterygoid fossa, 5 (4.4–5.6); width of mesopterygoid fossa, 2.3 (2.1–2.7); breadth across molars, 5.5 (5.3–5.9). Length of tail is slightly greater than length of head and body (Álvarez 1961; Merriam 1898; Schmidly et al. 1988). Mean body masses (g) and ranges (in parentheses) for males ($n = 19$) and females ($n = 18$), respectively, were 25.2 (22–30) and 23.6 (20–29—Álvarez 1963).

Peromyscus levipes varies considerably in several morphological traits; in the states of San Luis Potosi and Hidalgo northward there is a gradual cline of decreasing measurements, except for ratio of length of tail to length of head and body. Specimens from several localities in San Luis Potosi are relatively shorter and darker dorsally than topotypes from Tlaxcala (Álvarez 1961). Specimens from mountains on the Mexican Plateau in the state of San Luis Potosi were paler than those from tropical slopes of the Sierra Madre Occidental (Álvarez 1961; Dalquest 1953).

DISTRIBUTION

Peromyscus levipes occurs in the mountain region of eastern Mexico (Fig. 3). It is found on both sides of the Sierra Madre Oriental from central Nuevo Leon and western Tamaulipas to central Veracruz and into the northern slopes of the Transversal Neovolcanic area of the states of Queretaro, Tlaxcala, Puebla, Distrito Federal, state of Mexico, and Morelos (Musser and Carleton 2005; Schmidly et al. 1988). No fossils of *P. levipes* are known.

FORM AND FUNCTION

The phallus of *Peromyscus levipes* is elongated and sharp. Glans is about two-fifths the length of hind foot, and 4.75 times longer than wide (Bradley and Schmidly 1987). Triangular spines, pointed at tip and about as wide as long, are present on dorsal and ventral surfaces. Fluting is absent. Baculum is rod-shaped, dorsoventrally curved, and has a triangular base 4–5 times wider than shaft (Bradley and Schmidly 1987). Baculum is about 1.2–1.3 times longer than glans, and tip of baculum is covered by a minute cartilaginous cap (Bradley and Schmidly 1987; Carleton 1977).

The phallus of *P. levipes* has 2 different epidermal conditions, with spines and spineless. The spineless condition was found in specimens from 9 locations in Queretaro and Hidalgo, and all 45 specimens exhibited this condition (Bradley et al. 1989). Individuals with the spineless condition do not differ biochemically (Bradley et al. 1989), craniometrically (Schmidly et al. 1988), or karyotypically (Houseal et al. 1987) from individuals with spines.

Measurements (mean ± *SE*, in mm, $n = 24$) of glans penis and baculum of *P. levipes* (Bradley et al. 1989) are: length of distal tract, 12.85 ± 0.18; length of glans, 8.48 ± 0.15; length of protractile tip, 2.11 ± 0.05; width of glans, 1.79 ± 0.03; length of baculum, 11.02 ± 0.18; length of cartilaginous tip, 0.16 ± 0.00; width of baculum at base, 1.52 ± 0.04, and width of baculum at midpoint, 0.37 ± 0.02. Detailed descriptions of 63 muscles of the cervical region of *P. levipes* are available (Esquivel 1981).

ONTOGENY AND REPRODUCTION

Peromyscus levipes usually produces 2–3 litters per year (Davis 1944). Between late March and early April, 1 pregnant female was collected with 2 embryos, 3.0 mm in length (Hooper 1953). Two pregnant juvenile females were caught in August (Davis 1944). In Morelos, reproductive activity was recorded during all months except March, with maximum reproductive activity occurring in July–November (García-Estrada et al. 2004; Romero-Almaraz et al. 2004). In Morelos, males with enlarged testes were collected in May (Álvarez-Castañeda 1996) and in June and August (Davis and Russell 1954).

ECOLOGY

Peromyscus levipes occupies oak–sweet gum forest, oak–pine forest, pinyon–juniper woodland, and scrub oak (Hooper 1953; Koestner 1941; Schmidly et al. 1988). *P. levipes* occurs along rock walls in a mixed forest association (Davis and Russell 1953, 1954), and in xerophytic vegetation in the Distrito Federal in central Mexico (Castro-Campillo

et al. 1992). In central Veracruz (Jalapa) and north of Puebla (Chignahuapan), *P. levipes* occurs in cloud forest with *P. beatae* (Schmidly et al. 1988).

Peromyscus levipes occurs in tall sacaton grass (*Mulhenbergia*), mixed grasses, and herbs along creeks, rocky bluffs, and lava flows; there is a decided preference for rocky areas (Davis 1944). Plants associated with *P. levipes* are *Bursera grandifolia*, *Daphnopsis americana, Enterolobium cyclocarpum*, *Euphorbia fulva*, *Ficus petiolaris*, *Guazuma ulmifolia, Licania arborea*, *Lysiloma divaricata*, *Neobuxbaumia mezcalaensis*, *Pachycereus weberi*, *Pithecellobium dulce*, *Sapindus saponaria*, *Stenocereus beneckei*, and *S. stellatus* (Romero-Almaraz et al. 2004).

