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Perognathus parvus.

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Perognathus parvus (Peale, 1848)

Great Basin Pocket Mouse

Cricetodipus parvus Peale, 1848:53. Type locality "Oregon," probably near The Dalles, Wasco Co. (Hall, 1981; Osgood, 1900).

Perognathus parvus: Cassin, 1858:48. First use of current name combination.

Perognathus monticola Baird, 1858:422. Type locality "west of Rocky Mountains, St. Marys? [=St. Marys Mission, Stevensville, Montana]"; regarded by Osgood (1900) as having been obtained at The Dalles, Oregon.

Perognathus columbianus Merriam, 1894:263. Type locality "Pasco, Plains of Columbia [Franklin Co.], Washington (on east side of Columbia river, near mouth of Snake river)."

Abromys lordi Gray, 1868:202. Type locality "British Columbia."

P[erognathus]. mollipilosus Coues, 1875:296. Type locality "Fort Crook [Shasta Co.], California."

Perognathus olivaceus Merriam, 1889:15. Type locality "Kelton [near N end Great Salt Lake, Box Elder Co.], Utah."

Perognathus laingi Anderson, 1932:100. Type locality "Anarchist mountain, near Osoyoos-Bridesville summit, about 8 miles east of Osoyoos lake, at about 3,500 feet altitude, latitude 49°08′ north, longitude 119°32′ west [British Columbia]."

CONTEXT AND CONTENT. Order Rodentia, Family Heteromyidae, Subfamily Perognathinae. The subfamily Perognathinae contains two genera, *Chaetodipus* and *Perognathus*, with the latter containing nine species (Hafner and Hafner, 1983). Eleven subspecies of *Perognathus parvus* currently are recognized (Hall, 1981) as follows:

P. p. bullatus Durrant and Lee, 1956:183. Type locality "Ekker's Ranch, Robber's Roost, 25 miles [airline] [*sic*] east of Hanksville, 6,000 feet, Wayne County, Utah."

P. p. clarus Goldman, 1917:147. Type locality "Cumberland [Lincoln Co.], Wyoming."

P. p. columbianus Merriam, 1894:263, see above.

P. p. idahoensis Goldman, 1922:105. Type locality "Echo Crater, 20 miles southwest of Arco, Butte County, southern Idaho."

P. p. laingi Anderson, 1932:100, see above.

P. p. lordi (Gray, 1868:202), see above.

P. p. mollipilosus Coues, 1875:296, see above.

P. p. olivaceous Merriam, 1889:53, see above (*amoenus* Merriam, *magruderensis* Osgood, and *plerus* Goldman are synonyms).

P. p. parvus (Peale, 1848:53), see above (*monticola* Baird a synonym).

P. p. trumbullensis Benson, 1937:181. Type locality "Nixon Spring, 6,250 ft., Mt. Trumbull, Mohave County, Arizona."

P. p. yakimensis Broadbooks, 1954:96. Type locality "Washington, Yakima County, sixteen miles NW Naches, Rocky Flat (or Rocky Prairie), 3800 feet elevation."

Honacki et al. (1982) noted that two nominal species of *Perognathus* in California (*P. alticola* and *P. xanthonotus*) probably are subspecies of *P. parvus*.

DIAGNOSIS. Representatives of the genus *Perognathus* are distinguished by their soft pelage, absence of spines or bristles, somewhat hairy soles on hind feet, greatly developed mastoids that extend beyond the occipital plane, auditory bullae meeting or nearly so anteriorly, ascending branches of supraorbital slender and threadlike, supraoccipital without lateral indentations by mastoids, and breadth of interparietal less than breadth of interorbital (Hall, 1981; Osgood, 1900). The diagnostic characteristics of *P. parvus* include lobed antitragus, length of hind foot >20 mm, occipitonasal length >24 mm, ears not clothed with white hairs, tail dark above and neither crested nor conspicuously tufted, and presence of an olivaceous lateral line (Hall, 1981).

GENERAL CHARACTERS. *Perognathus parvus* (Fig. 1) is the largest member of the genus (Best, in press). Tail length is 110 to 120% of the length of the head and body (Blair et al., 1968). Hind legs are elongate but not to the extent observed in bipedal heteromyids such as *Dipodomys* and *Microdipodops*. Great Basin pocket mice, and other heteromyids, have external, fur-lined cheek pouches used to carry seeds and other food items to be cached. Grooved upper incisors in *P. parvus* are shared with other heteromyids except *Liomys* and *Heteromys* (McLaughlin, 1984).

Means and ranges (in parentheses) of measurements (in mm) for 18 *P. p. trumbullensis* from Mohave Co., Arizona (Hoffmeister, 1986) were: length of body, 84.2 (80 to 88); length of tail, 88.4 (77 to 95); length of hind foot, 23.2 (22 to 25); occipitonasal length, 26.9 (26.0 to 27.9); frontonasal length, 17.8 (17.0 to 18.6); nasal length, 10.3 (9.6 to 10.9); interorbital length, 6.2 (6.0 to 6.5); mastoid length, 14.3 (13.7 to 14.9); zygomatic breadth, 12.8 (12.3 to 13.6); length of mastoid bulla, 9.2 (8.7 to 9.5); alveolar length of maxillary toothrow, 3.9 (3.7 to 4.2); width of interparietal, 5.1 (4.6 to 5.5); length of interparietal, 3.4 (2.9 to 4.1); and distance between stylomastoid foramina, 11.3 (10.8 to 11.8). The ratio of length of tail to length of body was 104.9% in this sample.

Males are slightly larger than females; Best (in press) reported 10 of 19 external and cranial characters were significantly larger in males. Means and extremes (in parentheses) of measurements (in mm) for five male and four female *P. p. olivaceous*, respectively, from the east shore of the Great Salt Lake, Utah (Durrant, 1952) were: total length, 174 (160 to 181), 172 (160 to 190); length of tail, 91 (85 to 97), 88 (85 to 90); length of hind foot, 23 (22 to 24), 21 (19 to 22); length of ear, 8 (7 to 9), 7.5 (6 to 9). Means for 31 males and 19 females, respectively, from Washington, were as follows: total length, 169, 164; length of tail, 90, 86; length of hind foot, 22.6, 21.8; length of ear, 5, 5 (Dalquest, 1948). Means and ranges (in parentheses) of body mass (in g) for 10 male and 10 female *P. p. olivaceous* from Nevada (Hall, 1946) were: 25.4 (21.5 to 31.0) and 20.5 (16.5 to 28.5).

