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Peromyscus leucopus.

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Peromyscus leucopus (Rafinesque, 1818)

White-footed Mouse

Musculus leucopus Rafinesque, 1818:446. Type locality pine barrens of Kentucky. Apparently restricted by Osgood (1909: 115–116) to the mouth of the Ohio River.

Peromyscus leucopus Thomas, 1895:192; first use of current name combination.

Cricetus myoides Gapper, 1830:204. Type locality between York and Lake Simcoe, Ontario, Canada.

Arvicola emmonsi DeKay, *in* Emmons, 1840:61. Type locality Massachusetts.

Peromyscus arboreus Gloger, 1841:95. Type locality unknown.

Mus michiganensis Audubon and Bachman, 1842:304. Type locality Erie Co., Michigan (=Ohio).

Hesperomys campestris Le Conte, 1853:413. Type locality New Jersey.

Hesperomys texana Woodhouse, 1853:242. Type locality vicinity of Mason, Mason Co., Texas.

Vesperimus mearnsi J. A. Allen, 1891*a*:300. Type locality Brownsville, Cameron Co., Texas.

Hesperomys affinis J. A. Allen, 1891*b*:195. Type locality Barrio, Oaxaca, Mexico.

Peromyscus canus Mearns, 1896:445. Type locality Fort Clark, Rinney Co., Texas.

Peromyscus tornillo Mearns 1896:445. Type locality Rio Grande, 6 mi above El Paso, El Paso Co., Texas.

Peromyscus musculoides Merriam, 1898:124. Type locality Cuicatlan, Oaxaca, Mexico.

Peromyscus cozumelae Merriam, 1901:103. Type locality Isla Cozumel, Yucatan, Mexico.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae (Cricetidae according to some authors), Subfamily Cricetinae, Genus and Subgenus *Peromyscus*. Member of the *P. leucopus* species group. Hall (1981) recognized 17 subspecies, as follows:

P. l. affinis (J. A. Allen, 1891*b*), see above (*musculoides* Merriam a synonym).

P. l. ammodytes Bangs, 1905. Type locality Monomoy Island, Barnstable Co., Massachusetts.

P. l. aridulus Osgood, 1909. Type locality Fort Custer, Big Horn Co., Montana.

P. l. arizonae (J. A. Allen, 1894). Type locality Fairbank, Cochise Co., Arizona.

P. l. castaneus Osgood, 1904. Type locality Yohaltun, Campeche, Mexico.

P. l. caudatus Smith, 1939. Type locality Wolfville, Kings Co., Nova Scotia, Canada.

P. l. cozumelae Merriam, 1901, see above.

P. l. easti Paradiso, 1960. Type locality 6.8 mi SE Pungo, Princess Anne Co., Virginia.

P. l. fusus Bangs, 1905. Type locality West Tisbury, Martha's Vineyard, Dukes Co., Massachusetts.

P. l. incensus Goldman, 1942. Type locality Metlaltoyuca, 800 ft, Puebla, Mexico.

P. l. lachiguiriensis Goodwin, 1956. Type locality San Jose Lachiguiri, about 4,000 ft, Oaxaca, Mexico.

P. l. leucopus (Rafinesque, 1818), see above (*brevicaudus* Davis a synonym).

P. l. mesomelas Osgood, 1904. Type locality Orizaba, Veracruz, Mexico.

P. l. noveboracensis (Fischer, 1829). Type locality New York (*myoides* Gapper, *emmonsi* DeKay, *arboreus* Gloger, *michiganensis* Audubon and Bachman, *campestris* Le Conte, and *minnesotae* Mearns are synonyms).

P. l. ochraceus Osgood, 1909. Type locality Winslow, Navajo Co., Arizona.

P. l. texanus (Woodhouse, 1853), see above (*mearnsi* J. A. Allen and *canus* Mearns are synonyms).

P. l. tornillo Mearns, 1896, see above (*flaccidus* J. A. Allen a synonym).

DIAGNOSIS. A relatively small species of *Peromyscus*; pelage brownish to grayish dorsally with darker middorsal stripe often present, whitish ventrally with hairs having dark bases, buffy pectoral spot often present; ears average in size and covered with short dark hairs; feet white dorsally, with six plantar tubercles; tail somewhat shorter to slightly longer than head and body, usually moderately covered with dark dorsal and white ventral hairs (Fig. 1); one pair of pectoral and two pairs of inguinal mammae; skull small (Fig. 2), with no interorbital shelf or ridging, auditory bullae not inflated, rostrum not inflated, and toothrows parallel or diverging anteriorly; accessory lophs and styles of teeth variable but usually present, anterocone usually undivided (Fig. 3); baculum elongate and having a broad base and a relatively large cartilaginous tip; glans penis bearing well-developed spines and a long protractile tip having a pair of dorsal lappets; a full complement of male accessory glands present but the preputial glands not visible macroscopically; sperm typical of genus; stomach discoglandular (Carleton, 1973; Hall, 1981; Hooper, 1957, 1958; Linzey and Layne, 1969, 1974).

GENERAL CHARACTERS. The following selected measurements (mm) give an indication of the considerable variation in size within *P. leucopus* (Hall, 1981 and others); total length, 130 to 205; length of tail, 45 to 100; hindfoot length, 17 to 25; skull length, 24.0 to 29.5; basonasal length, 21.3 to 26.7; length of maxillary toothrow, 3.4 to 4.5; breadth across molars, 3.6 to 5.7; greatest rostral breadth, 3.8 to 5.7; width of anterior palatine foramen, 1.0 to 2.5; length of anterior palatine foramen, 3.5 to 6.0.

Various combinations of mensural characters and of those described in the diagnosis distinguish *P. leucopus* from most species of the genus within its range. External characters alone are usually sufficient to distinguish *P. leucopus* from all other species of *Peromyscus* except *P. maniculatus*, *P. polionotus*, and *P. gossypinus* (Hall, 1981).

