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Peromyscus difficilis (Rodentia: Cricetidae)

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Abstract: *Peromyscus difficilis* (J. A. Allen, 1891) is a cricetid rodent commonly called the southern rock deermouse or Zacatecan deermouse. It is of medium body size for the genus (28–43 g), with large ears and a long, evenly bicolored tail that is always slightly longer than the head plus body length. It is 1 of 56 species in the genus *Peromyscus* and includes 5 subspecies. *P. difficilis* is a Mexican endemic distributed throughout the Sierra Madre Occidental and Sierra Madre Oriental, southward through the mountainous regions of Guanajuato, Puebla, Hidalgo, and Veracruz, into northern and central Oaxaca. Habitat preferences range from dry, semiarid hills to montane forests. *P. difficilis* is not of special conservation concern. DOI: 10.1644/867.1.

Key words: cricetid, endemic rodent, Mexico, southern rock deermouse, Zacatecan deermouse

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Peromyscus difficilis (J. A. Allen, 1891)
Southern Rock Deermouse

Vesperimus difficilis J. A. Allen, 1891:298. Type locality "Sierra de Valparaiso, Zacatecas, Mexico."
[*Peromyscus*] *difficilis*: Trouessart, 1897:518. First use of current name combination.
P. felipensis Merriam, 1898:122. Type locality "Cerro San Felipe, Oaxaca, Mexico (alt. 10,200 ft)."
P. amplus Osgood, 1904:62. Type locality "[San Juan Bautista] Coixtlahuaca, Oaxaca, Mexico."
P. d. petricola Hoffmeister and de la Torre, 1959:167. Type locality "12 mi. E. San Antonio de las Alazanas, 9000 ft., Coahuila, Mexico."
P. d. saxicola Hoffmeister and de la Torre, 1959:168. Type locality "Cadereyta, 2100 meters, Querétaro, México."

CONTEXT AND CONTENT. Order Rodentia, suborder Myomorpha, superfamily Muroidea, family Cricetidae, subfamily Neotominae, tribe Reithrodontomyini, subgenus *Peromyscus*; *truei* species group (Musser and Carleton 2005). The genus *Peromyscus* currently includes 56 nominal species (Musser and Carleton 2005). The *truei* species group includes *P. attwateri* (Texas deermouse), *P. difficilis*, *P. gratus* (saxicoline deermouse), *P. nasutus* (northern rock deermouse), *P. pectoralis* (white-ankled deermouse), and *P. truei* (piñon deermouse—Durish et al. 2004). Hall (1981) listed 8 subspecies for *P. difficilis*; however, Zimmerman et al. (1975, 1978) elevated *P. nasutus* to species status (also supported by Avise et al. [1979] and Carleton [1989]) with 2 subspecies, *P. n. griseus* and *P. n. penicillatus*. Currently 5 subspecies of *P. difficilis* are recognized (Musser and Carleton 2005), as follows:

P. d. amplus Osgood, 1904:62. See above.
P. d. difficilis (J. A. Allen, 1891:298). See above.
P. d. felipensis Merriam, 1898:122. See above.
P. d. petricola Hoffmeister and de la Torre, 1959:167. See above.
P. d. saxicola Hoffmeister and de la Torre, 1959:168–169. See above.

Fig. 1.—An adult male *Peromyscus difficilis* from 3 km S El Frijol Colorado, Veracruz, México. Photograph taken by J. A. Fernández.

DIAGNOSIS

Peromyscus difficilis (Fig. 1) can be distinguished from sympatric congeners by combinations of morphological characters. Where *P. difficilis* co-occurs with *P. bullatus* (Perote deermouse) in the Perote region of Veracruz, the 2 species can be distinguished by the generally larger body size and significantly longer occipitonasal length of *P. difficilis* (ranges in mm—total length of adults 210–245; occipitonasal length 29.6–32.2) compared with those of *P. bullatus* (total length of adults 178–224; occipitonasal length 27.4–28.6—González-Ruíz and Álvarez-Castaneda 2005; González-Ruíz et al. 2005).

Chromosomal and molecular evidence have been used to suggest that *P. difficilis* and *P. nasutus* are sibling species (Avise et al. 1979; Bradley et al. 2007; Zimmerman et al. 1975, 1978), and these species may be sympatric in the northernmost portion of the *P. difficilis* distribution (Durish et al. 2004; Janecek 1990). According to Hoffmeister and de la Torre (1961), subspecies of *P. difficilis* average ≥219 mm in total length (range and *SD* were not provided by Hoffmeister and de la Torre [1961]), whereas subspecies of *P. nasutus* average ≤200 mm in total length. Also, the pelage of *P. difficilis* is generally darker (yellowish orange heavily overlaid with black) than that of *P. nasutus* (yellowish orange to burnt orange, only lightly overlaid with black). Length of hind foot generally is >24.5 mm in *P. difficilis* and <24.5 mm in *P. nasutus* (Hoffmeister and de la Torre 1961), and the baculum in *P difficilis* is generally longer (range 14.4–18.5 mm) than in *P. nasutus* (range 13.2–16.2 mm—Burt 1960; Tamsitt 1958).