Coloration of pelage is variable within and among populations. Osgood (1900) characterized *P. parvus* as being dichromatic to some degree. He described in detail gray and buff phases, but noted that various intermediate color stages occur between these extremes. Hall (1981:531) succinctly described coloration as "upper parts approx. pinkish buff or ochraceous buff, thinly to heavily overlaid with blackish; underparts white to buffy"; the tail is distinctly bicolored. Pelage characters that vary geographically include color of the dorsum and belly, hue and intensity of the lateral line, and conspicuousness of the light auricular patches (Cowan and Guiguet, 1956; Iverson, 1967; Osgood, 1900).

The skull (Fig. 2) is large and slightly rounded in dorsal profile. Nasals are long, tympanic bullae inflated, interparietal pentagonal, and premaxillae extend posterior to nasals (Durrant, 1952).

DISTRIBUTION. Great Basin pocket mice occupy almost the entire Great Basin Region of western North America. The distribution of *P. parvus* extends from south-central British Columbia

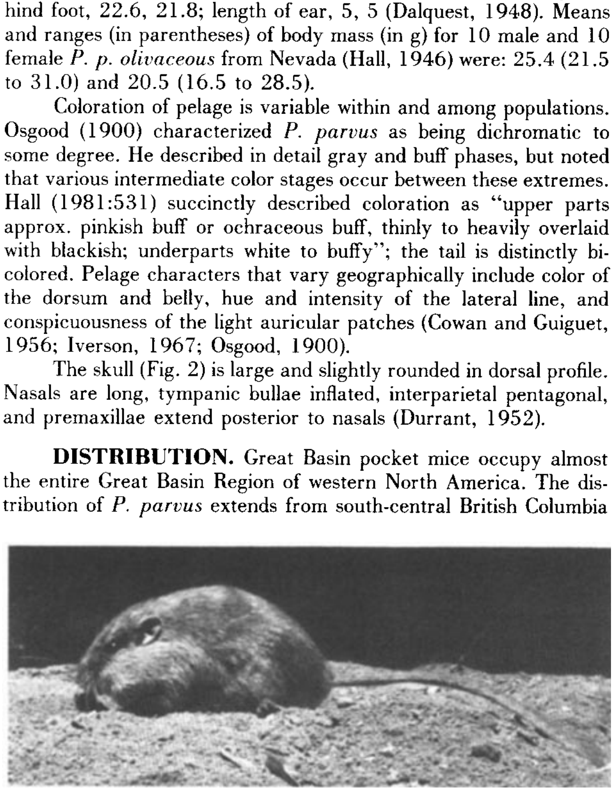

FIG. 1. Photograph of an adult female *Perognathus parvus* from 1 mi S, 3 mi W Terrebonne, Deschutes Co., Oregon.

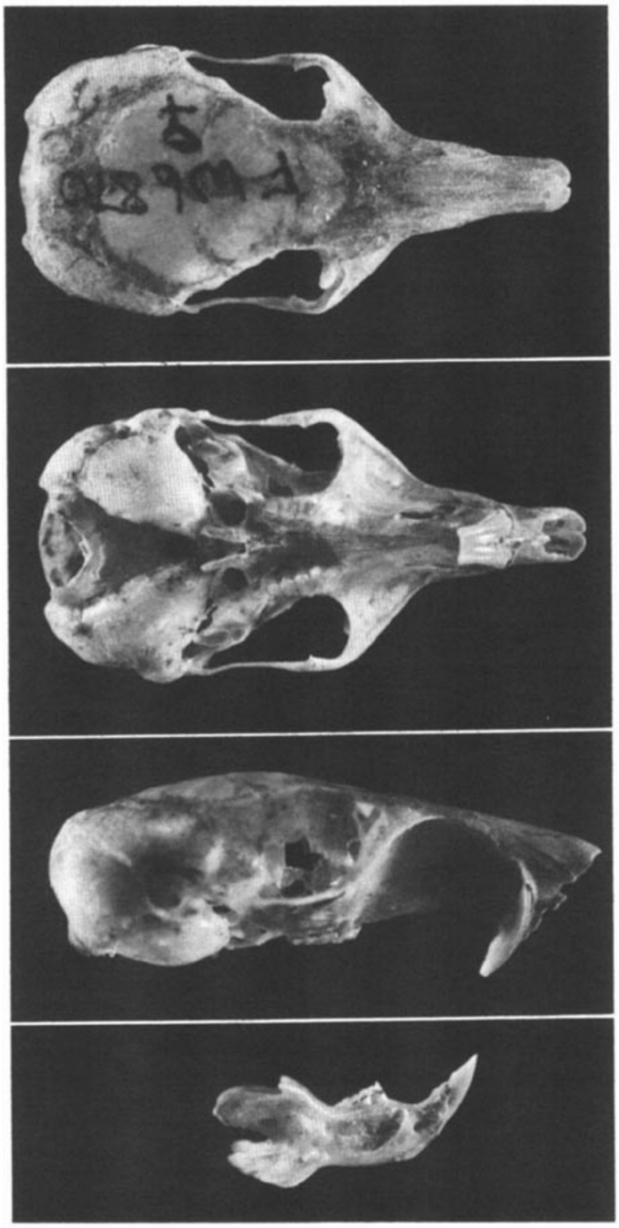

FIG. 2. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of an adult female *Perognathus parvus* (Oregon State Univ., Department of Fisheries and Wildlife mammal collection 6870) from 1½ mi N Fields, Harney Co., Oregon. Occipitonasal length is 26.3 mm.

southward through central and eastern Washington and Oregon, southern Idaho, southwesternmost Montana and Wyoming, most of Utah and Nevada, northern Arizona, and northeast and east-central California (Fig. 3). *P. parvus* is described as a species of the Upper Sonoran, Transition, and Lower Boreal life zones (Bailey, 1936; Dalquest, 1948; Grinnell, 1913, 1933; Ingles, 1965; Osgood, 1900).

FOSSIL RECORD. The first fossils of *Perognathus* are of Miocene age (Hoffmeister, 1986; Kurtén and Anderson, 1980; Savage and Russell, 1983; Wood, 1935); however, the fossil record of *P. parvus* extends only from the late Irvingtonian and Rancholabrean of the Pleistocene to the Recent (Kurtén and Anderson, 1980). *P. parvus* is presumed to be descended from *Perognathus maldei*, a fossil form of the late Pliocene (Kurtén and Anderson, 1980; Savage and Russell, 1983). Martin (1984) described *P. stevei* from deposits of Hemphillian age at McKay Reservoir, Oregon; he considered the new species similar to *P. maldei* and Recent *P. parvus*. *P.* cf. *parvus* is reported from Smith Creek Cave, White Pine Co., Nevada (Miller, 1979) and *P. parvus* is reported from the Wasden site, Bonneville Co. and Moonshiner Cave, Bingham Co., southern Idaho (Kurtén and Anderson, 1980); all of these sites are within the current distribution of the species. Guilday (1969) concluded that semidesert conditions apparently prevailed at the time of deposition at the Wasden site.