In Illinois, the longer and wider calcaneum of *P. leucopus* was distinguishable from that of *P. maniculatus* in all instances (Stains, 1959). Guilday and Handley (1967) reported that in unworn lower

FIG. 1. *Peromyscus leucopus noveboracensis* from Long Island, New York. Photograph by J. V. Baumgartner.

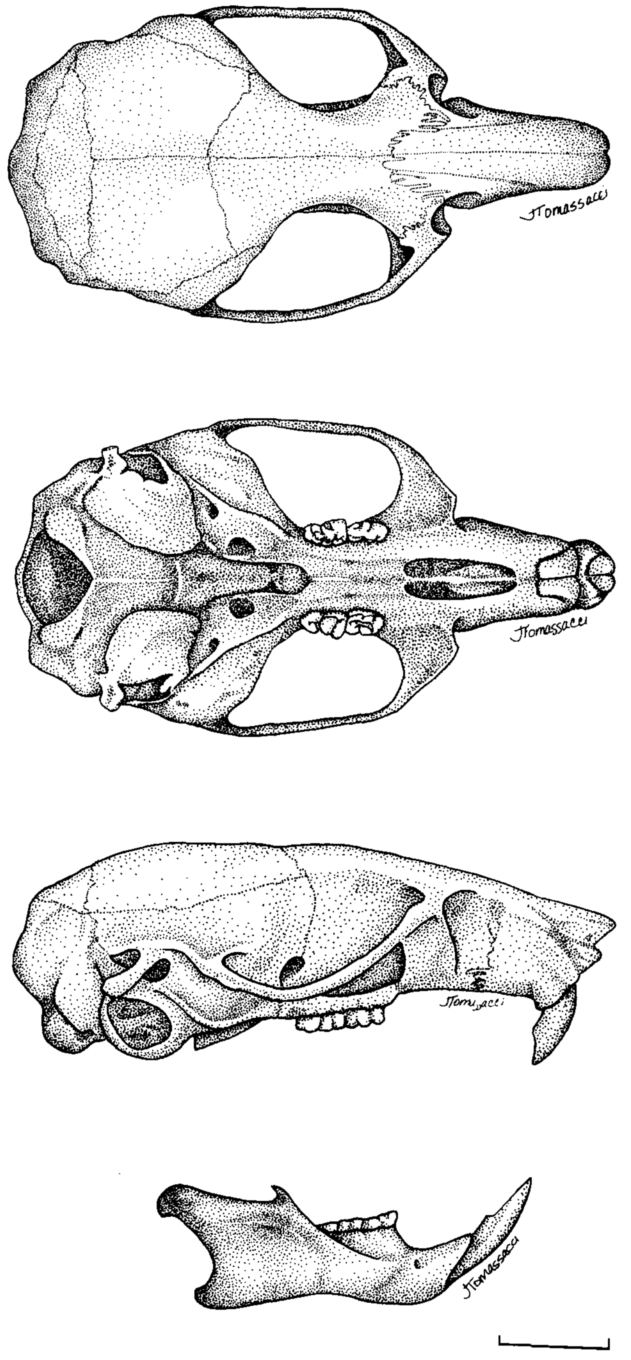

FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Peromyscus leucopus leucopus*, CSULB 4714, from 4 mi SE Bastrop, Morehouse Parish, Louisiana. Scale equals 5 mm.

first molars the anteroconid in *P. leucopus* was symmetrical, whereas in *P. maniculatus* the labial side of the anteroconid was not well developed. In Chihuahua, Mexico, Anderson (1972) could best distinguish *P. leucopus* from *P. maniculatus* by total length, maximum length of the incisive foramen, and the pterygoid fossa. Aquadro and Patton (1980) provided positive identification of live individuals of *P. leucopus* and *P. maniculatus* in areas of sympatry based on the presence of salivary amylase electromorphs.

Discriminant functions based on various combinations of external and skull measurements have proved useful for separating specimens of *P. leucopus* and *P. maniculatus*, as demonstrated by Choate (1973) for populations from New England, by Choate et al. (1979) for those from Kansas, by Stromberg (1979) for those from Wisconsin, and by Thompson and Conley (1983) for those from New Mexico.

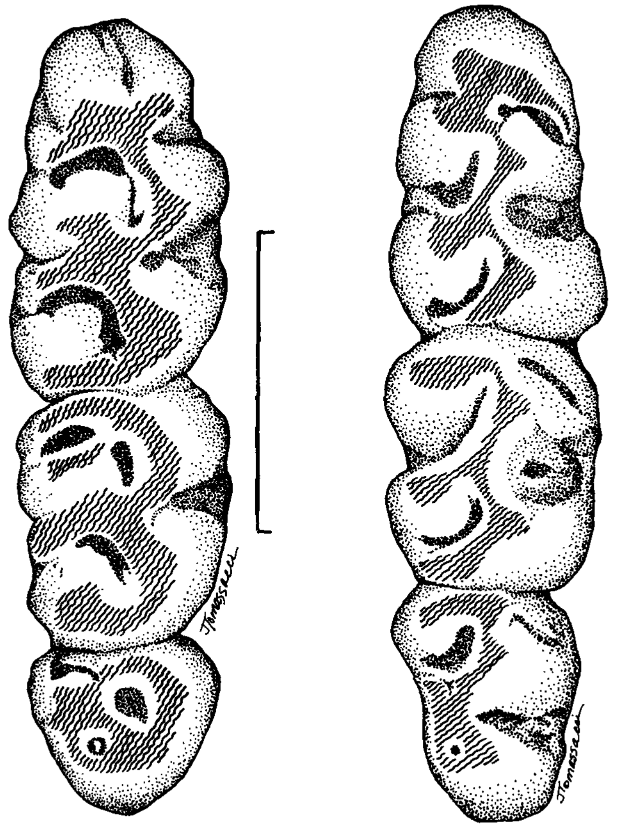

FIG. 3. Occlusal views of the right upper (on left) and left lower (on right) molars of *Peromyscus leucopus noveboracensis* from Lake Geneva, Walworth Co., Wisconsin. Scale equals 1 mm.