Peromyscus difficilis shares a similar distribution with *P. gratus* in many parts of Mexico, and where the 2 species are sympatric, *P. difficilis* can be distinguished from *P. gratus* by its generally larger body size (mm; total length of *P. difficilis* = 228, range 210–245; total length of *P. gratus* = 195, range 158–214) and its significantly longer occipitonasal length (30.7, range 29.6–32.2 in *P. difficilis*; 27.1, range 25.8–28.3 in *P. gratus*—González-Ruíz et al. 2005; Hoffmeister 1981).

Where *P. difficilis* occurs sympatrically with *P. melanophrys* (plateau deermouse), the species can be distinguished by the smaller size of *P. difficilis* (mm; total length of *P. difficilis* [mean of 15 males] = 234; total length of *P. melanophrys* [mean of 15 males] = 248—Dalquest 1953 [range and *SD* not provided]). The pelage of *P. melanophrys* also is distinctly more yellow than that of *P. difficilis* (Dalquest 1953). *P. difficilis* can easily be distinguished from *P. maniculatus* (North American deermouse) and *P. melanotis* (black-eared deermouse) by its much larger body size (total length usually >200 mm in *P. difficilis* and <200 mm in *P. maniculatus* and *P. melanotis*) and a tail that is longer than its head and body length (Hall 1981).

GENERAL CHARACTERS

Peromyscus difficilis is a medium-sized rodent with large ears and a long, evenly bicolored tail that is slightly but always longer than total head and body length. Dorsal coloration varies from brownish (ochraceous buff) to blackish, with dusky hairs arranged in fine lines. Coloration of the flanks is the same as the back except for presence of a well-defined lateral line, and its underparts are white to blackish suffused with silver. The ears are large, but when dry are shorter than the hind foot (Hall 1981; Hoffmeister and de la Torre 1961; Osgood 1909). *P. difficilis* has a narrow, blackish orbital ring, a long rostrum with nasals about 11 mm, large auditory bullae, and a supraorbital border not beaded or sharp-angled (Fig. 2; Hoffmeister and de la Torre 1961). Ranges of recorded external measurements (mm) were: total length 180.0–260.0; length of tail 91.0–145.0; length of hind foot 22.0–28.0; and length of ear 17.5–28.0 (Hall 1981). *P. difficilis* includes 5 subspecies that can be separated by a combination of morphological characters.

Peromyscus difficilis amplus *Osgood, 1904*.—Color of upper body uniform ochraceous buff with a fine, blackish overlay; lateral line broad; forehead and orbital region from base of vibrissae to ears grayish; underparts creamy white with a well-developed ochraceous-buff pectoral spot; tail evenly bicolored, dorsal tail stripe dark. Skull large with somewhat inflated braincase, anterior part depressed; large auditory bullae; long nasals; large toothrow and long postpalatal area. Measurements (mm; mean and range) of 10 adult topotypes from San Juan Bautista Coixtlahuaca, Oaxaca (Osgood 1904), were: total length 248 (235–260); length of tail 136 (128–145); and length of hind foot 27 (26–28). Means (mm) of cranial characters for same specimens were: greatest length of skull 30.4; basilar length 23.0; zygomatic width 10.4; least interorbital constriction 4.5; length of nasals 11.3; length of bony palate 4.6; length of palatine slits 6.2; length of diastema 7.9; postpalatal length 10.2; and alveolar length of maxillary toothrow 4.8. Mean measurements (mm) of 3 adult males and 5 adult females from the vicinity of Tlaxcala (Hoffmeister and de la Torre 1961) were: total length 234.5; length of tail 122.5; length of hind foot 24.9; length of ear (dry) 21.4; greatest length of skull 30.3; basilar length 23.2; zygomatic width 13.8; least interorbital constriction 4.7; length of nasals 11.5; length of bony palate 4.5; length of palatine slits 6.2; length of diastema 7.6; postpalatal length 11.1; and alveolar length of maxillary toothrow 4.9.

Specimens assigned to *P. d. amplus* from 2 km west and 3 km west of Limon, Veracruz, are notable for their large external ears and tympanic bullae. Measurements (mm; mean and range) of 16 adult males and 14 adult females, respectively, were: length of hind foot 25.8 (25.0–28.0), 25.6 (25.0–27.0); length of ear 26.0 (25.0–28.0), 25.5 (23.0–27.0); and length of ear (dry) 21.5 (19.5–23.9), 21.9 (20.0–24.2—

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Peromyscus difficilis* (Louisiana State University Museum of Natural Science [LSUMZ] 5749) from 3 km SW San Isidro, San Luis Potosí, México. Greatest length of skull is 29.6 mm.

Hooper 1958; Osgood 1909). Specimens from the nearby town of Perote and 2.4 km south of Perote, Veracruz, have the largest tympanic bullae and ears reported for *P. difficilis* (Hooper 1958; Osgood 1909). However, 10 topotypes from San Juan Bautista Coixtlahuaca, Oaxaca, also have large external ears and tympanic bullae, indicating that specimens from the Limon–Perote region of Veracruz are not unique in these 2 characters (Hall and Dalquest 1963). *P. d. amplus* differs from *P. d. difficilis* externally by its larger body size and dull, reddish color (Hoffmeister and de la Torre 1961).