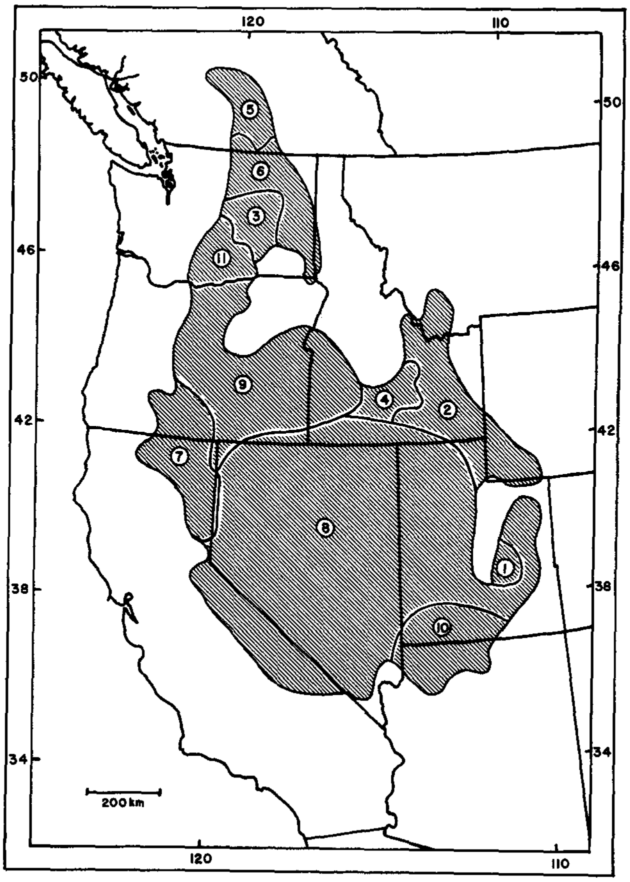

FIG. 3. Distribution of *Perognathus parvus*. Subspecies are: 1, *P. p. bullatus*; 2, *P. p. clarus*; 3, *P. p. columbianus*; 4, *P. p. idahoensis*; 5, *P. p. laingi*; 6, *P. p. lordi*; 7, *P. p. mollipilosus*; 8, *P. p. olivaceus*; 9, *P. p. parvus*; 10, *P. p. trumbullensis*; 11, *P. p. yakimensis*. Map modified from Hall (1981).

FORM AND FUNCTION. Many species of *Perognathus*, including *P. parvus*, possess a sebaceous glandular region on the underside of the tail centered about one-fourth to one-third the distance from the base (Quay, 1965). The glandular region may be 1 mm thick and constitute 20% of the diameter of the tail in some *Perognathus*; however, in *P. parvus*, the glandular region is relatively small. Quay (1965) suggested that development of the glandular region might be correlated to some degree with sex, age, and season, and possibly be of some taxonomic significance. He suspected that the localized concentration of sebaceous glands indicated a more specialized function than production of secretions for skin and hair conditioning, and he suggested that the "perineal drag" behavior in *Perognathus* (Eisenberg, 1963) actually might involve the sebaceous caudal glands.

The molars are tuberculate and rooted, and p4 is smaller than m3 (Osgood, 1900). The dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20.

The male reproductive system in *P. parvus*, as in other members of the genus *Perognathus*, exhibits extreme conservatism morphologically; a full complement of accessory reproductive glands is present (Hafner and Hafner, 1983). The baculum of *P. parvus*, like that of other *Perognathus*, has ". . . a relatively large, bulbous basal end that tapers rapidly into the slender shaft which turns up at a nearly right angle distally, and terminates in a point" (Burt, 1960: 40). The basal end is almost circular in cross section. Means and ranges (in parentheses) of length and height (in mm) at base for nine adults (presumably from Washington) were (Burt, 1960): 8.0

(7.5 to 8.4) and 0.9 (0.7 to 1.0), respectively; the baculum in *P. parvus* is the largest in the genus.

Although *Perognathus* was reported to have a single annual molt (Hall, 1946; Hall and Kelson, 1959; Osgood, 1900), Speth (1969) presented evidence that *P. parvus* in captivity has the potential for two molts annually. Duration of the winter molt (February–March) averaged 35 days (range, 15 to 63) and that of the summer molt (June–August) averaged 31 days (range, 11 to 90). In both adults and juveniles, new hair first appears on the dorsum immediately posterior to the ears; from that point the molt progresses posteriorly and ventrally, but another spot of new hair appears on the pate and rapidly becomes confluent with that on the dorsum (Speth, 1969:288, Fig. 1). Regions near the opening to the cheek pouches, the knee, and the base of the tail are last to molt. A molt may be complete, arrested at various stages, complete except for small spots, or complete except for scattered hairs. Pregnancy and lactation may interfere with completion of the molt (Speth, 1969).

Perognathus parvus and its congeners commonly enter torpor for various periods at all seasons; even in midsummer it is common to find that specimens caught in live traps are torpid. *P. parvus* maintained in captivity from September to March at 5°C and on a 12L:12D photoperiod with food available entered torpor spontaneously (Meehan, 1978). Initially, the bouts occurred daily, but gradually arousal and periods of euthermia became infrequent and bouts of torpor of 5 days became common. From this, Meehan (1978:5169) estimated that *P. parvus* remained in torpor for ". . . nearly 90% of the period of winter dormancy." Animals maintained at 6 and 19°C entered spontaneous torpor at about equal frequency during summer, but in autumn those maintained at 6°C became torpid significantly more frequently. At an ambient temperature (T_a) between −2 and 2°C, *P. parvus* can maintain a body temperature near 2°C at extremely low metabolic cost (MacMillen, 1983); through torpor animals are able to conserve sufficient energy to reduce food requirements between November and March from 300 to 50 g of seeds (Meehan, 1978). Meehan (1978) suggested that spontaneous torpor was initiated by low foraging success.