Linzey et al. (1976) employed a combination of measurements, with emphasis on length and width of anterior palatine foramina, length of hindfoot, and skull length, for separating *P. leucopus* from *P. gossypinus*. Martin (1967) was partly successful in separating the species by comparison of mandibular dimensions. Possible hybridization compounds the task of positively identifying all specimens in collections (Dice, 1937; McCarley, 1954), especially those without chromosomal or biochemical data.

DISTRIBUTION. The range of the white-footed mouse (Fig. 4) extends from southern Alberta, Saskatchewan, Maine, and Nova Scotia, southward through the eastern half of the United States to South Carolina, Georgia, and Alabama, and westward through New Mexico to central Arizona, thence southward through Chihuahua, Coahuila, and Durango and southward to the Yucatan Peninsula (Hall, 1981). The species is not recorded from the Gulf Coast Plain of North Carolina, South Carolina, Georgia, and Alabama or from any locality in Florida. A hiatus in the known range occurs in coastal Tabasco and in adjacent areas of Campeche and Veracruz in Mexico. Ranges of several insular and other mainland forms are partly or completely isolated from those of nearby populations.

FOSSIL RECORD. *Peromyscus* fossils usually consist of lower jaws or isolated teeth, requiring that identification depend on tooth size and morphology. Although molar size in *P. leucopus* varies little, morphological aspects, such as the presence or absence of accessory lophs and styles, vary considerably, making specific identification of these fossils a challenging task. Specimens assigned to *P. leucopus* are known only from Pleistocene deposits. Hibbard (1968) summarized the fossil record of *P. leucopus* and *cf. P. leucopus*, which then included specimens from Texas, Maryland, Wisconsin, Virginia, and Pennsylvania. Subsequent publications have recorded specimens from Missouri (Saunders, 1977), New Mexico (Harris, 1970), Tennessee (Guilday et al., 1969), Texas (Dalquest

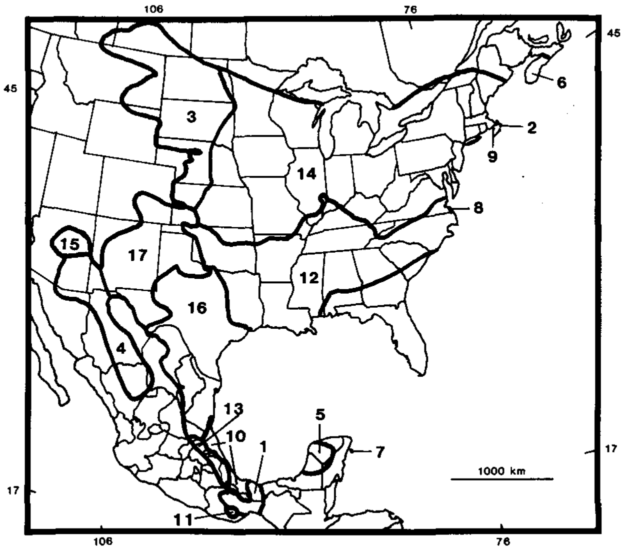

FIG. 4. Distribution of *Peromyscus leucopus*. Subspecies are: 1, *P. l. affinis*; 2, *P. l. ammodytes*; 3, *P. l. aridulus*; 4, *P. l. arizonae*; 5, *P. l. castaneus*; 6, *P. l. caudatus*; 7, *P. l. cozumelae*; 8, *P. l. easti*; 9, *P. l. fusus*; 10, *P. l. incensus*; 11, *P. l. lachiguiriensis*; 12, *P. l. leucopus*; 13, *P. l. mesomelas*; 14, *P. l. noveboracensis*; 15, *P. l. ochraceus*; 16, *P. l. texanus*; 17, *P. l. tornillo*. Map adapted from Hall (1981).

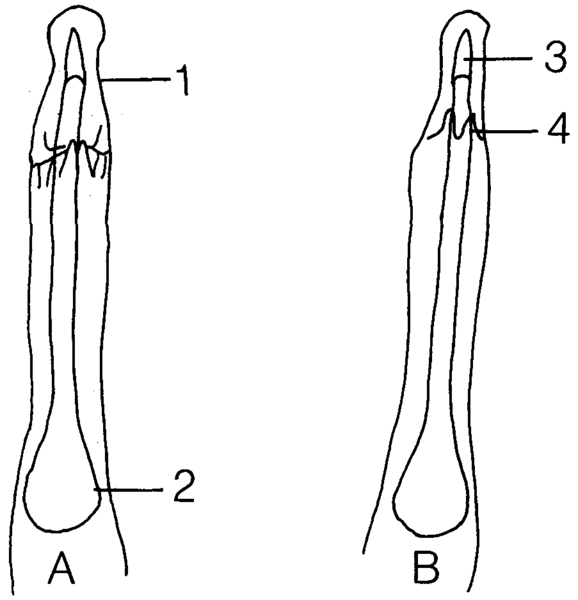

FIG. 5. Ventral (A) and dorsal (B) views of glans penis of *Peromyscus leucopus*. Numbers are: 1, protractile tip; 2, baculum; 3, cartilaginous tip; 4, dorsal lappet. Distance between lines labelled 1 and 2 equals 10 mm. Specimen no. 10870 in Museum of Zoology, Louisiana State University.

et al., 1969; Martin, 1968; Roth, 1973), and Virginia (Guilday et al., 1977).

