

Peromyscus boylii (Rodentia: Cricetidae)

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Abstract: *Peromyscus boylii* (Baird, 1855), the brush deer mouse, is a common cricetid rodent in the southwestern United States and Mexico. It is a member of the *Peromyscus boylii* species group and has had a complicated taxonomic history because many former subspecies have been elevated to species. It is a medium-sized *Peromyscus* with small ears and a long, slightly bicolored and slightly haired tail that ends in a tuft of long hairs. It prefers brushy habitat, showing an affinity for oak–scrub oak and canyon–creek bottoms. It is not of special conservation concern. DOI: 10.1644/838.1.

Key words: brush mouse, cricetid, North America, peromyscine, rodent

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Peromyscus boylii (Baird, 1855) Brush Deer mouse

Hesperomys boylii Baird, 1855:335. Type locality “middle fork of the American River, California,” near Auburn, Eldorado Co., California.

Sitomys robustus J. A. Allen, 1893b:335. Type locality “Lakeport, Lake Co., Cal.”

Sitomys rowleyi J. A. Allen, 1893a:76. Type locality “Nolan’s Ranch, Utah.”

Sitomys major Rhoads, 1893:831. Type locality “Squirrel Inn, San Bernardino Co.” California.

Sitomys rowleyi pinalis Miller, 1893:331. Type locality “Granite Gap, Grant County, New Mexico.”

P[eromyscus]. b[oylii]. rowleyi: Mearns, 1896:139. First use of current name combination.

Peromyscus gaurus Elliot, 1903a:157. Type locality “San Antonio, San Pedro Martir mountains, Lower California, Mexico.”

Peromyscus parasiticus Elliot, 1903b:244. Type locality “Lone Pine, Inyo County, California.”

Peromyscus metalicolla Elliot, 1903b:245. Type locality “Providencia Mines, Northwestern Sonora, Mexico.”

Peromyscus boylei Osgood, 1909. Incorrect subsequent spelling of *Hesperomys boylii* Baird, 1855.

P[eromyscus]. b[oylii]. glasselli Burt, 1932:171. Type locality “San Pedro Nolasco Island (latitude 27°58’N., longitude 111°24’W.), Gulf of California, Sonora, Mexico;” known only from type locality.

P[eromyscus]. b[oylii]. utahensis Durrant, 1946:167. Type locality “5 mi. above lower power station, Millcreek Canyon, 5,800 ft., Salt Lake County, Utah.”

CONTEXT AND CONTENT. Order Rodentia, suborder Myomorpha, superfamily Muroidea, family Cricetidae, subfamily Neotominae, tribe Reithrodontomyini, subgenus *Peromyscus*; *boylii* species group (Musser and Carleton 2005). The genus *Peromyscus* includes 56 nominal species (Musser



Fig. 1.—An adult male *Peromyscus boylii rowleyi* from lower Robertson Creek at the Hastings Natural History Reserve, Monterey County, California (22.5 km southeast of Carmel Valley, 36°22’N, 121°22’W). Photograph by Matina C. Kalcounis-Rueppell, 27 July 2002.

and Carleton 2005). The *boylii* species group includes *P. boylii*, *P. beatae*, *P. levipes*, *P. madrensis*, *P. simulus*, *P. stephani*, *P. schmidlyi*, and 2 unnamed species from Nayarit and Michoacán, Mexico (Bradley et al. 2004; Tiemann-Boege et al. 2000). Many of the taxa listed as subspecies by Osgood (1909) and Hall (1981) have been elevated to species in the *boylii* species group, including *P. levipes* (Schmidly et al. 1988), *P. madrensis* (Carleton 1977; Carleton et al. 1982), *P. simulus* (Carleton 1977; Roberts et al. 2001), and *P. beatae* (Schmidly et al. 1988); or to other species outside of the *P. boylii* species group, including *P. attwateri*, in the *P. truei* species group (Schmidly 1973); *P. aztecus* (Alvarez 1961; Carleton 1979; Hooper 1968) and *P. spicilegus* (Carleton 1977; Roberts et al. 1998), both in the *P. aztecus* species group; and *P. sagax*, currently in no species group (Bradley et al. 1996; Tiemann-Boege et al. 2000). The following taxa, listed as subspecies of *P. boylii* by Osgood (1909) and Hall (1981), have been realigned (as subspecies) with other *Peromyscus* species: *P. spicilegus evides* (actually recognized as a full species by Hall [1981] following Musser [1964]) and *P. boylii cordillerae* under *P. aztecus* (Carleton 1979); *P. boylii ambiguus* under *P. levipes* (Castro-Campillo et al. 1999); and *P. boylii sacarensis* under *P. beatae* (Bradley et al. 2000; Carleton 1979; Schmidly et al. 1988). Currently, 4 subspecies are recognized in *P. boylii* (Bradley and Schmidly 1999; Tiemann-Boege et al. 2000):

- P. b. boylii* Baird, 1855:335. See above.
P. b. glasselli Burt, 1932:171. See above.
P. b. rowleyi Allen, 1893a:76. See above.
P. b. utahensis Durrant, 1946:167. See above.

NOMENCLATURE NOTES. The species name *boylii* honors Charles Elisha Boyle, who collected the specimens that Baird (1855) described as *Hesperomys boylii* (Jennings 1987). The species name was changed to *boylei* by Osgood (1909) and subsequently both spellings have been used. The correct spelling of the species name is Baird's original latinization of Boyle to *boylii* (see nomenclature note in Carleton [1989]). The common name of "brush" may refer to the "brush of hair at the tip" of the tail (Baird 1855:335) or to the preference for "brush" (e.g., Stephens 1906:106) or "brushy" (Grinnell 1933:176) habitat. The genus name *Peromyscus* is derived from the Greek words *pera* meaning pouch or bag, *mys* meaning mouse, and *iscus* as a diminutive (Brown 1956).

Because many of the subspecies listed by Osgood (1909) and Hall (1981) have been elevated to species, some published information about *P. boylii* now is more appropriately attributed to other species (e.g., Anderson 1972; Baker and Phillips 1965; Brown 1963a, 1963b, 1964a, 1964b; Brown and Conaway 1964; Garner 1967; Hooper 1957, 1958; Linzey and Layne 1969; Long 1961; Rogers and Engstrom 1992; Whitaker 1968). Therefore, careful attention should be paid when interpreting this literature with respect to *P. boylii*.

DIAGNOSIS

The following diagnoses of *Peromyscus boylii* from sympatric species in the United States are from Schmidly (1977) and Davis and Schmidly (1994), unless otherwise noted. *P. boylii* can be differentiated from *P. maniculatus*, *P. leucopus*, *P. crinitus*, and *P. truei* (east of the Sierra Nevada) by a length of tail > total length of body. West of the Sierra Nevada, where the tail of *P. truei* is longer than its head and body, *P. boylii* is distinguished from *P. truei* by ears that are 70–80% as long as the hind foot rather than longer than the hind foot, by a tail that is less heavily haired but with more pronounced annulations, and by auditory bullae that are less inflated (Hoffmeister 1981). *P. boylii* is sympatric with and easily confused with other members of the subgenus *Peromyscus*. It can be differentiated from *P. pectoralis* by a tufted tip of the tail, by dark-colored ankles (dusky as opposed to white), by V-shaped rather than truncate posterior tips of the nasals, and by a baculum with a shorter spine at the distal end (Schmidly 1972). *P. boylii* has smaller ears and shorter fur than *P. difficilis*, as well as flanks that are distinctly bright yellow brown to ochraceous buff as opposed to the gray color on *P. difficilis*. *P. boylii* is distinguished from *P. attwateri* by a shorter hind foot (<24 mm) and a darker venter (slaty as opposed to white—Schmidly 1973). As a supplement to the criteria for distinguishing *P. boylii* from *P. maniculatus*, *P. leucopus*, *P. truei*, and *P. difficilis* in New Mexico, provided in Findley et al. (1975), Thompson and Conley (1983) provided a classification equation based on discriminant function analysis of ear length, length of maxillary tooththrow, mandible length, tail length, bullar depth, rostral length, body mass, and length of mandibular tooththrow.