Peromyscus difficilis difficilis *(J. A. Allen, 1891).*— Color of the upper body is dark with little ochraceous and heavily overlaid with black. Measurements (mm; means) of 12 adult males and 13 adult females from Batopilas, La Unión, and Guadalupe y Calvo, Chihuahua (Hoffmeister and de la Torre 1961), were: total length 219.2; length of tail 119.3; length of hind foot 25.9; length of ear (dry) 21.8; greatest length of skull 28.9; basilar length 21.8; greatest breadth of braincase 13.2; least interorbital constriction 4.5; length of nasals 11.2; length of bony palate 4.3; length of palatine slits 6.2; length of diastema 7.5; postpalatal length 10.1; and alveolar length of maxillary toothrow 4.6.

Mean body mass (g; with ranges) of 12 adult males and 12 adult females of *P. d. difficilis* from southeastern Coahuila (Baker 1956) were: 35.0 (28.3–42.8) and 33.3 (28.7–40.0), respectively. The mean and range measurements (mm) of 5 adult males and 6 adult females, respectively, from 10 km east of San Antonio de las Alazanas, Coahuila, were: total length 230.0 (223.0–237.0), 237.0 (227.0–250.0); length of tail 122.0 (115.0–126.0), 125.0 (112.0–138.0); length of hind foot 24.0 (22.0–25.0), 24.0 (23.0–25.0); length of ear 24.0 (23.0–28.0), 24.0 (23.0–26.0); greatest length of skull 30.1 (29.5–30.7), 30.5 (29.9–31.3); basilar length 23.2 (22.8–23.4), 23.4 (22.9–24.4); least interorbital constriction 4.6 (4.5–4.8), 4.6 (4.4–4.8); length of nasals 12.0 (11.5–12.5), 12.3 (11.6–13.1); length of bony palate 4.3 (4.2–4.6), 4.4 (4.3–4.6); length of palatine slits 6.7 (6.4–7.2), 6.8 (6.6–7.1); length of diastema 7.8 (7.5–8.0), 7.9 (7.7–8.0); postpalatal length 10.9 (10.8–11.0), 11.1 (10.6–11.7); and alveolar length of maxillary toothrow 4.9 (4.7–5.0), 4.8 (4.7–5.0).

Peromyscus difficilis felipensis *Merriam, 1898.*—Dorsal coloration dark (darkest of all subspecies); lateral line obscure; orbital ring and spot at base of vibrissae black; underparts, lips, and side of nose white with plumbeous basal fur showing through; pectoral region usually salmon; tail bicolored. Skull large; braincase well rounded; auditory bullae large and inflated. External measurements (mm) of the holotype were: total length 238.0; length of tail 125.0; and length of hind foot 27.5 (Osgood 1909). External measurements (mm; ranges) of 10 adult topotypes (Osgood 1909) were: total length 241.5 (225.0–248.0); length of tail 127.0 (118.0–132.0); length of hind foot 26.8 (25.5–27.5); and length of ear (dry) 20.4 (19.0–21.7). Mean measurements (mm) of 5 adult males and 1 adult female from Contreras, Distrito Federal (Hoffmeister and de la Torre 1961), were: total length 243.8; length of tail 134.8; length of hind foot 26.8; length of ear (dry) 21.5; greatest length of skull 31.1; basilar length 23.6; greatest breadth of braincase 14.5; least interorbital constriction 4.5; length of nasals 12.0; length of bony palate 4.6; length of palatine slits 6.3; length of diastema 8.1; postpalatal length 11.1; and alveolar length of maxillary toothrow 4.8. *P. d. felipensis* can be distinguished from *P. d. amplus* by its larger skull and much darker coloration (Hoffmeister and de la Torre 1961).

Peromyscus difficilis petricola ***Hoffmeister and de la Torre, 1959.***—Body long with relatively short tail; pelage on dorsum with dark peppery appearance, lacking the ochraceous of some of the other subspecies; auditory bullae greatly inflated; broad braincase and interorbital region; skull long, particularly the nasal bones, toothrows, and palatine slits. Mean measurements (mm) of 3 adult males and 4 adult females from the type locality (see synonymy) were: total length 224.3; length of tail 115.5; length of hind foot 23.4; length of ear (dry) 21.4; greatest length of skull 30.0; basilar length 22.6; greatest breadth of braincase 13.9; least interorbital constriction 4.6; length of nasals 11.5; length of bony palate 4.4; length of palatine slits 6.4; length of diastema 7.7; postpalatal length 10.7; and alveolar length of maxillary toothrow 4.8 (Hoffmeister and de la Torre 1959).

Peromyscus difficilis saxicola ***Hoffmeister and de la Torre, 1959.***—Dorsal coloration brownish red or ochraceous, with a reduced overlay of black; ears brownish; dorsal tail stripe mottled brown; underparts whitish; tail long; head and body length averages 70.5–77.0% of tail length. *P. d. saxicola* differs from other subspecies in having a smaller skull, including shorter nasal bones, palatines, and palatine slits; braincase and interorbital region narrower than in other subspecies. Mean measurements (mm) of 4 adult males and 5 adult females from type locality (see synonymy) were: total length 232.5; length of tail 134.7; length of hind foot 23.7; length of ear (dry) 21.6; greatest length of skull 29.3; basilar length 22.4; greatest breadth of braincase 13.5; least interorbital constriction 4.5; length of nasals 11.2; length of bony palate 4.2; length of palatine slits 6.1; length of diastema 7.5; postpalatal length 10.7; and alveolar length of maxillary toothrow 4.5 (Hoffmeister and de la Torre 1961).