FORM. The skull of *P. leucopus* lacks supraorbital ridges and inflated auditory bullae. The teeth possess accessory lophs, styles, and an undivided anterocone. The hyoid apparatus resembles that of other *Peromyscus*. No interspecific variation exists in the muscles of *P. leucopus*, *P. maniculatus*, and *P. difficilis* (all in the subgenus *Peromyscus*), but 17 differences occur between those of *P. leucopus* and *P. eremicus* (subgenus *Haplomylomys*). Organization of the carotid arteries in *P. leucopus* resembles closely that of other *Peromyscus*, especially *P. maniculatus*. The baculum and glans penis of *P. leucopus* (Fig. 5) resemble those of most other members of its subgenus, differing mainly in size (summarized primarily from Klingener's [1968] review). Linzey and Layne (1969) found that *P. leucopus* and *P. gossypinus* possess microscopic preputial glands; other species studied in the subgenus *Peromyscus* lacked these glands. In contrast, members of the subgenus *Haplomylomys* have well-developed, macroscopic preputials. *P. leucopus* spermatozoa resemble those of most other *Peromyscus* in having a recurved hook on the head (Linzey and Layne, 1974). The stomach of *P. leucopus* resembles that of most other *Peromyscus* in having a small glandular patch (discoglandular) with no pouch-like evagination (Carleton, 1973). Doty and Kart (1972) found midventral sebaceous glands in *P. maniculatus* and *P. polionotus* but not in *P. leucopus*, *P. gossypinus*, or other species studied.

FUNCTION. When placed on restricted water rations, *P. leucopus* conserves water primarily through reduction in urine volume. As urine volume decreases in response to water deprivation, evaporation becomes the principal avenue of water loss (Chew, 1951).

Water consumption in *P. leucopus* varies with ambient temperature, thermal history, and likely with other factors such as diet and reproductive state. When subject to an environment of 15°C and 75% relative humidity and fed rolled oats, total water intake (drinking, water in food, metabolic water) was 4.8 g/day, or 0.2 g g^{-1}day^{-1} (Getz, 1968*a*). At higher T_A and lower relative humidity *P. leucopus* seemingly used water loss by vaporization for thermoregulation; at a T_A of 34.2°C and 43.5% relatively humidity the mice drank 13.4 g/day (Chew, 1951).

Restricted availability of drinking water does not lead to significant dehydration of tissues in *P. leucopus*; weight losses observed under these conditions may result from a reduction in digestion and assimilation of food (Chew, 1951) and from metabolism of body fat when mice are exposed to low T_A and placed on restricted water rations (Deavers and Hudson, 1977). Chew (1951) found that some individuals of this species survived a weight reduction of 32 to 45%; those dying still retained a water content of 66% in their tissues. Body mass was maintained when the mice were allowed 39% of the usual intake of drinking water. On 1.7 ml of free water/day (26% of unrestricted intake of drinking water) and at a T_A of 27.6°C, the mice survived but lost weight (Chew, 1951).

The low water turnover rate of *P. leucopus* led Chew (1951), Deavers and Hudson (1977), and Getz (1968*b*) to suggest that such capability allowed this species to exist in relatively xeric habitats such as dry uplands. Although total water requirements are low, gain of water from oxidation of food is only moderate and sufficient water in succulent foods must be available, especially during dry conditions as in late summer and early fall (Getz, 1968*b*).

Production of CO_2 measured continuously through a 24-h period (12L:12D) at a T_A of 22°C was 78.4 ml/h (3.7 ml h^{-1}g^{-1}) during the light phase and 88.5 ml/h during the dark phase. Production of CO_2 peaked at approximately 2200 h (period of light was 0600 to 1800) but a lesser peak occurred at 0300 to 0400 h (Baker, 1974).

Thermal neutrality of *P. leucopus* acclimated to a T_A of 20 to 25°C for 4 months extended from 27.5 to 35°C, with oxygen consumption lowest at 30°C; oxygen consumption increased between 35 and 38°C and increased linearly with decreasing temperature below thermal neutrality. Thermal conductance below thermal neutrality averaged 0.23 cc O_2 g^{-1}h^{-1} per °C (Glaser and Lustick, 1975).

Food consumption in *P. leucopus* increases at lower T_A (Sealander, 1952) and is especially high when females nurse larger than average litters (Millar, 1975). Lactating females require an average of 25% more energy than males or non-lactating females (Baar and Fleharty, 1976).

The white-footed mouse exhibits daily torpor under field and laboratory conditions (Lynch et al., 1978*a*), although there is individual variation possibly having a genetic basis (Hill, 1975). Deprivation of food was considered a necessary stimulant for torpor in addition to low temperature (Morhardt and Hudson, 1966), but Hill (1975) found that torpor occurred regularly in some individuals on unrestricted food rations and that food deprivation induced torpor in those mice not exhibiting spontaneous torpor. Under field conditions the incidence of torpor was highest from mid-December to mid-February in Connecticut; in early January, 20 of 36 mice were torpid, but torpor did not occur when the T_A was higher than 3°C

(Lynch et al., 1978*a*). During winter, 96% were in groups of two to six animals; all mice in a group were either torpid or were active. Torpor usually lasted for at least 3 h and occurred during morning hours; individuals commonly alternated several days of daily torpor with several days without torpor. Minimum thoracic temperature during torpor was 17.3°C and minimum heart rate was 60/min, compared with 35°C and 700/min for mice before and following torpor (Gaertner et al., 1973). Arousal was slower, minimum thoracic temperature higher, and heartbeat irregular during fasting-induced torpor. Hill (1975) reported oxygen consumption of torpid mice remained below 2.0 $cm^3g^{-1}h^{-1}$ for 4.3 to 12.7 h/day in some individuals. Torpor saved 440 to 1,900 calories per episode on the average under laboratory conditions, but the value of torpor under field conditions is not known (Hill, 1975). Frequency of torpor increased 9-fold among cold-exposed mice (13°C) subjected to 16L:8D (Lynch et al., 1978*b*). A 2.5-fold increase in the frequency of torpor occurred in mice exposed to chronic administration of melatonin (Lynch et al., 1978*b*).