In east-central Mexico, *P. boylii* is easily confused with *P. beatae* and *P. levipes*. Morphologically, *P. boylii* differs from *P. beatae* as follows: it is smaller, of lighter color, has a shorter molar tooththrow (3.6–4.2 versus 4.2–4.9 mm), a narrower zygomatic breadth (12.3–13.8 versus 13.6–15.4 mm), a vertical infraorbital plate, a foramen along the ophthalmic arterial canal, a mesostyle on the left M2, and no ectolophid on the left m1 (Schmidly et al. 1988). Compared to *P. levipes*, *P. boylii* is lighter in color, has a shorter molar tooththrow (3.6–4.2 versus 4.2–4.8 mm), and a narrower zygomatic breadth (12.6–13.5 versus 12.9–15.2 mm). *P. boylii* also possesses a less-angular lateral border of the parietals, a mesostyle on the right M2, and an ectolophid on the left m1 (Schmidly et al. 1988). *P. boylii* differs from *P. beatae* and *P. levipes* in that *P. boylii* has a larger glans penis (ca. half the length of the hind foot) with slight fluting on its dorsal and ventral surfaces and triangular spines that are of equal height and width, and a longer baculum that is dorsoventrally curved with a shaft that is narrow relative to length (Bradley and Schmidly 1987). These 3 species differ karyologically, as well: *P. boylii* has a monomorphic low

fundamental number (FN) of 52, *P. beatae* a polymorphic low FN = 48–54 (Houseal et al. 1987), and *P. levipes* a polymorphic high FN = 58–60 (Schmidly et al. 1988). They also can be distinguished based on allozyme (Rennert and Kilpatrick 1986, 1987; Sullivan et al. 1991) and cytochrome-*b* and D-loop sequence analyses (Bradley et al. 2000; Castro-Campillo et al. 1999; Tiemann-Boege et al. 2000).

In west-central Mexico, *P. boylii* differs from *P. spicilegus* by having smaller body and cranial morphological dimensions, paler color, and no supraorbital shelf (Baker and Greer 1962; Carleton 1977; Carleton et al. 1982). *P. boylii* differs from *P. simulus* by having larger external and cranial dimensions in addition to being paler in color and lacking the supraorbital shelf that is only slightly developed in *P. simulus* (Baker and Greer 1962; Carleton 1977; Carleton et al. 1982). *P. boylii* is difficult to distinguish from *P. schmidlyi* but is slightly smaller in body size and has lighter coloration (Bradley et al. 2004).

GENERAL CHARACTERS

Peromyscus boylii (Fig. 1) is of medium size with small ears and a long, slightly bicolored (dusky drab above, white to gray below—Zelovoff 1988) and slightly haired tail (such that the rings of hair on the skin are evident—Zelovoff 1988) that ends in a tuft of long hairs (Bradley and Schmidly 1999). The skull (Fig. 2) and postcranial skeleton of *P. boylii* are described in detail by Carleton (1980). That analysis included some specimens that are no longer recognized as *P. boylii* (e.g., specimens now classified as *P. levipes*), and data for *P. boylii* (sensu stricto) cannot always be positively distinguished. Because of the systematic and taxonomic history of *P. boylii* (e.g., elevation of many subspecies to species), we specify subspecies and specimen localities for mensural and qualitative characters and only report on *P. boylii* (sensu stricto). If the published sources did not provide specimen localities, we used our judgment in deciding whether to include material herein and we note to the reader instances where origins of specimens are unknown.

The following morphological measurements (mean and range; mm) are from 10 adult topotypes of *P. b. boylii* (sexes not distinguished) from the Middle Fork of the American River, Eldorado County, California: total length, 197 (183–202); length of tail vertebrae, 103 (92–112); length of hind foot, 22 (21–23); and length of ear from notch (dry), 16.4 (15.3–17.5—Osgood 1909). The following means and ranges (mm) are from 11 specimens of *P. b. rowleyi* collected in Aguascalientes, Mexico: total length, 194.3 (175–210); length of tail, 103.6 (89–115); length of hind foot, 20.1 (12–22); length of ear, 19.0 (18–21); greatest length of skull, 26.5 (25.8–27.0); length of rostrum, 10.9 (10.6–11.5); length of nasal, 9.5 (9.0–10.0); width of zygomatic, 12.9 (12.6–13.5); maximum width of braincase, 12.3 (11.9–12.7); width of mastoid, 11.4 (11.1–11.8); minimum interorbital width, 4.3



Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Peromyscus boylii boylii* (Museum of Vertebrate Zoology [MVZ] 156578) from Hopland Field Station, Mendocino County, California (30°00'N, 123°05'W). Greatest length of skull is 27.3 mm. Photograph by Matina C. Kalcounis-Rueppell.

(4.2–4.6); length of molar toothrow, 3.9 (3.7–4.2); length of incisive foramen, 4.5 (4.2–5.1); length of auditory bulla, 5.2 (5.0–5.6); depth of braincase, 9.4 (9.1–10.0); length of mesopterygoid fossa, 4.5 (4.0–4.9); length of bony palate, 4.1 (4.0–4.5); width of rostrum, 4.6 (4.4–4.8); width of molars, 5.4 (5.2–5.5); width of postdental palate, 4.0 (3.8–4.3); and width of mesopterygoid fossa, 2.4 (2.3–2.5—Schmidly et al. 1988).

Dimensions (mean and range; mm) of 23 or 24 specimens of male *P. b. rowleyi* from western San Luis,

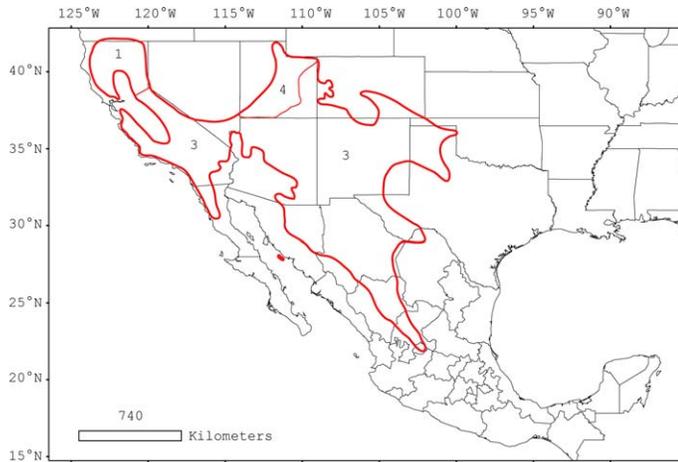


Fig. 3.—Geographic distribution of *Peromyscus boylii*. Subspecies are: 1, *P. b. boylii*; 2, *P. b. glasselli*; 3, *P. b. rowleyi*; 4, *P. b. utahensis*. Map redrawn from Carleton (1989) and Bradley and Schmidly (1999) with modifications from Hoffmeister (1986), Cockrum (1982), and Cockrum (1960) for Arizona; Stephens (1906), Jameson and Peeters (1988), and Grinnell (1933) for California; Armstrong (1972), Warren (1910), and Svoboda et al. (1988) for Colorado; Hall (1946) for Nevada; Bailey (1931) and Findley et al. (1975) for New Mexico; Caire et al. (1989) for Oklahoma; Verts and Carraway (1998) and Grinnell (1933) for Oregon; Davis and Schmidly (1994) and Schmidly (1977) for Texas; Durrant (1946), Barnes (1927), and Durrant (1952) for Utah; and Tiemann-Boege et al. (2000) for Mexico. The position of San Pedro Nolasco Island, Gulf of California, Sonora, Mexico (27°58'N, 111°24'W) is approximate.