The ability of desert heteromyids, including *P. parvus*, to survive solely on a diet of dry seeds is well established (Schmidt-Nielsen et al., 1948*a*), although *P. parvus* consumes succulent forage and insects at least seasonally (Jameson, 1954; Kritzman, 1970). Desert heteromyids conserve water by excreting urine composed of approximately 22% electrolytes (human urine is about 6%), but do not have a physiological water store that can be drawn upon during unfavorable conditions (Schmidt-Nielsen et al., 1948*b*). However, during these periods, water balance is maintained by ingestion of preformed water contained in dry seeds and by that derived through metabolism (Schmidt-Nielsen et al., 1948*a*). *P. parvus* maintained at 5°C lost 1.39 ± 0.06 g of water through respiration and produced 1.39 g of metabolic water if carbohydrates were the source of all heat produced; however, at T_a of 30°C, 3.34 ± 0.24 g of water was lost through respiration but only 0.67 g of water was produced (Anderson, 1970). Guthrie (1973) found that euthermic *P. parvus* subjected to 0% humidity at T_a between 0 and 20°C maintained a positive water balance, but torpid animals did not. Rubin (1979) found that *P. parvus* could maintain a positive water balance over a wider range of temperatures than larger related species. At 29°C, total water lost equaled total water gained for *P. parvus* maintained solely on seeds containing approximately 10% water by weight (Rubin, 1979). Rubin (1979) suggested that because small species of granivores such as *P. parvus* can maintain a positive water balance at higher temperatures, they can feed earlier in the evening and avoid competition with larger granivores.

For *P. parvus* from southern Washington, the relationship (ax + b) between metabolic rate (ml O_2 g^{-1} h^{-1}) and T_a between 0 and 30°C was $11.5 - 0.24\ T_a$ for active mice, $8.6 - 0.24\ T_a$ for resting mice, $7.0 - 0.165\ T_a$ for mice in their nests, and $0.38 + 0.014\ T_a$ for torpid mice (Schreiber, 1978). For those from southern California, the relationship for T_a between −5 and 30°C was $6.115 + 0.149\ T_a$ for euthermic animals (Meehan, 1978). Oxygen consumption by euthermic individuals in nests at T_a about 3°C was almost 4 ml g^{-1} h^{-1}. Among torpid individuals at T_a above 0°C, oxygen consumption was independent of T_a, but below 0°C the metabolic rate increased; at −5°C, oxygen consumption was 1.5 ml g^{-1} h^{-1} (Meehan, 1978). Estimated daily energy requirements for maintenance were 9.87 kilojoules for males and 11.00 kilojoules for females in winter, and 29.12 and 27.41 kilojoules for the two sexes, respectively, in summer (Schreiber, 1978). Summer torpor reduced these requirements by about 3%; winter energy requirements were reduced 40 to 43% by torpor. Schreiber (1978) estimated that male *P. parvus* in southern Washington ingested 10,669 kilojoules/year; females ingested 10,301 kilojoules/year, requirements provided by 873 to 999 cheatgrass (*Bromus tectorum*) seeds/day in spring and summer, and about 775 seeds/day in fall and winter. Torpor reduces winter requirements to an average of about 400 seeds/day. *P. parvus* consumes 4 to 10% of its body mass/day and must cache 50 to 65 g of cheatgrass seeds to survive the winter (Schreiber, 1978). Thus, according to Schreiber (1978) the average annual production of cheatgrass seed in southern Washington will support about 80 *P. parvus*/ha. Coefficients of digestibility (digested portion of ingested food) for *P. parvus* fed rolled oats was 94.6 ± 0.18% for adults and 95.3 ± 0.35% for subadults; the coefficient of digestibility for subadults fed cheatgrass seed was 84.1 ± 1.2% (Schreiber, 1979*a*). Coefficients of digestibility for *P. parvus* are related to the proportion of the diet consisting of fiber (Withers, 1982). The average capacity of one cheek pouch for five *P. parvus* from east-central California with a mean body mass of 17.8 g was 0.93 ± 0.17 cm^3. Thus, both pouches combined are of sufficient volume, as in other heteromyids, to contain seeds equivalent to the daily energy requirement (Morton et al., 1980).

The nature of experimental diets (millet seed, soybeans, or bran cereal) affected amounts of food consumed, production of fecal material, assimilation of energy, production of urine, and osmotic concentration of urine, but not water content of feces. Captive *P. parvus* fed millet seeds and deprived of water were able to maintain their body mass, but those fed soybeans or bran cereal were not (Withers, 1982). When deprived of water, experimental animals fed soybeans and bran cereal consumed less food, produced less fecal material and almost no urine, and produced much more concentrated urine; however, those fed millet seed, consumed slightly more food, produced equal amounts of fecal material, and produced slightly less urine of lower osmotic concentration when deprived of water (Withers, 1982). Withers (1982) concluded that *P. parvus* and other desert rodents could not survive indefinitely on a diet that contained little preformed water if assimilation efficiency were less than 85%.

The median lethal dose at 30 days ($LD_{50\ 30}$ with confidence interval in parentheses) of gamma radiation for *P. parvus* was 856 (811–897) rad, considerably greater than for *Microtus oregoni*, but somewhat less than for *Peromyscus maniculatus* (O'Farrell, 1969). The estimated $LD_{50\ 30}$ suggests that *P. parvus* is considerably less resistant to effects of ionizing radiation than *P. formosus* (=*Chaetodipus formosus*) and *P. longimembris* (Gambino and Lindberg, 1964), although methods used to calculate dosages were not directly comparable. Survival of *P. parvus* exposed to radiation seems related to season; the effect of season may be related to increased stress from reproduction or reduced stress associated with hibernation (O'Farrell et al., 1972). Among free-living *P. parvus*, mortality from radiation and natural causes was not additive, thus was considered synergistic (O'Farrell et al., 1973). Changes in body mass of *P. parvus* exposed to radiation were variable; in general, those receiving dosages <900 rad initially gained weight even though some receiving only 600 rad died (O'Farrell, 1969). At death, mean body mass of groups of *P. parvus* exposed to different dosages ranged from 76.5 ± 4.6 to 84% of that at the time of exposure. Commencing about 7 days after exposure, cheek pouches of *P. parvus* receiving 700 to 1,600 rad everted for about 4 days suggesting that the radiation affected the tone of the muscles that operate them. Doses of 400 to 1,400 rad caused depilation ranging from ". . . slight slippage to total loss . . ." of hair within 7 days of exposure; extent of depilation seemed related directly to dosage (O'Farrell, 1969:163). Among survivors, new hair commenced to appear the second week but was white or gray instead of the normal olivaceous. Similar changes in color were not noted in *Microtus oregoni*, *M. miurus*, and *Peromyscus maniculatus*.

ONTOGENY AND REPRODUCTION. In a 6-year study conducted in Washington, the first evidence of estrus in *P. parvus* occurred in April each year, but the first pregnancy was noted during April in 2 years and during May in 4 years (O'Farrell et al., 1975). In the same study, lactation was detected in May each year but was last observed during July in 1 year, September in 3 years, and October in 1 year; trapping was not conducted later than May during 1 year. In Idaho in 1967, pregnancy was evident in live specimens handled between 26 May and 2 August; lactation was detected between 27 June and cessation of trapping on 8 September (Speth et al., 1968). Above 1,200 m in British Columbia, first pregnancies in *P. parvus* were noted by the end of the third week of May, but below 1,200 m not until the end of the first week of June; no pregnancies were detected at high elevations after the first week of August, but occurred until near the end of August at low elevations (Iverson, 1967). Lactation extended from early June at both elevations to early August at high elevations and late August at low elevations (Iverson, 1967). Kritzman (1970) reported similar findings for *P. parvus* in Washington.