Melatonin also affects reproduction, thermoregulation, molting, nest building, food consumption, and brown fat deposition (Lynch and Epstein, 1976; Lynch et al., 1980). Abnormal effects created by pinealectomy were reversed by subcutaneously implanted beeswax pellets impregnated with melatonin. Pineal gland function is affected by variables known to affect various physiological and behavioral processes (Lynch et al., 1978*b*).

White-footed mice exposed to 9L:15D exhibited a "fall" molt and gonadal regression after 6 to 10 weeks acclimation. Onset of molting occurred 2 weeks earlier in mice maintained at a T_A of 5°C than in mice exposed to a T_A of 26°C, although molting eventually occurred following exposure to 12L:12D (Lynch, 1973). Gonadal response, however, was not influenced by low T_A (Lynch, 1973).

Spleen weight varied directly with body length but showed no relationship with sex, season, or cause of death (Davis et al., 1961). Compared with spleens of non-pregnant females, those of mice in late pregnancy were 50% heavier, and cells in nodules of these spleens were characterized by large vesicular nuclei, possibly the result of active production of gamma globulin. Spleens of young mice and those of parasitized by botfly (*Cuterebra*) larvae also were relatively large (Timm and Cook, 1979).

Peromyscus leucopus has heavier adrenal glands than *P. maniculatus bairdii* in absolute and relative terms (Christian, 1967). Christian (1967) suggested that the interspecific differences in adrenal masses reflected fundamental differences in total metabolism and in behavior. Absolute adrenal mass was sufficient in most instances to differentiate these species.

Hemoglobin concentration and hematocrit ratios in *P. leucopus* were significantly higher in winter and early spring than in summer, but there were no changes in mean corpuscular hemoglobin concentration (MCHC) or in erythrocyte diameters (Sealander, 1962). The relatively constant values in MCHC were interpreted as resulting from concomitant changes in hemoglobin concentrations and hematocrit ratios. Adult mice had higher values for hemoglobin concentration and hematocrit than juveniles (Sealander, 1964).

Adrenocortical activity in *P. leucopus* was not correlated with population density when densities were varied experimentally from 10.1 to 60.7 mice/ha (Clulow et al., 1969). The latter authors interpreted absence of a correlation as excluding population regulation by means of a behavioral-physiological mechanism involving adrenal activity.

A minimum visual angle of 4.1 ± 0.6 min of arc at a distance of 20 cm, as measured by optokinetic response, was reported by King and Vestal (1974). The authors concluded that among species of *Peromyscus* studied there was no relationship between visual acuity and habitat.

Chloral hydrate (0.77 mg/g) is a relatively safe and effective anesthetic for *P. leucopus* (Baumgardner and Dewsbury, 1979). Ether or chloroform results in high mortality rates. R. W. Hill (pers. comm.) obtained good results with methoxyflurane (metofane) as an anesthetic for neonatal and juvenile *P. leucopus*.

ONTOGENY AND REPRODUCTION. Resorption of embryos in *P. leucopus* is infrequent but transmigration of blastocysts was noted in 24% of litters in Missouri (Brown, 1964).

The minimum gestation period of non-lactating females is 22 to 23 days (Svihla, 1932). Among lactating females, gestation is extended as much as 14 days (Svihla, 1932), possibly from a delay in blastocyst implantation induced by effects of lactation and nursing on hormones controlling implantation, as in *Rattus* (Zeilmaker, 1964). Compared with *P. leucopus* from Michigan, those from southern Mexico exhibited a shorter gestation period. Among lactating females, there was no correlation between the number of young being nursed and the duration of the gestation period of the next litter; litter size and length of gestation period of that litter were not correlated in either population (Lackey, 1978*a*).

Mean litter size in *P. leucopus* is 5.0 in Ontario (Coventry, 1937), 4.3 in Michigan (Lackey, 1978*a*), 3.7 in Missouri (Brown, 1964), and 3.5 in southern Texas (Guetzow and Judd, 1981), and 3.0 for eight specimens from northern Tamaulipas, Mexico. The apparent latitudinal trend is reversed in southern Mexico where litter size was 5.4 for females trapped in December and January; in August, however, litter size was 3.9 (Lackey, 1978*a*). Seasonal variation in mean litter size was not considered a consequence of variation in age and body size of females. Davis (1956) found that litter size in a New Jersey population varied with age and body size of breeding females.

The breeding season in northern populations is strongly seasonal, with peaks in spring and late summer in Michigan (Burt, 1940), whereas in southern Texas (Judd et al., 1978) and in the state of Campeche, Mexico (Lackey, 1978*a*) the breeding season is year-round. Lower frequencies of pregnant females in northern populations during midsummer were interpreted as a reflection of many young females in the population (Cornish and Bradshaw, 1978; Long, 1973) or cessation of reproductive activity by all females (Burt, 1940). The male reproductive cycle in northern populations exhibits a seasonal pattern similar to that of females (Cornish and Bradshaw, 1978).

Postnatal development was described by Layne (1968), and extensive observations and measurements were reported by Lackey (1973, 1978*a*) for laboratory stocks derived from populations from Mexico and Michigan. Eruption of incisors, opening of ear meatus, and opening of eyes, but not elevation of pinnae, occurred at a younger age in Mexican mice. These events were correlated positively with litter size in Michigan mice, but among Mexico mice the correlations were negative (except elevation of pinnae). Females from Mexican stock averaged becoming sexually mature at 37.7 days, compared with 44.4 days for Michigan mice, but males exhibited no significant differences in rate of sexual development.