Durango, Mexico, are: length of skull, 26.8 (25.7–27.7); length of rostrum, 8.8 (7.9–9.4); width of zygomatic, 13.4 (12.9–14.0); length of maxillary tooththrow, 4.1 (3.9–4.4); total length, 189.0 (176–201); length of tail, 97 (88–107); and length of hind foot, 21.6 (20–23—Carleton 1977). Mean measurements for male and female *P. b. rowleyi*, respectively, from the Davis Mountains, Jeff Davis County, Texas, are: total length, 195.5 ($n = 47$), 195.5 ($n = 47$); length of tail, 103.0 ($n = 47$), 103.1 ($n = 47$); length of head and body, 92.1 ($n = 50$), 92.5 ($n = 55$); length of hind foot, 21.6 ($n = 52$), 21.7 ($n = 55$); length of ear, 18.9 ($n = 45$), 18.8 ($n = 55$); length of skull, 27.5 ($n = 50$), 27.4 ($n = 56$); length of basilar, 21.9 ($n = 52$), 22.0 ($n = 56$); length of rostrum, 10.4 ($n = 52$), 10.4 ($n = 55$); length of nasal, 10.5 ($n = 52$), 10.5 ($n = 55$); width of orbital constriction, 4.2 ($n = 55$), 4.2 ($n = 56$); width of mastoid, 11.5 ($n = 52$), 11.5 ($n = 55$); width of zygomatic, 13.3 ($n = 52$), 13.3 ($n = 55$); length of maxillary tooththrow, 4.1 ($n = 55$), 4.1 ($n = 56$); length of palatal foramen, 5.5 ($n = 55$), 5.5 ($n = 56$); length of bony palate, 4.0 ($n = 55$), 4.0 ($n = 56$); depth of skull, 9.4 ($n = 50$), 9.4 ($n = 55$); and length of bullae, 5.1 ($n = 52$), 5.2 ($n = 56$ —Schmidly 1973). Only the length of the maxillary tooththrow differs statistically between males and females. Mean measurements (mm) from 10 adult (sexes not identified) *P.*

b. utahensis (previously regarded as *P. b. rowleyi*) from Bluff City, San Juan River, Utah, are: total length, 191 (180–207); length of tail vertebrae, 99 (91–109); length of hind foot, 21.6 (21–23); and length of ear from notch (dry), 17.2 (16.6–18—Osgood 1909). Measurements (mm) from the type specimen of *P. b. glasselli* (male) captured on San Pedro Nolasco Island, Gulf of California, Sonora, Mexico (Burt 1932), are: total length, 188; length of tail vertebrae, 97; length of hind foot, 23; length of ear from crown, 16; greatest length of skull, 26.5; length of condylobasal, 23.6; basilar length of Hensel, 20.2; width of zygomatic, 13.1; length of interorbital constriction, 4.0; dimensions of interparietal, 9.4 by 3.5; length of nasals, 10.6; length of bony palate shelf, 3.6; and length of maxillary tooththrow, 4.2.

DISTRIBUTION

Peromyscus boylii inhabits the mountainous regions of the southwestern United States and northern Mexico, generally above 1,500 m (Fig. 3). In California, *P. boylii* is found throughout the state except for the Central Valley and the Mohave Desert. The distribution of *P. boylii* also includes the eastern shore of Lake Tahoe and the southern part of Nevada, the southeastern and southwestern parts of Colorado, and the central and eastern parts of Utah. In Arizona, *P. boylii* is found on mountain slopes throughout the state except the southwestern corner. In New Mexico, *P. boylii* is found throughout the state except at low elevations in the southeast. The distribution of *P. boylii* is restricted to the mountains of the Trans Pecos region in Texas, and in Oklahoma, it has been recorded only from the extreme northwestern portions of the panhandle in the Black Mesa region. In Mexico, *P. boylii* extends southward along the Mexican Plateau through the Sierra plains and northern Sierra, the eastern slopes of the Sierra Madre Occidental, the western slopes of the Sierra Madre Oriental, and the Altiplano. Along the Mexican Plateau the range passes through the states of Sonora, Chihuahua, Coahuila, Durango, Zacatecas, and Aguascalientes. *P. boylii* is known from San Pedro Nolasco Island, Sonora, Mexico, in the Gulf of California.

FOSSIL RECORD

The majority of fossil localities (FAUNMAP Working Group 1994) fall within the current distribution of *Peromyscus boylii* (Fig. 3), except for Friesenhahn Cave, Bexar County, Texas; Schulze Cave, Edwards County, Texas; and San Josecito Cave, Nuevo León, México. These fossil localities likely include fossils of *P. attwateri*, *P. levipes*, and perhaps *P. beatae*, and therefore are not discussed herein.

The oldest records are from Fowlkes Cave and Dry Cave. Material of *P. boylii* from Fowlkes Cave, Culberson

County, Texas, represents a late Pleistocene deposit dated as <35,000 and >10,000 years of age (Dalquest and Stangl 1984). Material of *P. boylii* from the Bison Chamber sublocality in Dry Cave, Eddy County, New Mexico, is dated at <14,470 and >10,730 years of age (Harris 1980, 1985, 1987); however, this record is questionable (Dalquest and Stangl 1984).

The majority of known localities of *P. boylii* fossil material are Holocene (<10,000 years old). Late Holocene material comes from Snaketown, Pinal County, Arizona (but questionable provenience—FAUNMAP Working Group 1994); Aldea Sierritas and Windy Wheat Hamlet Montezuma County, Colorado; Guadalupe Ruin, Sandoval County, New Mexico; several localities in Rio Arriba County, New Mexico (LA 12056, LA 12063, LA 12066, LA 12070, and LA 12072), and Leighton Ranch, Union County, New Mexico (Dalquest et al. 1990; FAUNMAP Working Group 1994; Haynes and Long 1976; Holbrook 1977; Olsen 1976; Pippin 1987).

FORM AND FUNCTION

Form.—*Peromyscus boylii* lacks internal cheek pouches (Carleton 1980), has a complete anterior longitudinal palatal ridge of high relief, and has 3 complete and 4 incomplete transverse palatal ridges (Carleton 1980). The distribution of gastric glandular epithelium is discoglandular. *P. boylii* has deep incisura angularis development, a bilocular stomach, a gall bladder, and no sulcus on the greater curvature of stomach (Carleton 1980).