DISTRIBUTION

Peromyscus difficilis is endemic to Mexico (Fig. 3) and is found throughout the Sierra Madre Occidental, Sierra Madre Oriental, and adjacent mountain ranges from southwestern Chihuahua and southeastern Coahuila, south through Durango and Zacatecas. Its range continues southward from Zacatecas into parts of San Luis Potosi and mountainous regions of Guanajuato, Puebla, Hidalgo, Tlaxcala, and Veracruz, into north-central Oaxaca (Hall 1981; Hoffmeister and de la Torre 1961; Osgood 1909).

The subspecies *P. d. difficilis* occurs in western Chihuahua, southward along the Sierra Madre Occidental into Guanajuato. *P. d. petricola* is found in the Sierra Madre Oriental of southeastern Coahuila, southwestern Tamaulipas, and probably northern San Luis Potosí and southern Nuevo León (Hoffmeister and de la Torre 1961). *P. d. amplus* occurs in the mountains of southern Hidalgo, the northern part of the state of México, Tlaxcala, Puebla, north-central Oaxaca, and west-central Veracruz. The range of *P. d. felipensis* appears to be fragmented; this species is found at high elevations (2,500–3,500 m) in the mountains surrounding the Valley of Mexico and also occurs at similar elevations in the mountains northeast of the city of Oaxaca (Cerro San Felipe and adjacent ranges). Finally, *P. d. saxicola* is restricted to Querétaro and northern Hidalgo (Goodwin 1954; Hall 1981; Hoffmeister and de la Torre 1961; Osgood 1909; Villa-Ramírez 1953). No fossils of *P. difficilis* are known.

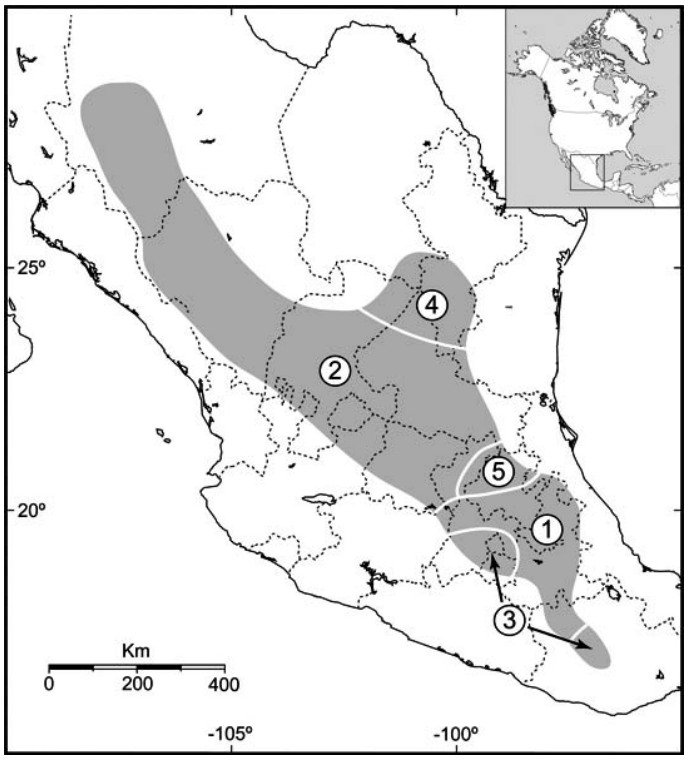

Fig. 3.—Geographic distribution of *Peromyscus difficilis* in México. Subspecies are: 1, *P. d. amplus*; 2, *P. d. difficilis*; 3, *P. d. felipensis*; 4, *P. d. petricola*; and 5, *P. d. saxicola*. Map redrawn from Hall (1981).

FORM AND FUNCTION

A study of nongeographic morphological variation in *Peromyscus difficilis amplus* from the northwestern part of the Cuenca Oriental (Puebla and Veracruz, México), found significant variation between age classes but no significant secondary sexual variation (Gaona 1997). The dental formula of *P. difficilis* is i 1/1, c 0/0, p 0/0, m 3/3, total 16 (Hooper 1957a). Upper incisors lack anterior grooves, and molars are bunodont. M1 and M2 have single, large lingual roots, and no labial roots. M3 has 2 medial roots, but no lingual or labial roots. In the lower jaw, m1, m2, and m3 have 2 medial roots, but no lingual or labial roots (Carleton

1980). The cusp arrangement on m3 has greatly reduced entoconid and hypoconid and wears to a C shape. In size, m3 is generally greater than 30% of the length of the molar toothrow (Carleton 1980). A detailed description of molar accessory structures is available in Hooper (1957a), who studied dental patterns in *P. difficilis* from 26 specimens from Sierra Fría, Aguascalientes, 32 specimens from Ixmiquilpan and Zimapan, Hidalgo, and 25 from the Distrito Federal.