Among males in Washington, testes became scrotal during February in one of 5 years and in March in the other 4 years; no animal with scrotal testes was captured after September during 3 years, August 1 year, and July 1 year (O'Farrell et al., 1975). Kenagy and Barnes (1984) reported that testes were about 67% of maximal mass when males emerged from torpor in spring but seminal vesicles were undeveloped. In Idaho, male *P. parvus* had scrotal testes when trapping commenced on 21 May; six of 29 males maintained scrotal testes throughout the summer (Speth et al., 1968). Iverson (1967) found that some adult male *P. parvus* at both low and high elevations in British Columbia were reproductively active when trapping commenced in April. The proportion of males with scrotal testes began to decline in June and reproductive activity ceased in August, about 2 weeks later at low-elevation sites than at high-elevation sites. Kritzman (1970) reported a similar relationship between cessation of reproductive activity and elevation in Washington.

In the laboratory, testes and seminal vesicles of males captured in spring and exposed to 16L:8D for 50 days were significantly larger than those exposed to 8L:16D; seminal vesicles of the latter animals were ". . . essentially inactive despite the presence of spermatogenic testes . . ." (Kenagy and Barnes, 1984:639). Testis development was initiated within 60 days in specimens captured when reproductively quiescent and subjected to either long or short photoperiods, or to continuous light or continuous darkness. In autumn, wild individuals, and those returned to the laboratory and exposed to 8L:16D, had undeveloped testes and seminal vesicles, whereas these organs increased in size and spermatogenesis usually commenced in animals exposed to 16L:8D (Kenagy and Barnes, 1984). From these and additional experiments, Kenagy and Barnes (1984: 642) concluded that reproduction in male *P. parvus* could be ". . . characterized as 'photoperiodic,' with an endogenous circadian rhythm of photosensitivity as its basis, and with an additional component of crude endogenous programming associated with recrudescence of gonads during winter," and was controlled ". . . by interactions between seasonally dependent responsiveness to the environment and spontaneous (endogenous) gonadal growth."

Twenty of 24 free-living males subjected to dosages of ionizing radiation ranging from 500 to 800 rad at the end of the breeding season in 1967 had scrotal testes during breeding seasons in 1968 and 1969 (O'Farrell et al., 1972); the animals were presumed to be fertile. However, none of 29 females subjected to the same treatment exhibited swollen vulvas or other evidence of reproduction during breeding seasons in 1968 to 1970 (O'Farrell et al., 1972).

Most authorities reported that adult *P. parvus* have one or two litters annually (Cowan and Guiguet, 1956; Dalquest, 1948; Duke, 1957; Larrison, 1970; O'Farrell et al., 1975; Speth et al., 1968), but Iverson (1967) found a sufficient number of females produced three litters to raise the mean to 2.06 litters annually on low-elevation study areas during 1964–1965 in British Columbia. During dry years, only one litter may be produced and some females may produce none (O'Farrell et al., 1975; Speth et al., 1968). For example, in Washington, estimates of mean number of litters produced annually were 0.3 (n = 44, with 30 not producing a litter and none producing more than one litter) during 1968 when precipitation was exceptionally low, 2.0 (n = 18, with all producing at least one litter and two individuals producing three) in 1969 when precipitation was considerably above average, and 1.1 (n = 70, with all but one having at least one litter and eight producing two) in 1970 when precipitation was a little above average (O'Farrell et al., 1975). Mean number of litters produced anually, thus the fecundity of the species, is correlated closely with precipitation and the resulting production of winter annuals. If precipitation is adequate, some juveniles born early in the breeding season may produce a litter in August (Iverson, 1967; O'Farrell et al., 1975; Speth et al., 1968).

Scheffer (1938) concluded from evidence alluded to but not presented that the length of the gestation period was between 21 and 28 days. Iverson (1967) attributed an estimate of 21 to 25 days for the gestation period of *P. parvus* to a personal communication from J. F. Eisenberg who reported a gestation period in a congener (*P. flavus*) of 26 days or less (Eisenberg and Isaac, 1963).

Reported litter sizes, based on counts of embryos, range from two (Scheffer, 1938; Speth et al., 1968) to eight (Dice, 1919; Hall, 1946; Scheffer, 1930, 1938) in *P. parvus.* Mean litter size, also based on counts of embryos was 5.0 (n = 3) for *P. parvus* from high elevations and 4.9 (n = 8) for those from low elevations in British Columbia (Iverson, 1967). For a population at Lind, Washington, mean litter size was 5.4 (n = 18) in 1921, 5.0 (n= 77) in 1923, and 5.3 (n = 37) in 1924, with an overall mean of 5.1 (Scheffer, 1938). Scheffer (1938) reported an overall mean litter size slightly higher (5.17) than that calculated from data he presented. Also in Washington, O'Farrell et al. (1975) calculated a mean litter size of 3.7 based on three litters born in traps. In Idaho, mean litter size was 4.7 (n = 3) in wild-bred females producing young in the laboratory (Speth et al., 1968). Hall (1946) reported a mean litter size of 5.5 (n = 33) for the species in Nevada. Iverson (1967) reported mean litter sizes based on counts of embryos slightly larger than those based on counts of pigmented sites of implantation, but differences were not significant. There is no postpartum estrus in *P. parvus*; pigmented sites of implantation reportedly persist about 3 weeks (Iverson, 1967).

Neonates born in captivity that survived and continued to gain weight during the first week of life weighed 2.2 g at 3 days postpartum (Speth et al., 1968). Seemingly, no additional description of the development of young *P. parvus* is available.