Descriptions of the male phallus (Hooper 1958), reproductive tract (Linzey and Layne 1969), and dentition (Hooper 1957) include some specimens no longer recognized as *P. boylii* (e.g., specimens now classified as *P. levipes*), and data for *P. boylii* (sensu stricto) cannot always be extracted from the sources. However, the following descriptions of the male phallus, reproductive tract, and dentition are for *P. boylii* (sensu stricto). *P. b. rowleyi* exhibits well-developed dorsal and ventral lappets and poorly developed fluting on the dorsal and ventral surfaces of the glans penis (Bradley and Schmidly 1987; Carleton 1977). Triangularly shaped spines, each with a height equal to its width, cover the surface of glans; these include medium-sized spines that are sparsely distributed dorsally and small spines densely distributed ventrally (Bradley and Schmidly 1987). Bradley et al. (1989) provide a qualitative description for *P. b. rowleyi* from Chihuahua, Aguascalientes, and Hidalgo, Mexico.

Mean dimensions (mm) of glans penes for specimens of *P. b. rowleyi* from western San Luis, Durango ($n = 7$); northern Pueblo Nuevo, Durango ($n = 3$); and Laguna del Progreso, Durango, Mexico ($n = 3$ —Carleton 1977), respectively, are: length of glans, 8.09, 8.46, 7.67; width of glans, 1.25, 1.33, 1.14; length of protractile tip, 2.20, 1.85,

2.23; and length of baculum, 10.55, 10.96, 9.68. The following means (mm) and ratios are from specimens of *P. b. rowleyi* ($n = 11$) collected in Aguascalientes, Mexico: length from base of ventral flexure to the distal tip of glans (length of the distal tract), 14.08; length of glans, 9.64; length of protractile tip, 2.52; greatest width of glans, 1.73; length of baculum, 11.89; length of cartilaginous tip of baculum, 0.17; greatest width at base of baculum, 1.31; greatest width of baculum at midpoint, 0.35; ratio of length of glans to width of glans, 5.60; ratio of length of glans to greatest width of baculum at midpoint, 6.79; ratio of length of cartilaginous tip to length of baculum, 0.015; and ratio of length of baculum to length of glans, 1.22 (Bradley and Schmidly 1987). Mean measures (mm \pm SE) from Chihuahua ($n = 2$), Aguascalientes ($n = 2$), and 2 locations in Hidalgo, Mexico ($n = 5$ and $n = 4$ —Bradley et al. 1989), respectively, are: length of distal tract, 13.07 ± 0.22 , 14.08 ± 0.44 , 13.67 ± 0.41 , 13.50 ± 0.39 ; length of glans, 8.97 ± 0.14 , 9.64 ± 0.32 , 9.25 ± 0.29 , 9.45 ± 0.19 ; length of protractile tip, 2.23 ± 0.07 , 2.52 ± 0.12 , 2.36 ± 0.11 , 2.51 ± 0.09 ; greatest width of glans, 1.82 ± 0.03 , 1.73 ± 0.06 , 1.63 ± 0.04 , 1.63 ± 0.07 ; length of baculum, 11.63 ± 0.26 , 11.89 ± 0.41 , 11.45 ± 0.48 , 12.11 ± 0.43 ; length of cartilaginous tip, 0.20 ± 0.02 , 0.17 ± 0.00 , 0.16 ± 0.01 , 0.17 ± 0.01 ; width of baculum at base, 1.39 ± 0.05 , 1.31 ± 0.07 , 1.16 ± 0.10 , 1.37 ± 0.08 ; and greatest width of baculum at midpoint, 0.38 ± 0.02 , 0.35 ± 0.02 , 0.39 ± 0.05 , 0.43 ± 0.02 .

Peromyscus boylii possesses medial ventral, lateral ventral, dorsal, and anterior prostate glands (Carleton 1980). Males also have a bulbourethral gland positioned between, and partly obscured by, the bulbocavernosus and ishiocavernosus muscles, compact coiled ampullary glands, and vesicular glands shaped like an inverted J. *P. boylii* lacks ampullae of ductus deferens. Measures of the male reproductive tract of *P. boylii* including accessory gland structures are presented in Linzey and Layne (1969); however, some specimens included are not *P. boylii* (sensu stricto).

Second, 3rd, and 4th interdigital plantar pads are grouped tightly, but the 1st is farther back on the heel and not opposite the 4th. The thenar and hypothenar pads are situated posteriorly and are strongly alternate. The plantar surface is thickly furred to the thenar pad (Carleton 1980). *P. boylii* possesses 3 pairs of mammae—1 pectoral and 2 inguinal (Bailey 1931; Carleton 1977, 1980).

The dental formula for *P. boylii* is $i 1/1$, $c 0/0$, $p 0/0$, $m 3/3$, total 16. Upper incisors are not grooved. In general, molars are bunodont. M1 has a single large lingual root and no labial root, M2 has a single large lingual root, and M3 has 3 roots. m1 has no lingual or labial root and m2 and m3 have 2 roots. m3 also is characterized by a greatly reduced entoconid and a hypoconid that wears to a C shape (Carleton 1980). Detailed descriptions of molar accessory structures are available in Hooper (1957). Frequency of

occurrence of molar accessory structures varies dramatically across populations of *P. boylii* (Hooper 1957; Schmidly 1973).

Function.—Body composition and energy equivalents (mean \pm SE, $n = 9$; per g dry mass basis) of *P. boylii rowleyi* from San Diego County, California, follow: dry body mass, 5.5 ± 0.8 (g); total body fat, 13.2 ± 1.7 (%); ash content, 13.8 ± 0.7 (%); total body caloric content, 5.1 ± 0.1 (kcal/g); ash-free caloric content 5.9 ± 0.1 (Kaufman et al. 1975). The chemical composition (mean \pm 2 SE, $n = 9$; mg per g dry mass) of *P. boylii rowleyi* from California and Nevada is as follows: nitrogen, 109.9 ± 7.0 ; calcium, 30.4 ± 3.3 ; sulfur, 32.3 ± 3.9 ; phosphorus, 18.9 ± 1.6 ; potassium, 10.8 ± 0.6 ; sodium, 2.8 ± 0.3 ; magnesium, 1.0 ± 0.1 (Wiener et al. 1977). The basal metabolic rate reported for *P. b. boylii* ($n = 20$) from Butte County, California, is 2.34 ± 0.3 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ and does not differ from that of *P. maniculatus* (Mazen and Rudd 1980).

ONTOGENY AND REPRODUCTION

To examine variation in morphological measures with age, Schmidly (1973) divided a sample of 154 *Peromyscus boylii rowleyi* into 6 relative age groups (chronological ages were not provided): group 1, M3 not completely erupted, juvenile pelage ($n = 1$); group 2, M3 completely erupted, no wear or little wear on cheek teeth, juvenile pelage ($n = 14$); group 3, molars partially worn, juvenile pelage or molting into adult pelage ($n = 33$ – 35); group 4, all major cusps worn smooth but pattern still identifiable, adult pelage ($n = 72$ – 77); group 5, many cusps obliterated by wear, adult pelage ($n = 16$ – 18); and group 6, all cusps obliterated ($n = 10$). Morphometrics (means, except for group 1; mm) for age groups 1–6, respectively, are: total length, 135.0, 167.9, 183.8, 195.6, 198.2, 201.6; length of tail, 63.0, 85.5, 96.2, 105.4, 108.8, 106.8; maximum length of skull, 23.4, 25.5, 26.6, 27.6, 27.8, 27.7; length of nasal, 8.1, 9.4, 10.0, 10.4, 10.8, 10.6; width of mastoid, 10.4, 11.2, 11.3, 11.6, 11.6, 11.5; and depth of skull, 8.6, 9.1, 9.3, 9.3, 9.5, 9.3.