In a low-disturbance area in Morelos, minimum number known alive (individuals/ha) during 14 months ranged from 16 to 41. Average residence time (range in parentheses; in days) for sexes combined, males, and females, respectively, was 175 (41–393), 217 (41–393), and 134 (41–228). Mean measurement of spatial activity (range in parentheses; in m^2) for males (n = 39) and females (n = 29), respectively, was 541.5 (44.2–3,623.1) and 577.5 (44.2–4,146.5—Romero-Almaraz et al. 2004). No significant differences in spatial activity were found between sexes in wet and dry seasons, and overall sex ratio did not differ from 1:1 (Romero-Almaraz et al. 2004). *P. levipes* preferred areas dominated by trees (73.4%) to those dominated by annual plants (5.6%), shrubs (11.5%), or tree–cactus associations (9.5%—Romero-Almaraz et al. 2004).

Peromyscus levipes has been taken in the same trapline as *P. melanotis* in Veracruz (Hall and Dalquest 1963) and *P. aztecus* in Hidalgo (Musser 1964). *P. levipes* occurs in sympatry with *P. boylii rowleyi* in Hidalgo (Houseal et al. 1987; Rennert and Kilpatrick 1986; Schmidly et al. 1988) and with *P. beatae* in Puebla (Houseal et al. 1987; Schmidly et al. 1988).

Ectoparasites infecting *P. levipes* include *Jellisonia bonia*, *J. grayi*, *J. hayesi*, *Pleochaetis mundus*, *Plusaetis dolens*, *P. mathesoni*, *P. parus*, and *P. sibynus* (family Ceratophyllidae); *Ctenophthalmus pseudagyrtes*, *Stenoponia ponera*, and *Strepsylla mina* (family Ctenophthalmidae); and *Atyphloceras tancitari* and *Hystrichopsylla orophila* (family Hystrichopsylidae—Acosta 2003; Whitaker and Morales-Malacara 2005). *P. levipes* has been found in pellets of barn owl (*Tyto alba*—Koopman and Martin 1959; López-Forment and Urbano 1977) and mottled owl (*Ciccaba virgata*—Koopman and Martin 1959).

GENETICS

Diploid number (2n) is 48, which is typical of the genus *Peromyscus*, but *P. levipes* exhibits some variation in autosomal morphology with FN ranging from 56 to 60 (Houseal et al. 1987; Schmidly et al. 1988). Karyotype includes 3–5 pairs of large to medium biarmed chromosomes, 2 pairs of small biarmed chromosomes, and 16–18 pairs of acrocentric chromosomes (Houseal et al. 1987; Schmidly et al. 1988; Schmidly and Schroeter 1974). The X chromosome is large and submetacentric, and the Y chromosome is small and submetacentric (Schmidly et al. 1988).

An examination of 19 populations for which chromosomal data have been reported (Houseal et al. 1987; Schmidly and Schroeter 1974) revealed that 58% of those populations were fixed for either FN = 58 (37%) or FN = 60 (21%). Thirty-seven percent were polymorphic for FN = 58–60, and 1 population (Cola de Caballo, Nuevo León) was polymorphic for FN = 56–58. Specimens with FN of 58–60 are only found in Queretaro and Hidalgo, with FN = 58 in San Luis Potosi, southeast of Hidalgo and northwest of Puebla, and with FN = 60 in the state of Mexico and central Veracruz (Houseal et al. 1987; Schmidly et al. 1988). In Jonacapa, Hidalgo, a population of *P. levipes* (FN = 58–60) occurred in sympatry with *P. boylii rowleyi* (FN = 52—Houseal et al. 1987; Rennert and Kilpatrick 1986; Schmidly et al. 1988), and in Chignahupan, Puebla, a population of *P. levipes* (FN = 58) occurred in sympatry with *P. beatae* (FN = 52–54—Houseal et al. 1987; Schmidly et al. 1988).

Kilpatrick and Zimmerman (1975) reported genetic polymorphism per population (P = 0.059) and heterozygosity per individual (h = 0.0392) for *P. levipes*; however, their analysis included specimens currently assigned to *P. beatae* and *P. levipes*. A population from Ciudad Victoria, Tamaulipas (n = 6), was polymorphic at 3 loci: phosphogluconate dehydrogenase (PGD-1), glutamate oxaloacetate transaminase (GOT-1), and albumin (ALB-1—Avise et al. 1974). In a sample of similar size, Kilpatrick and Zimmerman (1975) did not observe any polymorphism at those 3 loci but did report polymorphism at 2 esterase loci (EST-5 and EST-7). Polymorphisms were reported at 2 loci, ALB-1 and transferrin (TRF-1) in 3 populations from Queretaro and Hidalgo (n = 3), and no variation was reported at 16 other loci (Kilpatrick and Zimmerman 1975). All populations of *P. boylii*, including *P. levipes*, were monomorphic for a null allele at the EST-1 locus (Kilpatrick and Zimmerman 1975).