Both stapedial and sphenofrontal foramina are present in *P. difficilis*, as well as a groove on the squamosal imparted by the ophthalmic artery (Carleton 1980). These characters reflect carotid circulation to the orbit and brain, and the condition in *P. difficilis* appears to represent the plesiomorphic state in the subfamily Neotominae. The foramen ovale is present in *P. difficilis*, as are large postglenoid and subsquamosal foramina. The mesopterygoid fossa has elongated sphenopalatine vacuities that extend over half of the length of the presphenoid bone. The posterolateral palatal pits are absent or have 1 or 2 small foramina. A pair of round palatine foramina are located at the junction of the maxillary and palatine bones, which may on occasion be accompanied by 1 or 2 minute foramina. The lateral pterygoid fossae are flat, and at an even level with the bony palate. The skull lacks temporal ridges and has a smooth supraorbital region, concave or parallel-sided, with an hourglass shape when viewed from the dorsal plane. The zygomatic spine and the postorbital process are absent, and the lacrymal bone is scarcely evident dorsally. The angular process of the dentary bone is directed posteriorly in the same plane as the ascending ramus. In the hyoid apparatus, the entoglossal process is a small knob, the basihyal is arched and the thyrohyal has a length that is greater than or equal to the basihyal bone. The accessory tympanum is large, the mastoid bullae are small, and the tympanic bullae are greatly inflated (Carleton 1980).

In the postcranial skeleton, *P. difficilis* has an entepicondylar foramen located above the medial epicondyle of the humerus. There are 13 thoracic and 6 lumbar vertebrae, and >36 caudal vertebrae. The 2nd thoracic vertebra has a pronounced neural spine. The tuberculum of the 1st rib is broad and round, and it contacts the transverse process of the 7th cervical and 1st thoracic vertebrae. The trochlear process of the calcaneum is broad and shelf-like and is positioned at the level of the posterior articular facet. The scapulae have supraspinous and infraspinous fossae, but a 3rd fossa located along the axillary border is absent. Between 37% and 41% of the tibia is fused to the fibula. The 2nd, 3rd, and 4th interdigital plantar pads are arranged in close proximity, but the 1st is set further back on the heel, not opposite the 4th. The plantar surface is naked or only lightly furred on the heel. *P. difficilis* possesses 3 pairs of mammary glands, 1 axillary and 2 inguinal (Carleton 1980).

Peromyscus difficilis lacks internal cheek pouches and has a complete anterior longitudinal ridge, with high relief, separating the inflexi labii superioris muscle. It has 3 complete and 4 incomplete palatal ridges. The stomach (described from 3 specimens from Aguascalientes—Carleton 1973) is bilocular and discoglandular with a deep incisura angularis and a disc-shaped glandular epithelium surrounded by a distinct bordering fold. The remainder of the antrum and corpus of the stomach is covered by cornified epithelium, and the greater curvature of the stomach lacks a sulcus. A distinct saccular gall bladder is present, located between the cystic lobes of the liver. The 1st section of the large intestine shows few to no coils in the area near its junction with the small intestine and cecum. The cecum is moderately long and internally simple.

The male phallus in *P. difficilis* is elongate, rod shaped, and about one-half the length of the hind foot (Hooper 1958). The diameter of the phallus is ≤15% of its length. It consists of a main body of comparatively dense tissues and a tapered, pliable tip. There are 2 acute dorsal lappets and 1 short and broad ventral one. The glans has no spines, but is covered with conical tubercles that may become spinous when the animal is sexually active. The baculum is long (about two-thirds the length of the hind foot) and is a simple rod with a basal region that is moderately expanded laterally and dorsoventrally flattened. The proximal margin of the baculum is convex in profile, and the tip is capped with a minute cone of cartilage. Dimensions (mm) of the phallus of *P. difficilis* (based on 1 specimen examined by Hooper [1958]) were: length of the glans 13.1; length of the baculum 17.5; and length of tip 0.2. The position of the urinary meatus is subterminal (Carleton 1980).

Male accessory reproductive glands in *P. difficilis* include the anterior, dorsal, and lateral–ventral prostates, bulbourethrals, ampullaries, and vesicular glands; preputial glands are absent or not visible macroscopically in *P. difficilis* (Carleton 1980). Measurements (mm; length by width) of male genital structures in *P. difficilis* (based on 1 specimen from Oaxaca—Linzey and Lane 1969) were: testis 10.0 by 6.0; ampullary gland 2.7 by 3.0; vesicular gland 7.0 by 2.0; anterior prostate 3.5 by 1.7; dorsal prostate 5.0 by 3.0; ventral prostate 3.0 by 2.5; bulbourethral gland 2.5 by 2.7; greatest length of deferent duct 15; and greatest length of urethra 26.5.

The sperm in *P. difficilis* is oblong in shape, widest at the middle, and tapers gradually to a narrow, hooked tip; the hook is short and only slightly recurved. In stained preparations with Heidenhain's iron hematoxylin, the head is uniformly stained except for a dark line extending along the base and slightly up the sides of the head. Measurements of sperm (mean ± *SD* in μm, with percentage of total sperm length in parentheses; $n = 10$ sperm—Linzey and Lane 1974) were: head length 5.4 ± 0.07 (6.8%); head width 2.6 ± 0.07 (3.3%); midpiece length 17.0 ± 0.08 (21.6%); and tail length 56.4 ± 1.24 (71.6%).

ONTOGENY AND REPRODUCTION

Peromyscus difficilis reproduces mainly from June through December, although the breeding season may extend through the spring months (Ceballos and Galindo 1984; Dalquest 1953). In southwestern Durango, increases in breeding activity are strongly associated with increases in rainfall (Galindo-Leal and Krebs 1997). Females collected from throughout the species' distribution have an average of 3 embryos per pregnancy. Nonpregnant breeding females are significantly heavier than nonbreeding females, and pregnancies are not known to occur in females that weigh <25 g. Breeding males also are heavier than nonbreeding males, with no males < 27 g showing signs of breeding activity. Most pregnant females are overwintered adults, and these individuals may have 1–3 pregnancies during a breeding season. Some females born early in a breeding season have 1 pregnancy before the breeding season ends (Ceballos and Galindo 1984; Galindo-Leal and Krebs 1997).