Peromyscus boylii has a postjuvenile molt. Molting begins laterally and progresses dorsally toward the head and tail. An average molt is completed in 25 days (range = 8–35 days—Storer et al. 1944).

Breeding season varies across the distribution range of *P. boylii* and within populations. In general, breeding activity by *P. boylii* is somewhat reduced during the hottest summer months. In the Sierra Nevada, California, breeding season is April–September (based on presence of embryos in females), with peak number of pregnant or lactating females in June, declining in July, and rising again in September (Jameson 1953; Storer et al. 1944). The percentage of reproductive-aged females with fresh corpora lutea is lowest in July (30%) and highest in May (86%) and September (80%—Jameson 1953). In California, it appears that the

breeding season of *P. boylii* is characterized by rapid appearance and decline of breeding individuals in the population (Jameson 1953). In central and southern California, breeding can be year-round and corresponds to months with most rainfall (Kalcounis-Rueppell 2000; Vaughan 1954). In central Arizona, reproductive activity occurs April through October, peaking in late summer and autumn (Abbott et al. 1999). In Texas, breeding activity occurs in March–May and October–December, with some winter breeding (Bailey 1931) and with 2 or more litters per female produced in some years (Cornely et al. 1981). In Durango, Mexico, 21 females collected from late June to early August showed no indication of breeding (Drake 1958).

Timing and duration of the breeding season appear to be related to mast production. In the Sierra Nevada, California, reproductive activity begins in April and ceases in July in years with virtually no mast or berry production, but extends from April into December in a year with lower than average mast production (Jameson 1953). Peak breeding activity in late summer and early autumn coincides with ripening of oak, pinyon pine, and juniper mast in Arizona. Similar to the events in California, mast failure in Arizona results in 96% fewer pregnancies in summer and 56% fewer pregnancies in autumn (Abbott et al. 1999).

Mean age at the onset of estrus for captive female *P. boylii* is 50.9 days ($n = 33$; minimum age = 37 days—Clark 1938). However, pregnancy does not occur until females reach ≥ 4 months of age (Clark 1938). In the northern Sierra Nevada, California, only females weighing ≥ 18.1 g possessed corpora lutea (Jameson 1953). Females of unknown age, but with juvenile pelage, exhibited lactation in New Mexico (Bailey 1931) and in the Sierra Nevada, California, some females show evidence of pregnancy before completion of the postjuvenile molt (Storer et al. 1944). In Arizona, early-born young of the year reproduce during the breeding season of their birth (Hoffmeister 1986).

The most comprehensive study of reproduction in *P. boylii* involved a postmortem examination of 830 *P. boylii* (male and female) in the northern Sierra Nevada, California (Jameson 1953); the following observations (unless otherwise cited) are from that study. The vulva is imperforate when a female is nonfecund, but is perforate during estrus. The vulva may be perforate or imperforate at any stage of gestation, although it is more likely to be perforate in very early and late stages of pregnancy. Recent corpora lutea, generally numbering 2–5 per set, vary in size from estrus to estrus. The percentage of females with recent corpora lutea reaches 86% in May, 80% in September, and 31% in July. During winter, ovulation occurs but oviducts remain in an anestrus condition with the vagina sealed. During the winter nonbreeding period, the uterine horns are nonvascularized and are ≤ 1.0 mm in diameter at the base. During the breeding season, diameter increases to ≥ 1.0 mm, and during

estrus, horns often exceed 2.0 mm in diameter. Following parturition, horns may remain at ≥ 2.0 mm in diameter and appear thickened, rugose, and collapsed. Number of ova per set does not increase seasonally nor does number of ova ovulated increase with body mass. Postpartum estrus occurs. No fat is stored during reproduction (Bailey 1931).

Males can have enlarged testes before completion of the postjuvenile molt (Storer et al. 1944). Testes of fecund males are ≥ 11 mm (Jameson 1953). Testes of adult males in Guadalupe Mountains National Park, Texas, from March to August, range from 5 to 15 mm (Cornely et al. 1981). During winter, in the northern Sierra Nevada, California, males are nonreproductive, evidence that winter ovulations noted in females may not be accompanied by copulation.

Gestation averages about 29 days \pm 2.6 SD for free-ranging, lactating females ($n = 9$; all nonprimiparous), for which dates of vulval perforation and of parturition were known in Monterey County, California (Kalcounis-Rueppell 2000). Shorter gestations also have been reported: 22–25 days (Zevuloff 1988) and 23 days (Bradley and Schmidly 1999). In the Sierra Nevada, California, livetrapping studies indicate interbirth intervals of 25–31 days (Storer et al. 1944).

Peromyscus boylii produces several litters each year (Davis and Schmidly 1994; Hoffmeister 1986), with a maximum of 4 reported for populations in the intermountain west (Zevuloff 1988). Litter size does not seem to vary within the breeding season (Jameson 1953). Litter sizes of *P. boylii* are small relative to those of other *Peromyscus* of similar body mass (reviewed in Millar 1989). Mean (\pm SE) embryo counts vary from 3.1 ± 0.1 ($n = 42$, range = 2–4) in the northern Sierra Nevada, California (Jameson 1953), to 3.2 ± 1.1 ($n = 56$, range = 1–6) in Arizona (Hoffmeister 1986), to 3.5 ± 2.9 ($n = 4$, range 3–4) in Utah (Long 1940). Similar litter sizes are reported for a limited number of specimens from the Arizona–New Mexico border with Mexico (3, 3, and 2 embryos [Mearns 1907], and 3 embryos [Miller 1893]).

Neonates from litters of 3, 3, and 4 young in the Sierra Nevada, California, were 30 mm long (crown to rump), pink and wrinkled, and naked except for vibrissae, with closed eyes and folded pinnae (Storer et al. 1944). The only published birth weight (2.2 g) for *P. boylii* is for 1 individual born in a litter of 4 to a captive female from New Mexico (Bailey 1931). Young wean at 3–4 weeks of age (Bradley and Schmidly 1999). Juveniles of *P. boylii* have blue-gray pelage and a body size (at 1st trapping) that is about one-third adult size (Storer et al. 1944). *P. boylii* is known to produce ultrasound in the wild (Kalcounis-Rueppell et al. 2006) and a likely function of this ultrasound is for heterothermic pups to communicate with their mothers.

Peromyscus boylii displays a promiscuous mating system. This conclusion is supported by observations on the patterns of home-range overlap and on comparative phylogenetic analyses that demonstrate this type of mating

system to be ancestral and common in peromyscine rodents (Kalcounis-Rueppell 2000; Kalcounis-Rueppell and Ribble 2007; Ribble and Stanley 1998). Paternity of litters has not been systematically studied in *P. boylii*. Population-level sex ratios (male : female) vary from 0.68 (Schwilk and Keeley 1998) to 1.11 (Matson 1974) in California, to 1.25 in Mexico (Drake 1958). Over 2 breeding seasons in California, sex ratio varied from 0.96 to 0.56 (Kalcounis-Rueppell 2000).