A population of *P. levipes* exhibited polymorphism at 7 loci (amylase [AMY-1], EST-1, EST-6, phosphoglucomutase [PGM-2 and PGM-3], glucose 6-phosphate dehydrogenase [G6PD-1], and isocitrate dehydrogenase [IDH-1]—Rennert and Kilpatrick 1987). The population in Cola de Caballo (*P. l. ambiguus*) showed some genetic differentiation from samples of *P. l. levipes* at the carbonic anhydrase (CAR-1), EST-7 loci (Rennert and Kilpatrick 1987). *P. levipes* can be distinguished from *P. b. rowleyi* by genetic markers at the TRF-1 and salivary amylase (AMY-1) loci and from *P. beatae* by markers at the IDH locus (Rennert and Kilpatrick 1987). *P. levipes* and *P. boylii rowleyi* shared common alleles at many loci, although some differences existed with TRF-1 and AMY-1 (Rennert and Kilpatrick 1987). Rogers' similar-

ity between *P. levipes* and *P. boylii rowleyi* was >0.89 (S = 0.95—Avise et al. 1974), although that analysis included in the sample of *P. levipes*, specimens currently recognized as *P. beatae* (Avise et al. 1974).

REMARKS

According to Carleton (1989), *P. levipes* is distributed in the mountain region of the central-southern part of Mexico to Central America, including the Mexican states of Nayarit, Jalisco, and Michoacán. However, populations previously recognized as *P. levipes* from Guerrero, Oaxaca, Chiapas, and the northern part of Central America are now considered to be *P. beatae* (Musser and Carleton 2005), based on karyotype (Houseal et al. 1987), allozymes (Rennert and Kilpatrick 1987), and cytochrome-*b* sequence data (Bradley et al. 2000).

Taxonomic positions of the following 5 populations assignable to *P. levipes* from Nayarit, Jalisco, and Michoacán are unclear: population of Ocota, Nayarit (FN = 65–68) differs from *P. levipes* based on morphological (Bradley et al. 1996; Carleton et al. 1982), karyotypic (Carleton et al. 1982; Houseal et al. 1987), and cytochrome-*b* sequence data (Bradley et al. 2004; Tiemann-Boege et al. 2000); population of Dos Aguas, Michoacán (FN = 65–68) differs from the other *boylii* species group based on data concerning karyotype (Houseal et al. 1987), allozymes (Rennert and Kilpatrick 1987), and cytochrome-*b* sequence (Bradley et al. 2004; Tiemann-Boege et al. 2000); population of Los Reyes, Michoacán, is fixed for FN = 66 (Houseal et al. 1987; Schmidly and Schroeter 1974); specimens from Volcán de Colima, Jalisco, have FN = 68 (Houseal et al. 1987); and 2 populations of Michoacán (Pátzcuaro and Los Azufres) are fixed for FN = 56 (Houseal et al. 1987). Cytochrome-*b* sequences from populations in Ocota, Nayarit, and Dos Aguas, Michoacán, are placed in a separate clade, and these populations could represent a different, undescribed species (Bradley et al. 2004; Tiemann-Boege et al. 2000). Specimens from Los Reyes, Michoacán, and Volcán de Colima appear to have a close relationship with Ocota and Dos Aguas populations; the population of Volcán de Colima is karyotypically indistinguishable from the Dos Aguas population (Houseal et al. 1987). Additional studies are needed to clarify the relationships between specimens from Los Reyes and Volcán de Colima and those from Ocota and Dos Aguas. Populations fixed for FN = 56 of Michoacán (Pátzcuaro and Los Azufres) have not been considered as belonging to any species of the *boylii* species group, but it is possible that these populations are related to specimens with FN = 54–56 of Durango, currently known as *P. schmidlyi* (Houseal et al. 1987). Rennert and Kilpatrick (1987) looked at allozymes from samples from the Los Azufres population and placed it with the population from Dos Aguas and a population of *P. levipes* (FN = 59 or 60) from Jonacapa, Hidalgo.

The specific name *levipes* is derived from the Latin words *leav*, which means smooth or nimble, and *ped*, which means foot. The translation would be nimble-footed mouse because it moves swiftly.

Note from the authors.—The reader will find in the literature some information on *P. levipes* from areas of western Mexico, which might be considered as missing from this account. Genetic analysis has shown that many different species are listed under the name *P. levipes*, and some are still currently undescribed (R. Bradley, in litt.). Because some publications include data from the western (multiple species of *Peromyscus*) and eastern (*P. levipes*) areas of Mexico, it was very difficult or impossible to extract data specific to *P. levipes*. We made our best effort to include in this account only data currently assigned to *P. levipes*.

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