ECOLOGY

Population characteristics.—Population densities of *Peromyscus difficilis* appear to remain low year round in the central portion of its distribution (Ceballos and Galindo 1984; Villa-Ramírez 1953). In contrast, densities of populations of *P. difficilis* in southwestern Durango fluctuate seasonally, with low densities (about 2 individuals/ha) at the end of the dry season (April–June) and during the 1st half of the wet season (June–August—Galindo-Leal and Krebs 1997). Population density increases during the 2nd half of the wet season (September–October) and continues increasing to an average of about 13 individuals/ha (range 8–29 individuals/ha) throughout the 1st half of the dry season (November–January).

Survivorship appears to be the same for both sexes of *P. difficilis*. Galindo-Leal and Krebs (1998) found that females respond better than males to experimental addition of food, with well-fed females showing both improved reproduction and improved survivorship relative to well-fed males during both wet and dry seasons. Populations of *P. difficilis* in southwestern Durango have nearly even sex ratios, and both sexes appear to have exclusive and nonoverlapping home ranges during the breeding season (Galindo-Leal and Krebs 1997).

Space use.—*Peromyscus difficilis* is scansorial to semiarboreal and occurs in a wide variety of habitats, ranging from dry, semiarid hills to montane forests. In southwestern Durango, *P. d. difficilis* inhabits dry, temperate oak–pine forests at 2,400–2,600 m elevation dominated by oak species such as *Quercus chihuahuensis*, *Q. convalata*, *Q. durifolia*, *Q. eduardii*, *Q. potosina*, *Q. rugosa*, and *Q. sideroxyla* and pine species including *Pinus arizonica*, *P. chihuahuana*, *P. engelmani*, *P. leiophylla*, and *P. teocote*. Dominant shrubs in this region include point-leaf manzanita (*Arctostaphylos pungens*) and guazapol (*Caenothus buxifolius*—Aragón et al. 2009; Ceballos and Galindo 1984; Galindo-Leal and Krebs 1997; Goodwin 1954).

In Chihuahua, *P. d. difficilis* occupies rocky habitats at elevations ranging from 2,100 to 2,600 m (Anderson 1972). In southeastern Coahuila, the same subspecies has been captured in mesic forests at high elevations (2,300–2,900 m), where it shows an affinity for rocky areas and relatively dry habitats, such as chaparral hillsides (Baker 1956). In Zacatecas, *P. d. difficilis* has been collected in montane forests at high elevations (2,300–2,900 m), where it shows a strong affinity for rocky outcrops and other protective groundcover (Diersing 1976; Hoffmeister and de la Torre 1961; Matson and Baker 1986). Finally, *P. d. difficilis* also is known from rocky areas within desert and semidesert habitats dominated by cacti and other xerophytes in San Luis Potosi (Dalquest 1953) and Jalisco (Riojas-López 2006). Near Ojuelos de Jalisco in extreme northeastern Jalisco *P. d. difficilis* occurs in nopaleras (communities of flat-stemmed *Opuntia* cacti of the species *O. duranguensis*, *O. joconostle*, and *O. robusta*) and in areas dominated by woody perennial legumes, such as huizache (*Acacia*) and garabatillo (*Mimosa*), and grasses (*Bouteloua*, *Aristida*, and *Muhlenbergia*). In parts of this region, arboreal opuntias (*O. chavena*, *O. hyptiacantha*, *O. leuchotricha*, and *O. streptacantha*) dominate the landscape forming dense, thorny associations with huizache and garabatillo. In 2006, about 80% of the land in this region was intensively grazed or under cultivation, and *P. difficilis* was restricted to the remaining patches of densely vegetated habitat with medium-to-tall herbaceous and shrubby cover (Riojas-López 2006).

Specimens of *P. d. petricola* were collected near Miquihuana in southwestern Tamaulipas (2,600 m elevation) among rocks and stumps in an oak forest (Alvarez 1963). Specimens of the same subspecies also were collected at a nearby locality 32 km north of Tula (1,800 m elevation) in extreme southwestern Tamaulipas, where they were found on a hillside dominated by juniper brush (*Juniperus flaccida*—Alvarez 1963).

The distributions of *P. d. amplus* and *P. d. felipensis*, both collected near Milpa Alta, Distrito Federal, by Navarro-Frías et al. (2007), appear to be associated with vegetation type. Whereas *P. d. amplus* was captured in dry, brushy environments at 2,500 m elevation, *P. d. felipensis* was collected in rocky areas within coniferous forests dominated by *Abies religiosa*, *Pinus hartweggii*, *P. leiophylla*, and *P. montezumae* at 3,100 m elevation. *P. d. felipensis* also has been associated with humid oak–pine forests in other regions of central and southern México, including Parres in the Distrito Federal, Santiago Cuatenco in the state of México, Lagunas de Zempoala near Huitzilac, Morelos, and Sierra Norte near Santa Catarina Ixtepeji, Oaxaca (Goodwin 1954; Müdespacher-Ziehl et al. 2005; Villa-Ramírez 1953).