ECOLOGY

Space use.—Generally, *Peromyscus boylii* shows an affinity for oak–scrub oak and canyon–creek bottoms. In Zion National Park, Utah, *P. boylii* is found in oak brush between 1,200 and 1,800 m (typically the Upper Sonoran zone in Utah) and overlaps extensively with *P. maniculatus* (Long 1940). In southwestern Utah, *P. boylii* is found only in pinyon–juniper communities and is absent in sagebrush, shadscale, blackbush, and creosote bush habitats (Honeycutt et al. 1981). In Canyonlands National Park in southeastern Utah, *P. boylii* is strongly associated with rocky habitats, as are other common *Peromyscus* species in the region (i.e., *P. crinitus*, *P. maniculatus*, and *P. truei*); unlike those species, *P. boylii* shows a strong secondary association with oak brush rather than with shrublands. *P. boylii* is most similar in habitat preference to *Neotoma mexicana*; these 2 species regularly co-occur in *Mahonia* thickets and saxicoline oak brush habitats (Armstrong 1979).

In the San Gabriel Mountains and the Sierra Nevada of California, *P. boylii* is found from about 500 to 1,900 m (Jameson 1951; Vaughan 1954). In the northern Sierra Nevada, *P. boylii* inhabits secondary-growth brush fields of manzanita (*Arctostaphylos patula* and *A. viscida*), deerbrush (*Ceanothus*), bearbrush (*Garya fremontii*), and small (diameter at breast height <30.5 cm) black oak (*Quercus kelloggii*), but is not found in adjacent coniferous forest. In the same region, *P. boylii* commonly inhabits ravines at elevations >900 m that contain oak woodland dominated by golden cup oak (*Q. chrysolepsis*), maple (*Acer macrophyllum*), and bay laurel (*Umbellularia californica*—Jameson 1951). In Monterey County, California, *P. boylii* is found in canyon bottoms dominated by live oak (*Q. agrifolia*), bay laurel, and California buckeye (*Aesculus californica*—Kalcounis-Rueppell and Millar 2002). In the Owens Lake Region, Inyo County, California, an ecotone lying between Upper and Lower Sonoran Desert life zones, *P. boylii* was not abundant in *Atriplex confertifolia* and *Franseria dumosa* vegetation but was numerous in creek canyons (Matson 1976) containing primarily golden cup oak, basin sagebrush (*Artemisia tridentata*), wingscale (*Atriplex canescens*), and rabbit brush (*Chrysothamnus nauseosus*—Matson 1974). In the Santa Monica Mountains of California, 6 months after a wildfire, captures of *P. boylii* were associated with neither of

the 2 predominant vegetation types (chaparral or coastal sage scrub) nor with distance from unburned areas (Schwilk and Keeley 1998).

Peromyscus boylii inhabits brushy chaparral rather than open juniper–pinyon stands in north-central Arizona (Abbott et al. 1999). In regions of discontinuous chaparral stands, *P. boylii* inhabits rocky pockets of vegetation. In the desert of central Arizona, *P. boylii* occurs more frequently on active floodplains characterized by more sandy soil, debris, a rocky substrate, and herbaceous cover than on inactive floodplain terrace (Ellison and van Riper 1998). On the upper floodplain terrace, *P. boylii* prefers areas with annual grass cover and rocky substrate, whereas on the lower terrace, *P. boylii* associates with herbaceous vegetation, exposed soil substrate, and annual grass cover (Ellison and van Riper 1998). *P. boylii* in east-central Arizona inhabits a range of scrub habitat associations from pinyon–juniper and juniper–oak to manzanita and Manzanita–oak, with a preference for manzanita-dominated microhabitats (Holbrook 1978, 1979a).

Peromyscus boylii in the Sandia Mountains of New Mexico is found in the Upper Sonoran zone and extends into the Transition zone (elevation = 1,980–2,133 m), where it resides in dense brushy areas regardless of plant species composition or exposure (Wilson 1968). In New Mexico, *P. boylii* is directly sympatric with more small mammal species than is *P. leucopus*, *P. maniculatus*, *P. truei*, or *P. difficilis* (Wilson 1968). *P. boylii* is most abundant in areas uninhabited by other *Peromyscus* species (Wilson 1968). In areas of overlap with *P. leucopus*, *P. boylii* primarily inhabits the brushy canyon slopes, whereas *P. leucopus* inhabits the canyon floor. Although *P. boylii* and *P. truei* both are captured in the pinyon–juniper zone, *P. boylii* appears restricted to dense brush within that zone, thus reducing contact between them (Wilson 1968).

In the Sierra Nevada, California, with density of *P. boylii* varying through the year between 2 and 17 individuals/ha, home ranges (minimum convex polygon; based on trapping), averaged over the year, were 0.11 ha for males ($n = 13$) and 0.17 ha for females ($n = 15$ —Storer et al. 1944). In a Durango, Mexico, population of 26 or 27 individuals/ha during the summer hiatus in breeding, home ranges (minimum convex polygon; based on trapping) were 0.11 ha for males ($n = 13$) and 0.17 ha for females ($n = 15$ —Drake 1958). Also in Durango, Mexico, through the year with peak population density of 20–46 individuals/ha, home ranges (minimum convex polygon; based on trapping) were 0.14 ha for males ($n = 9$) and 0.05 ha for females ($n = 10$ —Alvarez and Arroyo-Cabrales 1990). In Mora County, New Mexico, with population density of 11 or 12 individuals/ha, home ranges (minimum convex polygon; based on radiotelemetry) were 0.47 ha for males ($n = 9$) and 0.26 ha for females ($n = 9$). These areas correlated negatively with density of *P. boylii* but positively with

densities of syntopic *P. truei* and *P. difficilis* (Ribble and Stanley 1998). In Monterey County, California, during 2 breeding seasons with population density from 40 to 72 individuals/ha, home ranges (minimum convex polygon; based on radiotelemetry) were 0.13 ha for males ($n = 6$) and 0.11 ha for females ($n = 9$) in 1997 and 0.15 ha for males ($n = 6$) and 0.13 ha for females ($n = 9$) in 1998 (Kalcounis-Rueppell 2000). A home-range estimate (minimum convex polygon from radiotelemetry) of 0.12 ha ($n = 20$) for *P. boylii* in Arizona was unaffected by season or sex (Gottesman et al. 2004). Male home ranges overlap with multiple females and males, whereas female home ranges show little intrasexual overlap (Ribble and Stanley 1998).

Peromyscus boylii climbs a variety of plants and structures and is common wherever shrubs and trees are present but is absent from large patches of grassland (Holbrook 1979b). When placed on an inclined surface in the dark, young *Peromyscus* tend to climb upward (Clark 1936). In southeastern California, females of *P. boylii* of all age classes were captured more frequently in trees than were males of the same age class; the ratio of 0.42 male : 1 female captured in trees was significantly different than the ratio of 1.11 male : 1 female captured on the ground (Matson 1974).