Postnatal growth in *P. leucopus* is rapid and largely completed within 6 weeks of birth. If mass and dimensions of animals 25 weeks old are considered adult, growth in mass and in body length of 6-week-old animals is 85% and 95% completed, respectively, and by 10 weeks, 93% and 98% completed (Lackey, 1978*a*). Postnatal growth in a population from southern Texas (Guetzow and Judd, 1981) and from a population in southern Mexico (Lackey, 1978*a*) were similar in most respects, suggesting little geographic variation in rates of growth. However, effects of litter size on postnatal growth rates were substantially greater in mice from Michigan than in those from southern Mexico.

The estrous cycle of *P. leucopus* resembles that of some other species of this genus, such as *P. californicus*, *P. crinitus*, and *P. eremicus*, in having a mean duration of 6.0 days (Dewsbury et al., 1977). Ovulation is spontaneous, but pseudopregnancy can be induced (Conaway, 1971). Vaginal smears resemble those of laboratory strains of *Rattus* and *Mus* (F. L. Osgood, Jr., cited in Asdell, 1964). There is a postpartum estrus (Svihla, 1932) during which a single copulation usually results in pregnancy under laboratory conditions (Dewsbury et al., 1979).

ECOLOGY. Northern populations of this species reach highest densities in brushy fields and in woodlots dominated by deciduous trees but typically have low densities in grassy fields (Hamilton and Whitaker, 1979) and in mature, mainly coniferous forests (Choate, 1973). In eastern Texas, McCarley (1963) found that *P. gossypinus* apparently excluded *P. leucopus* from lowland habitats that *P. leucopus* occupies in regions further west where *P. gossypinus* is absent. In regions characterized by prairie or semi-desert, the white-footed mouse usually is most abundant in riparian areas and in ravines (Blair, 1954; Kaufman and Fleharty, 1974; Wilson, 1968). The habitat of *P. leucopus* typically includes a canopy (if only of brush), woody debris, and often rocks (Barry and Francq, 1980; Van Deusen and Kaufman, 1977). In Tamaulipas, Mexico, Alvarez (1963) commonly found *P. leucopus* in forested and brush habitats throughout the state under 365 m. In Veracruz, *P. leucopus* was found primarily in fields of brush and weeds and in sugar cane fields but not in tall grass; other habitats included newly cleared areas with fallen logs. In that area, *P. leucopus* "rarely enters deep forest" (Hall and Dalquest, 1963:303). Lackey (1978*b*) reported similar habitat use by populations in Campeche in the southern part of the Yucatan Peninsula, but Birney et al. (1974) reported *P. leucopus* as common in second-growth thorn forest and in fields planted to henequen in the northern part.

The population dynamics of *P. leucopus* do not differ consistently or dramatically from those of other species of *Peromyscus* (Terman, 1968). The genus as a whole is characterized by less variation in population density than that reported for a variety of other small terrestrial mammals such as *Microtus pennsylvanicus* and *Reithrodontomys megalotis* (Terman, 1966).

Population regulation in *P. leucopus* under various environmental and demographic conditions was attributed to food limitation (Bendell, 1959); to spatial limitations imposed by territoriality, especially among resident breeding females (Burt, 1940; Metzgar, 1971); and possibly to a reduction in recruitment of breeding-aged individuals caused by a decline in reproductive activity or to reduced juvenile survivorship, as suggested by Terman (1965) for *P. m. bairdii.* These studies suggest that population regulation mechanisms are effective only at relatively high population densities. Replacement in depopulated areas may occur through adjustment in boundaries of nearby territories and by immigration of transient mice when the population density of residents is low (Metzgar, 1971; Stickel, 1946).

Mortality in this species usually leads to a complete population turnover annually, although there may be seasonal differences in mortality (Snyder, 1956); a reliable measure of mortality is difficult to obtain because of the possibility of disappearance of individuals through emigration (Terman, 1968). Winter mortality may be relatively low compared with that in spring and summer (Lackey, 1973). Snyder (1956) reported an inverse relationship between population density and mortality in a Michigan population but could not identify causative factors.

Home range size varies seasonally, with the largest areas recorded during the breeding season and the smallest during winter. Estimates of home-range size vary greatly; the average is approximately 0.1 ha. Males usually have larger home ranges than females although exceptions have been reported (Stickel, 1968). Other variables affecting home-range size include food supply, age, and population density (Stickel, 1968).

Insects were the most frequently occurring food class in stomach contents of *P. leucopus* throughout the year in a study in New York; starchy matter (mast, seeds) and green vegetation followed in frequency in late fall and winter, whereas fruit was next after insects in frequency in spring and summer. All other items occurred in a frequency less than 10% (Hamilton, 1941). In Indiana, seeds, insects, and unidentified vegetation occurred most frequently, representing 43%, 30%, and 25% of the diet, respectively, on a volume basis (Whitaker, 1966). Cultivated foods and grass seeds appear to be used infrequently in Indiana, even in non-forest habitats (Mumford and Whitaker, 1982). In an Illinois forest, seeds were the principal items consumed in spring and autumn but in summer and fall arthropods were the most frequent (Batzli, 1977). The ratio of the lengths of the small intestine to the hindgut and the ratio of the mucosal surface area of the small intestine to that of the hindgut of *P. leucopus* point to an omnivorous diet. In these characteristics, *P. leucopus* ranked between largely herbivorous *Microtus* and largely insectivorous and carnivorous *Blarina* (Barry, 1977).