In the northwestern part of the Cuenca Oriental in Puebla and Veracruz, *P. d. amplus* is found in semiarid to temperate environments from 2,300 to 2,600 m elevation dominated by halophilic grasses and shrubs, acahuales (dense stands of *Cecropia obtusifolia* in disturbed soils), and isolated junipers (*Juniperus deppeana*—Gaona 1997; Hooper 1957b). Where *P. d. amplus* and *P. d. saxicola* co-occur in Veracruz, both species are restricted to arid, rocky regions, including lava flows and rocky cliffs.

Diet.—*Peromyscus difficilis* is granivorous and insectivorous (Aragón et al. 2009; Ceballos and Galindo 1984; Galindo-Leal and Krebs 1997). Seeds and cactus fruits constitute major components of the diet of *P. d. difficilis* in San Luis Potosi (Dalquest 1953).

Diseases and parasites.—The nematodes *Vexillata vexillata*, *Stilestrongylus peromysci*, *Protospirura mexicana*, and *Carolinensis huehuetlana* have been collected from *Peromyscus difficilis* (Falcón-Ordaz and Sanabria 1995, 1996, 1997, 1999). A new genus and species of digenean helminth, *Caballerolecythus ibunami*, was described from the intestines of specimens of *P. difficilis* and *Liomys irroratus* (Mexican spiny pocket mouse) collected at Piñonal, municipality of El Carmen Tequexquitla, Tlaxcala (Lamothe-Argumedo et al. 2005).

In southwestern Durango, *P. difficilis* is parasitized by botflies (*Cuterebra*), with warbles generally occurring on the backs and sides of the mice. Adult females had higher infestation rates in the breeding season (autumn) when they are more sedentary, whereas adult males had higher infestation rates during the nonbreeding season (winter) when they are more sedentary (Galindo-Leal 1997). Two species of sucking lice (Anoplura), *Hoplopleura hesperomydis* and *Polyplax auricularis*, have been collected from *P. difficilis* (Mortan and Hoff 1957).

Fleas (Siphonaptera) representing at least 5 families have been collected from *P. difficilis*—Ctenophthalmidae: *Anomiopsyllus sinuatus*, *Ctenophthalmus haagi*, *C. micropus* (T. M. Pérez-Ortíz, pers. comm.), *C. pseudagyrtes*, *C. tecpin*, *Epitedia wenmanni*, *Meringis arachis*, *Stenoponia ponera*, *Strepsylla mina*, *S. taluna*, *S. villai*, and *S. davisae*; Hystricopsyllidae: *Atyphloceras tancitari*, *Hystrichopsylla llorentei*, and *H. occidentalis*; Ceratophyllidae: *Jellisonia breviloba*, *J. grayi*, *J. hayesi*, *J. ironsi*, *J. wisemani*, *Kohlsia martini*, *K. pelaezi*, *Pleochaetis mundus*, *P. paramundus*, *Plusaetis apollinaris*, *P. asetus*, *P. aztecus*, *P. dolens*, *P. mathesoni*, *P. sibynus*, *P. soberoni*, and a species in the genus *Thrassis*; Leptopsyllidae: *Peromyscopsylla hesperomys*; and Pulicidae: *Echidnophaga gallinacea* and *Euhoplopsyllus glacialis* (Acosta 2003, 2005; Acosta et al. 2008; Ayala-Barajas et al. 1988; Barrera 1953, 1968; Hastriter 2004; Tipton and Mendéz 1968).

Interspecific interactions.—In southeastern Coahuila, *Peromyscus difficilis difficilis* was collected commonly in association with *Neotoma mexicana* (Mexican woodrat) and *Eutamias bulleri* (currently *Tamias bulleri* [Buller's chipmunk]), and less commonly with *Peromyscus truei* and *P. boylii* (brush deermouse—Baker 1956). In an area with dense plant cover dominated by arboreal nopaleras (*Opuntia*) in northeastern Jalisco, rodent species occurring sympatrically with *P. d. difficilis* included (in order of abundance) *Reithrodontomys fulvescens* (fulvous harvest mouse), *L. irroratus*, *Chaetodipus nelsoni* (Nelson's pocket mouse), *Reithrodontomys megalotis* (western harvest mouse), *Dipodomys ordii* (Ord's kangaroo rat), *Chaetodipus hispidus* (hispid pocket mouse), *Peromyscus melanophrys*, *Peromyscus gratus*, and *Perognathus flavus* (silky pocket mouse—Riojas-López 2006). At a 2nd, more-open site in northeastern Jalisco dominated by shrubby nopalera, short grasses, and herbaceous legumes, rodent species captured in association with *P. d. difficilis* included (in order of abundance) *Dipodomys phillipsi* (Phillips's kangaroo rat), *R. megalotis*, *P. flavus*, *D. ordii*, *P. gratus*, *R. fulvescens*, *P. melanophrys*, *C. nelsoni*, *L. irroratus*, and *Peromyscus maniculatus*. Finally, at a 3rd site in the same region, this one a cultivated nopalera consisting mainly of *Opuntia megacantha*, rodent species associated with *P. d. difficilis* (in order of abundance) were *R. megalotis*, *R. fulvescens*, *D. phillipsi*, *D. ordii*, *Sigmodon fulviventer* (tawny bellied cotton rat), *P. gratus*, *P. maniculatus*, *P. melanophrys*, *P. flavus*, *Sigmodon hispidus* (hispid cotton rat), and *L. irroratus* (Riojas-López 2006).