Diet.—*Peromyscus boylii* is an omnivore. Analysis of stomach contents of 480 *P. boylii* across all seasons in the northern Sierra Nevada, California, revealed that diet varied seasonally and largely reflected locally available items. In winter, diet was composed of seeds (mainly acorns of *Quercus kelloggii*), berries (manzanita [*Arctostaphylos patula*] and silktassel [*Garrya fremontii*]), and arthropods (caterpillars, heteropterans, and spiders). During times of deep snow, *P. boylii* browsed on silktassel and ceanothus (*Ceanothus cuneatus*) leaves. Small amounts of fungi, mammals, birds, and lizards (*Sceloporus graciosus*) also were eaten. In spring, *P. boylii* consumed smaller quantities of seeds, no berries, and a higher proportion of insects (cutworm [*Protorthodes rufula*], geometrids, coccids, and isopterans) than in the winter. In a year with little mast production, most seeds that were consumed had already sprouted. Leaves of herbs were eaten, and manzanita flowers were found in 1 individual. In summer, manzanita berries, when available, replaced seeds as a dietary staple and caterpillars and pentatomid bugs were components of the diet. In autumn, *P. boylii* preferred acorns, Douglas fir (*Pseudotsuga taxifolia*) and ponderosa pine (*Pinus ponderosa*) seeds, and manzanita berries when available. In a year with no acorn, cone, or berry production, *P. boylii* subsisted on acorns from the previous year and manzanita seeds. Additionally, fungi replaced fruits and seeds when these were unavailable. Insects comprised a smaller portion of the diet in autumn (Jameson 1952). In Monterey County, California, the diet of *P. boylii* consists largely of coast live oak (*Q. agrifolia*) acorns (Kalcounis-Rueppell and Millar 2002).

The diet of *P. boylii* in New Mexico consisted of arthropods (32%), juniper fruit (25%), juniper pollen cones

(8%), prickly pear tissue (7%), and juniper mistletoe (7%—Smartt 1978; see also Bailey 1931). *P. boylii* in Texas consumes hackberries, juniper berries, pine nuts, cactus fruits, Douglas fir seeds, and acorns (Davis and Schmidly 1994; Schmidly 1977). *P. boylii* consumes primarily juniper berries within the juniper belt of Utah (Barnes 1927), and cactus fruit, acorns, conifer seeds, berries, fungi, and insects in other parts of the intermountain west (Zeloff 1988).

Although omnivorous, *P. boylii* appears to favor acorns when they are available (Kalcounis-Rueppell and Millar 2002; Schmidly 1977). Year-to-year variation in population densities correlates with mast abundance (Abbott et al. 1999; Jameson 1953). Where *P. boylii* feeds on pinyon pine (*Pinus edulis*) nuts, its seed caching is probably important for seed dispersal and establishment (Pearson and Theimer 2004). Unlike sympatric *P. difficilis*, and unlike conspecifics in California (Jameson 1952), *P. boylii* in New Mexico does not shift to insectivory in the summer (Holbrook 1978).

Diseases and parasites.—Internal parasites of *Peromyscus boylii* (sensu stricto) include cestodes (*Hymenolepis horrida*, *Mesocestoides kirbyi*, *M. variabilis*, and *Mesocestoides* larvae), and nematodes (*Gongylonema peromysci* and *Heligmosomum*—Whitaker 1968). *P. boylii* in California serves as intermediate host for the leukocyte-born protozoan *Heptazon peromysci* (Apicomplexa: Protozoa—Levine 1982).

Several species of ticks in various stages of development parasitize *P. boylii*, including nymphal *Dermacentor occidentalis*, larval *Ixodes pacificus*, adult *I. spinipalpis*, and adult *I. augustus* (Whitaker 1968; see also Medina et al. 2006). Parasite loads of 3.0 *I. pacificus* and 1.3 *D. occidentalis* per infested *P. boylii* have been reported (Burkot et al. 1999). *P. boylii* also hosts chiggers (*Odontacarus villosus* [Goff and Loomis 1973], *O. hirsutus*, *Chatia ochotona*, *Euschoengastia criceticola*, *E. lacerta*, *E. peromysci*, *E. pomerantzi*, *E. radfordi*, *Neotrombicula dinehartae*, *N. jewetti*, and *Pseudoschoengastia occidentalis*) and mites (*Androlaelaps casalis*, *A. fahrenheitsi*, *Brevisterna utahensis*, *Bryobia praetiosa*, *Dermanyssus becki*, *Eubrachylaelaps circularis*, *E. debilis*, *Eubrachylaelaps*, *Haemogamasus nidi*, *H. pontiger*, *Hermannia*, *Hirstionyssus affinis*, *H. occidentalis*, *Ornithonyssus bacoti*, and other *Ornithonyssus* [Whitaker 1968]). *P. boylii* in Utah was more heavily infested with *E. circularis* and *A. fahrenheitsi* than were other *Peromyscus* species (Whitaker 1968). Other ectoparasites of *P. boylii* include lice (*Hoplopleura ferrisi* and *Polyplax auricularis* [Whitaker 1968]), and numerous species of fleas (*Aetheca wagneri*, *Atyphloceras echis*, *A. felix*, *A. multidentatus*, *A. nudatus*, *Catallagia decipiens*, *C. mathesoni*, *Catallagia* sp., *Corypsylla kohlsi*, *Epitedia stanfordi*, *Hoplopsyllus anomalus*, *Hystrichopsylla dippiei*, *H. gigas*, *H. occidentalis*, *Malariaeus sinomus*, *M. telchinus*, *Megathroglossus procus*, *Monopsyllus eumolpi*, *M. wagneri*, *Opisodasys keeni*, *O. nesiotus*, *Orchopeas howardi*, *O. leucopus*, *O. sexdentatus*, *Peromyscopsylla ebrighti*, *P. hemisphaerium*, *P. hesperomys*, *P. adelpha*, *Pleochaetis*

sibynus, *Rhadinopsylla sectilis*, and *Stenoponia ponera* [Whitaker 1968; see also Medina et al. 2006 and Davis et al. 2002]).

Several species of ticks and fleas carried by *P. boylii* are vectors for bacteria of human concern. In Oregon and California, infection rates of *P. boylii* with the tick-transmitted Lyme disease spirochete *Borrelia burgdorferi* range from about 4% ($n = 24$ [Burkot et al. 1999] and $n = 27$ [Vredevoe et al. 2004]) to 22.2% ($n = 14$ —Brown and Lane 1996). *P. boylii* in Colorado tested positive for antibodies to *Ehrlichia* that causes human granulocytic ehrlichiosis. *P. boylii* in the western United States can have plague (*Yersinia pestis* = *Pasturella*) or host plague-infested fleas (Whitaker 1968 after Allred 1952). *P. boylii* in Ventura County, California, hosts a high flea species diversity with low infestation rate, but 5 of 9 flea species are important in plague epidemiology (Davis et al. 2002).