ECOLOGY. *Perognathus parvus* is a species of arid and semiarid habitats (Bailey, 1936; Davis, 1939). Benson (1937) described it as a Great Basin species, living on more or less sandy ground where sagebrush (*Artemisia tridentata*) is the dominant plant. *P. parvus* generally occurs in desert and grassland habitats and is excluded from heavily forested habitats on mountain ranges therein. In eastern Washington, *P. parvus* is common in sandy areas dotted with shrubs, but occasionally is found in dry, grassy sites (Dalquest, 1948). It also may be abundant locally in rocky areas where it can be trapped high on talus slides, many meters from the nearest soil (Dalquest, 1948). In eastern California, Oregon, and Washington, *P. parvus* inhabits "slopes and flats of the Sagebrush, Scrub, and Pinyon-Juniper Woodland, saltbrush, and greasewood" (Ingles, 1965:221). O'Farrell (1975*b*) described the habitat of *P. parvus* in south-central Washington as shrub-steppe associated with light-textured soils. In eastern Washington and northern Idaho, Rickard (1960) captured *P. parvus* only in semidesert and grassland habitats (*Artemisia rigida/Poa*, *A. tridentata/Agropyron*, and *Agropyron/Poa* associations); the apparent absence of *P. parvus* from *Festuca*-dominated grasslands was attributed to heavy-textured soils that inhibit burrowing by pocket mice. Feldhamer (1979) found *P. parvus* strongly influenced by edaphic factors; presence of the species was correlated positively with percent sand and negatively with percent clay. *P. parvus* also was restricted to communities dominated by sagebrush and greasewood (*Sarcobatus vermiculatus*), and was absent as residents from grassland and marsh habitats (Feldhamer, 1979). O'Farrell (1975*a*) found *P. parvus* more abundant in lower elevation habitats dominated by annuals than in higher elevation habitats dominated by perennials. Deacon et al. (1964) reported taking *P. parvus* infrequently in juniper-piñon (*Juniperus utahensis-Pinus monophylla*) communities at elevations as high as 2,530 m in southern Nevada. Linsdale (1938) took *P. parvus* adjacent to creeks, on wet ground, and in *Microtus* runways, and suggested that the species is not restricted entirely to arid or semiarid habitats.

On the basis of frequency of capture in various habitats, Feldhamer (1979) caught more *P. parvus* than expected at sites with >40% ground cover. Gano and Rickard (1982) found the species 3 times more abundant on unburned than on burned study plots where fire had killed bitterbrush (*Purshia tridentata*) and sagebrush.

The diet of Great Basin pocket mice reportedly consists ". . . mainly of seeds of a great variety of plants, including grasses, little wild beans, borages, sunflowers, and other composite plants, pigweeds, nettles, docks, *Solanum* seeds, and even wild plants of the mustard family" (Bailey, 1936:247). Cheek pouches of one specimen from Ontario, Oregon, contained 960 seeds of *Solanum* and three of *Amaranthus* (Bailey, 1936). Seeds of introduced plants such as Russian thistle (*Salsola iberica*), wild mustard (*Sisymbrium altissimum*), and pigweed (*Amaranthus* and *Chenopodium*) also are eaten (Scheffer, 1938). In southern Washington, grass seeds (principally *Bromus*, *Agropyron*, and *Festuca*) composed about 88% of the contents of cheek pouches (Kritzman, 1974). Near Mt. Shasta, California, *P. parvus* consumed seeds of snowbush (*Ceanothus velutinus*) more commonly than those of other species (Smith, 1942).

In spring, before grass seeds ripen, insects are incorporated into the diet of *P. parvus* (Kritzman, 1974; O'Farrell et al., 1975). In a rocky sagebrush habitat in California, stomachs of 14 of 18 *P. parvus* collected in April contained remains of insects; stomachs of 11 contained only insect remains, but, although nine *P. parvus* had seeds in their pouches, only two carried insects (Jameson, 1954). In British Columbia, stomach contents of *P. parvus* in lowland populations were composed of about 50% seeds, 25% vegetative material, and 25% animal material, whereas in upland populations the three items composed about 40, 40, and 20%, respectively (Iverson, 1967). Vegetative and animal materials usually are not found in cheek pouches or caches (Iverson, 1967), but Kritzman (1970) reported the occurrence of some green material and insect larvae in cheek pouches of *P. parvus* in early spring. These findings suggest that examination of materials in cheek pouches may not always provide a reliable depiction of the diet of *P. parvus* and that the species is more opportunistic and generalized in its feeding than the appellation "desert granivore" implies.

Numbers of *P. parvus* exhibit a strong positive correlation with precipitation falling between October and April, likely because of the influence of precipitation on seed resources (Dunigan et al., 1980; Hedlund and Rickard, 1981; O'Farrell et al., 1975). Estimates of density for populations of *P. parvus* include an annual average of 28.5/ha (peak 42/ha) in south-central Washington (Hedlund and Rogers, 1980) and 82.3/ha in the Yakima Valley, Washington (Gray, 1943), the latter approximating the maximum number that can be supported by an average annual seed crop (Schreiber, 1978). O'Farrell et al. (1975) estimated sustained densities in excess of 80/ha during years that precipitation was above average.

Perognathus parvus frequently is the numerically dominant species within small mammal communities in the Great Basin, especially in the northern portion of its range where it often composes more than 90% of the individuals collected (O'Farrell et al., 1975; Rogers and Hedlund, 1980; Small and Verts, 1983; Verts and Carraway, 1986). Because of its smaller size and periodic bouts of torpor, *P. parvus* expends only one-fourth to one-third as much energy as *Peromyscus maniculatus* and *Onychomys leucogaster* (Schreiber, 1979*b*). Nevertheless, at the community level, because of its abundance, *P. parvus* is the prime energy mover; the annual contribution of *P. parvus* to community energy exchange is nearly 4 times that of *Peromyscus maniculatus*, 11 times that of *O. leucogaster*, and 17 times that of *Reithrodontomys megalotis* (Schreiber, 1979*b*). However, Schreiber (1979*b*) believed that *P. parvus*, even at high densities, did not affect its primary food resource (cheatgrass) significantly (Schreiber, 1978).

Perognathus parvus is captured most frequently in association with *Peromyscus maniculatus*, *Onychomys leucogaster*, and *Reithrodontomys megalotis*, and less frequently with *Tamias minimus*, *Spermophilus townsendii*, *Ammospermophilus leucurus*, *Thomomys talpoides*, *Dipodomys ordii*, *D. microps*, *Microdipodops megacephalus*, *Peromyscus truei*, *Neotoma cinerea*, *Microtus montanus*, *M. longicaudus*, *Lemmiscus* (=*Lagurus*) *curtatus*, and *Mustela frenata* (Feldhamer, 1979; Kritzman, 1974; O'Farrell, 1975*a*, 1975*b*; O'Farrell and Clark, 1986; Rickard, 1960; Scheffer, 1938; Schreiber, 1979*b*). *Perognathus parvus* and *Peromyscus maniculatus* are the most abundant and ecologically widespread small mammals in sagebrush communities in the Great Basin (Kritzman, 1974; O'Farrell 1975*a*, 1975*b*; O'Farrell et al., 1975), although in sagebrush-shadscale (*Atriplex*) habitats in northeastern Nevada *P. parvus* and *D. microps* were the predominant small mammals; *Peromyscus maniculatus* and *A. leucurus* generally were in a secondary role (O'Farrell and Clark, 1986).