In oak–pine forests near Milpa Alta, Distrito Federal, rodents collected in the same trap lines that yielded *P. d. felipensis* included *Reithrodontomys chrysopsis* (volcano harvest mouse), *R. megalotis*, *R. sumichrasti* (Sumichrast's harvest mouse), *Peromyscus melanotis*, *Neotomodon alstoni* (volcano deermouse), and *Microtus mexicanus* (Mexican vole—Navarro-Frías et al. 2007). In central México, *P. d. difficilis* has been collected in the same areas with *Baiomys taylori* (northern pygmy mouse), *L. irroratus*, *P. boylii*, and *P. truei* (Ceballos and Galindo 1984). In the Oriental Basin of Veracruz, *P. d. amplus* was collected in association with the endemic *Peromyscus bullatus* (González-Ruíz et al. 2005). Additional associations of *P. difficilis* with *B. taylori*, *L. irroratus*, *Neotoma albigula* (white-throated woodrat), and *P. truei* have been reported (Villa-Ramírez and Cervantes 2003). In central México, common predators of *P. difficilis* include the ring-tailed cat (*Bassariscus astutus*), skunks, snakes, and owls (Ceballos and Galindo 1984).

GENETICS

Cytogenetics.—All populations of *Peromyscus difficilis* examined to date have a diploid number (2n) of 48 chromosomes, as do all other species of the genus *Peromyscus* (Committee for Standardization of Chromosomes of *Peromyscus* 1977). However, fundamental number (FN) varies within *P. difficilis* as follows: *P. d. amplus* from Totalco, Veracruz, has FN = 66, including 2 pairs of metacentric autosomes, 8 subtelocentric pairs, and 13 telocentric pairs (Arellano-Meneses et al. 2000). The X

chromosome in *P. d. amplus* is subtelocentric and the Y is telocentric. *P. d. difficilis* from 29 km west of El Salto, Durango, has FN = 58, with 17 acrocentric and 6 biarmed pairs (Robbins and Baker 1975). Heterochromatin in *P. d. difficilis* from this locality in Durango is restricted to centromeric regions. *P. d. petricola* from near Concepción del Oro, Zacatecas, has FN = 56 (Zimmerman et al. 1975). Finally, *P. d. felipensis* from the states of Mexico and Morelos has FN = 76 with 1 metacentric, 1 submetacentric, 13 subtelocentric, and 8 telocentric autosomes, and a population of the same subspecies from southeast of Oaxaca has FN = 76 with 2 metacentric, 13 subtelocentric, and 8 telocentric autosomes (Müdespacher-Ziehl et al. 2005). In *P. d. felipensis*, the X chromosome is subtelocentric and the Y chromosome is metacentric.

Molecular genetics.—In a comparison of allelic differentiation at 23 protein loci in *Peromyscus difficilis* from Zacatecas and *P. nasutus* from Colorado, Zimmerman et al. (1978) reported a genetic identity (*I*—Nei 1972) of 0.943 (roughly equivalent to 94% genetic similarity) between these sibling species. However, an earlier allozyme study that included a larger number of loci of the rapidly evolving esterase class revealed a considerably lower genetic identity ($I = 0.86$) between *P. difficilis* and *P. nasutus* (Zimmerman et al. 1975).

Analysis of sequence differentiation in the mitochondrial cytochrome-*b* gene of 31 species of *Peromyscus* by Durish et al. (2004) showed an average sequence divergence (2-parameter model of Kimura [1980]) of 1.09% among the subspecies *P. d. amplus*, *P. d. difficilis*, and *P. d. saxicola* and an average sequence divergence of 7.70% between *P. difficilis* from Aguascalientes and *P. nasutus* from New Mexico and Texas. Maximum-likelihood analysis of DNA sequence data from the same gene in 44 species of *Peromyscus* by Bradley et al. (2007) divided the *P. truei* species group into 2 clades, the *P. difficilis* clade (containing *P. attwateri*, *P. difficilis*, *P. nasutus*, and *P. ochraventer* [El Carrizo deermouse]) and the *P. truei* clade (*P. gratus* and *P. truei*).

Population genetics.—Based on an examination of allozyme variation at 22 protein loci, Avise et al. (1979) reported a mean heterozygosity of 0.8% and mean polymorphism of 4.8% in a population ($n = 18$ individuals) of *Peromyscus difficilis difficilis* from Yerbaniz, Durango. Although these values are low relative to those measured in most other mammal populations (Powell 1975), the study by Avise et al. (1979) was unusual in that it included only a single esterase locus. A study by Zimmerman et al. (1975) that included 3 esterase loci and 2 other rapidly evolving loci (transferrin and 6-phosphoglutamate dehydrogenase) showed variation at 4 of these 5 loci.

CONSERVATION

Peromyscus difficilis is considered of "Least Concern" by the International Union for Conservation of Nature and Natural Resources (Castro-Arellano and Vázquez 2008). This species is not listed in any risk category by any Mexican or international conservation agency.

REMARKS

Several articles published on populations of *Peromyscus difficilis* from the United States are not included in this account because these populations are now considered to be *P. nasutus* (Carleton 1980; Durish et al. 2004; Musser and Carleton 2005).

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