Peromyscus boylii serves as a reservoir for hantavirus. In Arizona, antibody prevalence (minimum number infected divided by minimum number alive) varied from 13.3% ($n = 98$ —Kuenzi et al. 1999) to 20.2% ($n = 287$ —Abbott et al. 1999). The absolute number of antibody-positive *P. boylii* peaks during periods of high population density (Abbott et al. 1999). However, the proportion of the population of *P. boylii* that is antibody-positive peaks during low population densities (Abbott et al. 1999). Individuals of *P. boylii* that are positive for the hantavirus antibody are more frequently males, heavier, and older than antibody-negative individuals (Abbott et al. 1999). Individuals of *P. boylii* that are antibody-positive survive longer, and males that are antibody-positive survive longer than antibody-positive females (Abbott et al. 1999). The higher antibody prevalence in males may be due to territoriality or aggression toward other males during breeding, or longer survival of males, or both (Abbott et al. 1999). Individuals acquire hantavirus antibodies in all months except December, January, and March, with 2 transmission peaks occurring from April to June and from September to October that correspond to the breeding season (Abbott et al. 1999) or to high population density (Kuenzi et al. 1999). The longer residence of dominant, antibody-positive males in patchy, optimal habitat may be an important variable contributing to hantavirus infection and the persistence of a reliable reservoir during low population densities (Abbott et al. 1999). *P. boylii* also is a reservoir of hantavirus in Texas (Mantooth et al. 2001) and it hosts Limestone Canyon virus, another *Peromyscus*-borne hantavirus that may not cause disease in humans (Sanchez et al. 2001).

Interspecific interactions.—Ecological interactions of *Peromyscus boylii* with sympatric species have received little attention. However, examination of data from east-central Arizona suggests that microhabitat use by *Neotoma stephensi* and *P. maniculatus* is influenced by *P. boylii* (Holbrook 1979a). Removal of *P. boylii* from juniper-oak shrubland and juniper-grassland resulted in an expansion in

the types of microhabitats utilized, and an increase in arboreal activity, by both *N. stephensi* and *P. maniculatus*. Removal of *N. stephensi* from a pinyon–juniper woodland and a Manzanita–oak shrubland resulted in minimal changes in habitat use and a decreased use of manzanita, but no change in arboreal activity, activity level, or spatial distribution by *P. boylii*.

Peromyscus boylii is an important prey item for Mexican spotted owls (*Strix occidentalis lucida*—Block et al. 2005). Life span of free-living *P. boylii* in central Arizona averages 3–4 months (depending on hantavirus antibody presence) with a range from 1 to 26 months (Abbott et al. 1999).

GENETICS

The standard karyotype for the genus *Peromyscus* is that of *Peromyscus boylii glasselli*. The diploid number (2n) is 48 and the fundamental number (FN) is 52 (Committee for Standardization of Chromosomes of *Peromyscus* 1977). Karyotypes presented for *P. b. boylii* (Lee et al. 1972), *P. b. rowleyi* (Houseal et al. 1987; Lee et al. 1972; Schmidly 1973; Schmidly and Schroeter 1974), and *P. b. utahensis* (Lee et al. 1972) are identical to those presented for *P. boylii* by Hsu and Arrighi (1966, 1968) and to those of *P. b. glasselli* (Committee for Standardization of Chromosomes of *Peromyscus* 1977). *P. boylii* has 1 pair of large biarmed (chromosome 1), 2 pairs of small biarmed (chromosomes 22 and 23), and 20 pairs of small to large acrocentric (chromosomes 2–21) autosomes. The X chromosome is large and subtelocentric, whereas the Y chromosome is medium sized and metacentric. The karyotype of *P. boylii* is consistent with the primitive karyotype for *Peromyscus* (biarmed for pairs 1, 22, and 23, and all other autosomes acrocentric—Greenbaum and Baker 1978; Robbins and Baker 1981; Stangl and Baker 1984).

Polymorphisms have been reported for serum albumin (Avisé et al. 1974; Jensen and Rasmussen 1971; Rasmussen 1968), esterase (Rasmussen 1968; Rasmussen and Jensen 1971), and transferrin (Rasmussen and Koehn 1966). Animals from Arizona, New Mexico, Texas, California, and Mexico (Durango and Sonora) exhibited the following polymorphic loci (most common alleles shown): ALB-1⁹⁷, ALB-1¹⁰⁰, TRF-1¹¹³, and IDH-1¹¹⁰ (Avisé et al. 1974), with the mean percentage of polymorphic loci in these populations of *P. boylii* ranging from 0.05 to 1.0 and mean percentage of heterozygous loci per individual ranging from 0.08 to 3.0 (Avisé et al. 1974). *P. boylii* in Arizona and Mexico (Hidalgo, Aguascalientes, and Chihuahua) was monomorphic at 27 loci and polymorphic at 12 loci, with up to 4 alleles (Rennert and Kilpatrick 1986, 1987; Sullivan et al. 1991). *P. b. utahensis* from Utah and *P. b. rowleyi* from Oklahoma, New Mexico, Texas, and Mexico (Chihuahua and Durango) shared the following monomorphic loci: hemoglobin beta I and beta II, ES-1, LDH-3, LDH-1, and

TRF1, whereas ALB-1⁹⁵, ES-5¹⁰⁰, ES-7¹⁰⁰, GOT-1⁹⁵, and 6 PGD-1⁸⁵ were fixed in *P. b. utahensis* (Kilpatrick and Zimmerman 1975). Polymorphisms were found in *P. b. rowleyi* with up to 5 alleles at the ES-7 locus and 2 alleles at the ES-6 and ES-5 loci (Kilpatrick and Zimmerman 1975). Populations of *P. boylii* exhibited ranges of heterozygosity from 0.02 to 0.05 (Kilpatrick and Zimmerman 1975).

Sequences of the mitochondrial genome corresponding to the region of the D-loop and cytochrome *b* demonstrate a sister taxa status between *P. boylii* and *P. simulus* (Bradley et al. 2000; Castro-Campillo et al. 1999). Analysis of variation in 1,143 base pairs of the cytochrome-*b* gene (Tiemann-Boege et al. 2000) supports other DNA sequence analyses (Bradley et al. 2000; Castro-Campillo et al. 1999) with respect to relationships of *P. boylii* to *P. simulus* and *P. beatae*. Additionally, a close relationship of *P. stephani* and *P. madrensis* to the *P. boylii*–*P. simulus* sister relationship was revealed, with *P. beatae*–*P. levipes* forming a sister taxon relationship with the clade containing *P. boylii*, *P. simulus*, *P. stephani*, and *P. madrensis* (Tiemann-Boege et al. 2000). Based on cytochrome-*b* sequence data, mean genetic distances (Tamura–Nei) of *P. boylii* with other species in the *P. boylii* species group are *P. beata*, 8.6; *P. levipes*, 8.8; *P. madrensis*, 3.6; *P. simulus*, 2.7; *P. stephani*, 4.2; and *P. schmidlyi*, 7.9 (Bradley et al. 2004; Tiemann-Boege et al. 2000). Recognition of 4 subspecies of *P. boylii* is generally supported by cytochrome-*b* sequence analysis. However, northern and southern forms of *P. b. rowleyi* are apparent (Tiemann-Boege et al. 2000).

In an evolutionary analysis of zona pellucida glycoproteins ZP1 and ZP2 among species of *Peromyscus*, *P. boylii* was found to have relatively high rates of amino acid substitution in ZP2 (relative to nonreproductive nuclear proteins), and *P. boylii* from Culberson County, Texas, had relatively high rates of substitution in both ZP1 and ZP2 (Turner and Hoekstra 2006). High rates of substitution may have implications for reproductive isolation from sister species (Turner and Hoekstra 2006).

CONSERVATION

Peromyscus boylii does not have any special conservation status and is listed as a taxon of Least Concern in the Lower Risk category (LC/LR—International Union for Conservation of Nature and Natural Resources 2008).

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