Studies of interspecific competition involving *P. parvus* have focused on its relationship with *Peromyscus maniculatus* (Ambrose and Meehan, 1977; Kritzman, 1970, 1974; O'Farrell, 1975*a*; O'Farrell et al., 1975). Competition between *P. parvus* and *Peromyscus maniculatus* probably is not intense owing, in part, to complementary local distributions attributable to independent responses to critical environmental factors. *P. parvus* is more abundant in hotter, drier lowland sites, whereas *Peromyscus maniculatus* occurs in greater numbers in more mesic, higher elevation sites (Kritzman, 1974; O'Farrell, 1975*a*). The greatest dietary overlap between these species occurs in spring when both feed on insects (Kritzman, 1974). Landeer et al. (1979) found a negative relationship between densities of populations of *P. parvus* and ants (Formicidae), and attributed it to less vegetative cover where density of ant populations was high rather than to interspecific competition for seeds. They further suggested that competition for seeds between ants and rodents may not be as intense in cold deserts of the Great Basin as in the hot Sonoran desert where such competition has been documented (Brown and Davidson, 1977).

Ectoparasites of *P. parvus* include two fleas, *Meringus shannoni* and *Monopsyllus wagneri* (O'Farrell, 1975*b*), eight species of mites, *Androlaelaps fahrenholzi*, *Ischyropoda armatus*, *Haemogamasus onychomydis*, *Kleemania* sp., *Proctylaelaps* sp., *Bakerdania* sp., *Geomylichus* sp. (Maser and Whitaker, 1980), and *Geomylidus perognathi* (Fain and Whitaker, 1980), and one tick, *Ixodes kingi* (Chamberlin, 1937). Endoparasites include stomach nematodes (*Protospirura* sp. and *Rictularia* sp.), a pinworm (*Syphacia* sp.), and an unidentified tapeworm (O'Farrell, 1975*b*).

Predators of *P. parvus* include rattlesnakes (*Crotalus* sp.), burrowing and short-eared owls (*Athene cunicularia* and *Asio flammeus*), coyotes (*Canis latrans*), weasels (*Mustela frenata* and *M. erminea*), skunks (*Mephitis mephitis*), badgers (*Taxidea taxus*), foxes (*Vulpes vulpes*, *V. macrotis*, and *Urocyon cinereoargenteus*; Banfield, 1974; Scheffer, 1938). Scheffer (1938) indicated that northern grasshopper mice (*Onychomys leucogaster*), and deer mice (*Peromyscus maniculatus*) preyed on *P. parvus*. Where dry-land farming is practiced and numbers of these species are low, Great Basin pocket mice may become a nuisance by consuming newly planted or sprouted seed and ripening grain, and by contaminating fields sown to one variety of grain with caches of seed gleaned elsewhere (Scheffer, 1938).

BEHAVIOR. Great Basin pocket mice are semifossorial granivores that limit ". . . their surface activities to the essentials of gathering sufficient food caches to sustain themselves, and breeding to sustain the species" (O'Farrell et al., 1975:27). On the surface, they run about ". . . on all fours like other mice . . ." making tracks with hind feet in front of those made by the forefeet (Bailey, 1936: 246). *P. parvus* uses its forefeet to fill rapidly its pouches with seeds that are transported to larders within the burrow where they are expressed from the pockets by use of the forefeet. Johnson and Jorgensen (1981) found that *P. parvus* ranked third among six heteromyid and two cricetine rodents in its ability to detect buried caches of 100 seeds of Indian rice grass (*Oryzopsis hymenoides*). These mice found 42.5% of caches buried 0.6 cm and 17.5% buried 1.3 cm beneath the surface of the soil; when soil moisture increased from 0.0092 to 0.280 g/g of soil, Great Basin pocket mice were able to find more caches.

In Washington, *P. parvus* constructs burrows slightly less than 25 mm in diameter that lead to globular nest cavities ". . . about the size of a baseball . . ." 13 to 30 cm below the surface (Scheffer, 1938:9). Nests contained ". . . finely broken weed twigs, perianths of Russian thistles, and seed husks or bits of dried grass" (Scheffer, 1938:9). Permanent burrows typically extend to a maximum depth of 1 m, have one or more storage chambers, a nest cavity, and several entrances (Bailey, 1936; Iverson, 1967), whereas "escape" burrows are simple, shallow (20 to 30 cm), lack nests and food caches, and have at least two entrances (Iverson, 1967). Dalquest (1948) described placement of burrows as typically at bases of shrubs whose tough roots provide physical protection, but Kritzman (1970: 42) considered *P. parvus* to choose ". . . with equal frequency, . . . exposed ground, places sparsely covered by plants . . . , or ground fairly effectively concealed by . . . shrubs" for burrowing where soils were sandy. Spoil mounds from burrow construction are miniatures of those constructed by pocket gophers (Geomyidae), even to the burrow opening commonly being plugged with loose earth (Scheffer, 1938). Secondary entrances may be left open (Bailey, 1936).

Great Basin pocket mice usually are active only during the warmer 8 or 9 months of the year, but there is considerable variation among individuals (Scheffer, 1938). In Washington, the mean date of vernal emergence from torpor by adults ranged from about the fourth week in March to the fourth week in April for males and from the third week in April to the first week in May for females during 4 years. Yearling animals emerged earlier than older adults. Emergence may be cued by soil temperature (O'Farrell et al., 1975). The mean duration of activity for adults ranged from about 60 to 90 days among years, but seemingly was not related to sex. O'Farrell et al. (1975:11) reported that Great Basin pocket mice "... were not trappable for 1 (1969–70) to 4 (1968–69) mo during midwinter, usually between November and February." However, they indicated subsequently (p. 13) that males "... dominated the trapping population between January and March."

During the active season, *P. parvus* is largely nocturnal or crepuscular although occasionally individuals may be seen abroad during daylight hours (Scheffer, 1938). Within an hour after sunset, traps are quickly filled with animals and, if released, the animals are recaptured repeatedly until near dawn (Scheffer, 1938). Moonlight seems to have a strong negative effect on the susceptibility of *P. parvus* to capture (R. J. Kline, per. comm.). Also, activity is reduced during inclement weather (Scheffer, 1938). The species is noted for its ease of capture; O'Farrell et al. (1975) recaptured 74% of the 1,855 *P. parvus* thought to have been born on their study areas. However, populations are believed to contain a component that is not trappable until the highly trappable component is removed (Small and Verts, 1983; Verts and Carraway, 1986).

Scheffer (1938:4) considered *P. parvus* to have a "milder" disposition than other groups of mice with which it is associated; he indicated that an individual of the species could be handled "... without danger of being bitten if careful not to grasp it tightly." Experience of one of us (BJV) and Broadbooks (1961) in handling and marking members of the species did not corroborate the purported docility of the species. After being handled, these pocket mice sandbathe vigorously (Scheffer, 1938). Kritzman (1970) reported that *P. parvus* formed "wallows" by sandbathing repeatedly in the same spot; she found wallows where ground cover was sparse.