The botfly, *Cuterebra fontinella* (*C. angustifrons* in some reports), occurs frequently in *P. leucopus* and possibly lowers fitness in subadult males temporarily (Timm and Cook, 1979). Baudoin (1976) reported increased survivorship of parasitized non-reproducing mice compared with parasitized reproducing mice; he suggested that parasitic castration of *P. leucopus,* if only temporarily, represented an adaptation by *C. fontinella* that improved its own survivorship through increased host survival. Timm and Lee (1981, 1982) questioned the occurrence of parasitic castration in *P. leucopus* and rejected the hypothesis that parasitic castration was an evolved strategy of the botfly; they concluded that reproduction in *P. leucopus* was affected only slightly and temporarily. Physiological effects of botfly parasitism on *P. leucopus* include lower erythrocyte count, hemoglobin concentration, and hematocrit percentage, and higher total leucocyte number (Dunaway et al., 1967). Prevalence of infestation is highest in summer; for example, 42.2% were infested in August in Virginia (Hensley, 1976). There is much variation in rates of infestation according to year, habitat, and sex and age of the host (Dunaway et al., 1967; Timm and Cook, 1979).

BEHAVIOR. White-footed mice are considered semi-arboreal because of their climbing in trees (Batzli, 1977; Nicholson, 1941) and possession of various arboreal adaptations. The tail is used as a prop and balancing organ during climbing. *P. leucopus* is more adept in crossing gaps and moving along narrow branches, can climb smoother tree trunks, and remains longer on an elevated platform with no pathway to the ground than various short-tailed, terrestrial species of *Peromyscus*; tail amputation reduced climbing ability of white-footed mice more than in terrestrial species (Horner, 1954). White-footed mice are better than *Clethrionomys gapperi* at climbing vertically and traversing a 5 mm diameter dowel (Getz and Ginzberg, 1968), but score lower than *P. gossypinus* in laboratory measures of climbing (Dewsbury et al., 1980).

In some parts of its range *P. leucopus* spends most of its active period on the ground, even in wooded habitat (Madison, 1977). Studies of nest-site selection by use of nest boxes in the field (Nicholson, 1941) and laboratory (Stah, 1980) suggest that *P. leucopus* usually select nest sites off the ground, but there are reports of nests at or near ground level in rock piles, logs, stumps, under trees, and in ground burrows (Mumford and Whitaker, 1982), including those of woodchucks (*Marmota monax*; Madison, 1977). In Veracruz, Mexico, nests were found under loosened bark of fallen trees (Hall and Dalquest, 1963). Wolff and Hurlbutt (1982) located nesting sites of *P. leucopus noveboracensis* and *P. maniculatus nubiterrae* by radiotelemetry and demonstrated that *P. leucopus* used ground nests significantly more often than *P. maniculatus.*

Nests built by white-footed mice consist of a variety of materials, including grass, leaves, hair, feathers, milkweed floss, shredded bark, and moss (Edwards and Pitts, 1952; Nicholson, 1941). Nest building by mice from various latitudes seems correlated with average midwinter temperatures at those latitudes (King et al., 1964). Nest-building behavior was most intense at a T_A of 5°C, and the most effective nest contained 13 g of nesting material, resulting in an energy saving of 5.1 Kcal/day at a T_A of 5°C (Glaser and Lustick, 1975). Hill (1972) found a positive correlation between the degree of maternal care of nestling young and the T_B of the young. Significant differences in measures of nest-building activity between *P. leucopus* and *P. floridanus* were correlated with differences in diversity of habitats and nest sites used by the two species (Layne, 1969). Microhabitat features affect nesting behavior more than direct climatic effects (Layne, 1969; Wolfe, 1970). *P. leucopus* maintained under a short photoperiod build larger nests than those under a longer photoperiod (Lynch, 1974).

Peromyscus leucopus is primarily nocturnal (Baumgardner et al., 1980) but occasionally is active during day in winter (Mumford and Whitaker, 1982). Orr (1959) found that individuals in an outdoor enclosure were more active at higher temperatures and relative humidities. *P. leucopus* in laboratory trials selected a higher mean floor temperature (32.4 + 1.3°C) than *Mus musculus, P. maniculatus gracilis,* or *P. maniculatus bairdi* (Ogilvie and Stinson, 1966). White-footed mice in Massachusetts were captured significantly more often than deer mice at higher temperatures and relative humidities, under overcast skies, and during light rain at night (Drickamer and Capone, 1977).

Food-hoarding behavior was reported to be well developed in *P. leucopus* (Hamilton and Whitaker, 1979; Mumford and Whitaker, 1982) but was minimal in other studies (Lanier et al., 1974; Nicholson, 1941). *P. leucopus* shows greater flexibility in feeding behavior compared with *P. maniculatus* (Drickamer, 1972). Laboratory measurement of feeding diversity of field-caught white-footed mice indicates that immigrant mice consume a wider range of foods than residents (Tardif and Gray, 1978).

The pattern of copulatory behavior shown by *P. leucopus* consists of no locking or intravaginal thrusting, with multiple intromissions before ejaculation and multiple ejaculations (Dewsbury, 1975*a*). Latency to initiate copulation is long, and the number of ejaculations before satiety and frequency of intromissions before first ejaculation is low compared with those of many other cricetids (Dewsbury, 1975*b*). The natural fertility rate in this species is low (Dewsbury and Lanier, 1976). A copulatory plug is found in the female after mating, which may reduce sperm competition or prevent sperm leakage (Baumgardner et al., 1982; Voss, 1979). *P. leucopus* probably are polygamous (Myton, 1974). In the laboratory, both sexes participate in parental care by sitting on pups and