In British Columbia, areas of home ranges computed by the boundary-strip method for 30 male and 17 female *P. parvus* captured five or more times averaged 894 and 656 m^2, respectively (Iverson, 1967). In Washington, areas of circular (radius = 2.45σ) and elliptical home ranges were 1,560 to 4,005 m^2 for males and 508 to 2,301 m^2 for females (O'Farrell et al., 1975). Broadbooks (1961) reported the mean and extremes (in parentheses) of the greatest diameters of home ranges of five adult males captured four to 10 times in northern Oregon as 148 m (60 to 297 m). Also, in Oregon, Feldhamer (1979) reported that the mean home-range area calculated by the standard-diameter method based on 2σ was 288.4 m^2 for males and 277.7 m^2 for females in greasewood habitats, and 336.9 and 267.2 m^2 for the two sexes, respectively, in sagebrush habitats. Although home-range size within studies varied with year, sex, age, population density, resource availability, and habitat (Feldhamer, 1979; Iverson, 1967; O'Farrell et al., 1975), differences in methods of calculating areas of home range prevent comparison between regions.

In samples of 16 of each sex, mean distances that centers of home ranges shifted between successive years were 16 ± 3 m (range, 2 to 43) for males and 6 ± 0.7 m (range, 1 to 10) for females (O'Farrell et al., 1975). This, combined with the ability of the species to home, was interpreted to indicate that *P. parvus* spatially partitioned occupied areas. However, Iverson (1967:52) considered the degree of overlap of home ranges of *P. parvus* to be greater "... than would be expected if spacing mechanisms were functioning." He also indicated (p. 56) that centers of home ranges were distributed randomly indicating that intraspecific interactions had "... no effect on the choice of burrow sites or on the location or configuration of the home range of another." Such is not in keeping with the agonistic intraspecific social patterns commonly attributed to *P. parvus* (Ambrose and Meehan, 1977; Kritzman, 1974; Scheffer, 1938) or with removal-induced changes in distribution of captures on a grid (Verts and Carraway, 1986).

Although Iverson (1967) suggested that animals did not seem to expand their home ranges when adjacent animals were removed, Small and Verts (1983) concluded that the rapid replacement of animals removed from a 1.8-ha grid was by immigrants from nearby areas. However, based on a similar study in which potential immigrants were marked, Verts and Carraway (1986) concluded that the increase in numbers of unmarked individuals caught after removal was not caused by an influx of animals from surrounding areas. O'Farrell et al. (1975) considered dispersers to represent only a small proportion of the total population; dispersers were biased slightly in favor of males.

None of four males had homed within 3 days after being displaced 0.82 km, but one of six males had homed by 3 days after being displaced 0.41 km. However, the individual that homed failed to home again when displaced 0.41 km in nearly the opposite direction (Broadbooks, 1961). Three *P. parvus* that escaped during handling were recaptured "... in their original home ranges within 2 wk of their escape" (O'Farrell et al., 1975:20).

Great Basin pocket mice are not considered social animals, as they invariably occupy separate nests in the wild. When caged together, they initially engage in vigorous sparring in an erect position, but later live together in a more or less amicable relationship (Scheffer, 1938). One of a pair of males caged together for several months (by BJV) kept the other animal completely shorn of hair; individual hairs, when cut, were stuck by one end to the adhesive surface of a piece of masking tape covering part of the hardware-cloth door to the cage.

Although *P. parvus* may develop a degree of tolerance for conspecifics, such indifference is not exhibited toward congeners (Blaustein and Risser, 1974) or other mice (Ambrose and Meehan, 1977; Blaustein, 1972; Huey, 1959; Kritzman, 1974). The greatest activity of a female *P. parvus* and a male *Microdipodops megacephalus* housed in the same cage, but on opposite sides of a hardware-cloth partition, was kicking sand at each other (Huey, 1959). In a paired encounter between members of these species, *P. parvus* attacked and was clearly dominant over *M. megacephalus*, but the combatants did not kick sand at each other (Blaustein, 1972). In 15 paired encounters with the smaller *P. longimembris*, *P. parvus* initiated attacks and was dominant in 13 instances (Blaustein and Risser, 1974). Blaustein and Risser (1974) believed that the agonistic behavior of *P. parvus* toward *P. longimembris* might be responsible for the two species being contiguously allopatric in regions where both occur (Hall, 1946). In paired encounters with *Peromyscus maniculatus*, *P. parvus* initiated attacks and *Peromyscus maniculatus* typically avoided *P. parvus* by moving to maintain maximum distance between the two individuals. *P. parvus* was dominant over *Peromyscus maniculatus* in 11 of 12 trials (Ambrose and Meehan, 1977), contrary to the conclusions regarding interspecific behavior of the two species based on field observations (Kritzman, 1974; O'Farrell et al., 1975). The vocal repertoire of *P. parvus* seems limited to a "*que, que, que,*" uttered as a faint whimper or a whine when handled too roughly or as a shrill squeal during agonistic interactions with conspecifics (Bailey, 1936).

GENETICS. Karyotypes of *P. parvus* have a diploid number (2N) of 54, but the number of autosomal arms (FN) ranges from 70 to 104 among various populations (Williams, 1978). In *P. p. columbianus* from east-central Washington all autosomes are biarmed; the X chromosome is a large submetacentric, the Y a small submetacentric. *P. p. clarus* in northeastern Utah has an autosomal complement of 12 biarmed and 14 uniarmed chromosomes; the X is a large subtelocentric, the Y a small acrocentric. *P. p. olivaceus* and *P. p. mollipilosus* from California have 11 biarmed and 15 uniarmed chromosomes; the sex chromosomes have the same morphology as those of *P. p. clarus*. A karyotype of *P. p. trumbullensis* from Arizona had 8 biarmed and 18 uniarmed autosomes and sex chromosomes similar to those of *P. p. clarus*, *P. p. mollipilosus*, and *P. p. olivaceus*. Williams (1978:606) considered the karyotype of the hypothetical ancestral *Perognathus* to be 2N = 56, FN = 54, and that *Perognathus* evolved by "... non-Robertsonian changes in the number of autosomal arms, either by pericentric inversions or arm additions," whereas *Chaetodipus* "... evolved primarily by changes in 2N, presumably by Robertsonian changes and tandem fusions ...." Further, he (p. 607) considered the karyotype of *P. parvus* to have diverged from that of *P. flavus* and *P. longimembris* "... by a single 2N reducing event (either a centric fusion in a common ancestral karyotype of 2N = 56, FN = 70, or a tandem fusion from a karyotype of 2N = 56, FN = 72)."

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