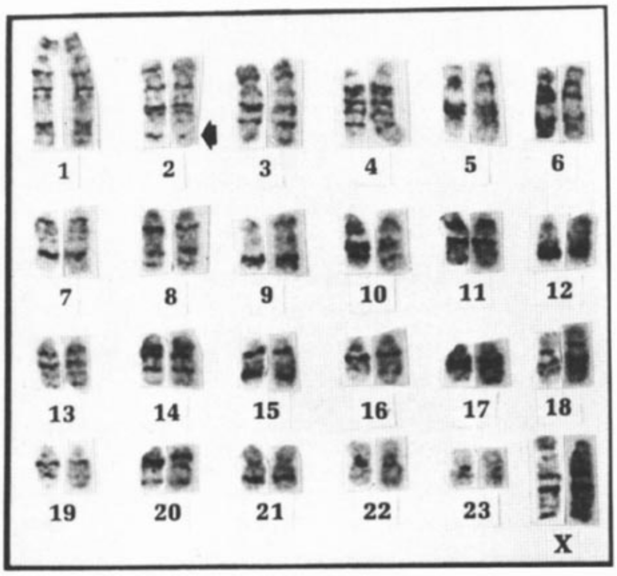

FIG. 6. Haploid G-banded karyotypes for two chromosomal subdivisions of *Peromyscus leucopus* (from Baker et al., 1983). The chromosome on the left of each pair is from the southwestern race; the one on the right is from the northeastern race. The arrow indicates a dark band observed only in *P. leucopus* among the 18 species of *Peromyscus* examined to date by G- and C-banding (Robbins and Baker, 1981).

licking them (Hartung and Dewsbury, 1979), although females attend pups more frequently than males (McCarty and Southwick, 1977). In forest enclosures and in the laboratory, pups in the company of their mothers maintained homeothermic temperatures irrespective of their ability to thermoregulate when alone (Hill, 1972). The extent and significance of parental care in the wild is unknown.

Behavioral regulation of population density in *P. leucopus* is supported by both field and laboratory studies. During the breeding season, home ranges of mice of the opposite sex overlap more than those of the same sex (Ormiston, 1983). Also, the frequency of establishment of home ranges by introduced subadult females was correlated negatively with density of resident adult females; the trend between introduced subadult males and the density of adult males was similar but not significant (Metzgar, 1971). In laboratory trials, breeding females, but not males, behaved aggressively toward 21- to 25-day-old conspecifics (Rowley and Christian, 1976*a*). Laboratory observations (Hill, 1977; Vestal, 1977) suggest that avoidance behavior may be involved in behavioral population regulation. Evidence for the occurrence of social interactions and dominance relationships under natural conditions is suggested by the observation of Vestal and Hellack (1978) that field-caught neighbors seem to recognize each other and show submissive behavior in laboratory encounters. Kin recognition was reported by Grau (1982). Repulsion of individuals can occur without direct contact and could be based on olfactory or other sensory modalities (Mazdzer et al., 1976, Orr, 1959). Sexual maturation of *P. leucopus* in the laboratory is delayed by the presence of urine or feces of conspecifics (Rogers and Beauchamp, 1976).

Getz (1969) concluded there was no evidence that aggression was a determinant of habitat segregation between *P. leucopus* and *Clethrionomys gapperi*. Increasing poulation density of *Microtus pennsylvanicus* in an outdoor enclosure altered use of space by *P. leucopus* (Bowker and Pearson, 1975), although, in laboratory trials, white-footed mice were aggressive toward and dominant over this species (Baenninger, 1973; Rowley and Christian, 1976*b*). Dominance by *P. leucopus* and *P. maniculatus nubiterrae* tested in the field was site-specific rather than species-specific (Wolff et al., 1983).

Young *P. leucopus* probably begin exploration of the area surrounding their birthsite between 16 and 25 days of age (Sheppe, 1966), and females abandon litters 20 to 40 days postpartum (Nicholson, 1941). Most juveniles initially disperse within a radius of about 100 m of their point of origin, but longer movements approaching 1 km also occur (Ormiston, 1983; Stickel and Warbach, 1960). Adults may make long distance movements during exploration or changes in location of home range (Ormiston, 1983). *P. leucopus* can cross bodies of water by crossing on ice or by swimming. Individuals have well-developed swimming abilities (Evans et al., 1978; King et al., 1968) and pass between islands up to 233 m apart (Sheppe, 1965).

Peromyscus leucopus is thoroughly familiar with its immediate environment and with those features that may be used in navigation, such as trees, logs, rocks, and other objects (Barry and Francq, 1980). Individuals orient toward trees that are proximally associated with a goal (Joslin, 1977). *P. leucopus* uses visual and olfactory cues to orient and home (Parsons and Terman, 1978). Population density and activity were positively related to measures of shrub cover or stem density in some studies (Kaufman and Fleharty, 1974; M'Closkey and Fieldwick, 1975; Stickel and Warbach, 1960), negatively related in some (Barry and Francq, 1980; Bongiorno and Pearson, 1964), and without relationship in others (Getz, 1961; Klein, 1960).

Peromyscus leucopus responds strongly to new objects placed within a familiar area, which may facilitate learning of new escape routes, feeding sites, nests, potential mates, and home-range areas. White-footed mice show weak neophobia, followed by neophilia that declines progressively (Sheppe, 1966).

GENETICS. *Peromyscus leucopus* has a diploid chromosome number of 48 and a fundamental number of 70 to 72 (Hsu and Arrighi, 1968). Two distinct karyotypes occur (Fig. 6), one in northeastern and north-central, and the other in southwestern United States (Baker et al., 1983; Robbins and Baker, 1981). The two races differ by three euchromatic pericentric inversions, a difference greater than that distinguishing various pairs of closely related species of *Peromyscus* (Robbins and Baker, 1981). Individuals from Tennessee, Oklahoma, and Mississippi exhibit karyotypes intermediate between the two types, suggesting the existence of an extensive area of hybridization between the two karyotype races. There is a greater similarity in karyotype between the northeastern race of *P. leucopus* and the cotton mouse, *P. gossypinus*, than between the two chromosomal races of *P. leucopus* (Baker et al., 1983). The karyotype of Latin American populations remains unknown.

Genetic differences between geographically close populations of *P. leucopus* often are observed (Bokoch and Eckroat, 1976; Price and Kennedy, 1980). Browne (1977) analyzed protein variation at 28 loci and found that the Bass Island populations in Lake Erie differed from mainland samples in exhibiting lower average individual heterozygosity and a lower proportion of polymorphic loci.

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