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SYSTEMATICS AND NOTES ON THE BIOLOGY OF PEROMYSCUS HOOPERI

DAVID J. SCHMIDLY, M. RAYMOND LEE, WILLIAM S. MODI, AND EARL G. ZIMMERMAN

No new information has been reported concerning Hooper's deer mouse (*Peromyscus hooperi*) since its original description (Lee and Schmidly, 1977). This was based upon 14 specimens (five adults) and included only brief comments from the collector's field notes regarding the habitat where certain specimens were captured. In November of 1976, a population of *P. hooperi* was discovered near Ocampo, in central Coahuila, México, less than 40 kilometers from the type locality. Subsequently (1978), a second population was found near the Coahuila-Zacatecas border along Mexican Highway 54. The Ocampo area was visited again in March of 1977 and 1978, and the present paper provides details of our studies of the aforementioned populations and records such ecological information as was obtained.

P. hooperi is known to occur sympatrically with three species of *Peromyscus* (*P. eremicus, P. pectoralis,* and *P. melanophrys*), and possibly will be found with another species (*P. maniculatus*). *P. melanophrys* is a large, distinctive mouse (total length in adults greater than 240 millimeters and hind foot greater than 25) with several cranial features (such as a trenchant supraorbital ridge) that clearly distinguish it from *P. hooperi. P. maniculatus* is distinguished from *P. hooperi* by its notably shorter tail (less than 78 in adults), substantially smaller skull, and more complex occlusal surfaces of the molar teeth. No further comparisons among *P. hooperi, P. melanophrys,* and *P. maniculatus* are presented nor

are deemed necessary. In general size and external appearance, however, *P. hooperi*, *P. eremicus*, and *P. pectoralis* closely resemble one another, and identification is difficult. We include herein information regarding the identification, geographic distribution, habitat, morphology, karyology, reproduction, ontogeny, and genetic variation of *P. hooperi*, as well as its systematic relationships to other species in the genus.

Methods and Materials

Unless noted otherwise, all specimens reported are housed in the Texas Cooperative Wildlife Collection (TCWC) at Texas A&M University. Most specimens were obtained during field surveys in Coahuila by personnel of the TCWC. Most animals were processed as conventional study skins and skulls; some complete skeletons and whole carcasses preserved in 10 per cent formalin also were prepared. Mice from several localities were returned to the University of Illinois and a colony was maintained while aspects of their karyology, growth, development, and reproductive biology were investigated. Live animals taken to North Texas State University provided tissue for electrophoresis.

Material at the Museum of Natural History, University of Illinois, Urbana (UIMNH), Museum of Natural History, University of Kansas (KU), and the National Museum of Natural History, Washington, D.C. (USNM) was examined for additional specimens of *P. hooperi* from the Mexican Plateau. Among those collections and the material in the TCWC, a total of 153 specimens of *P. hooperi* is known at this writing, from 14 localities in Coahuila and Zacatecas as follows: *Coahuila*: 1) Sierra del Pino (5 mi. S, 3 mi. W Acebuches), 1891 m., 1 (KU); 2) 3 mi. N, 4 mi. E San Francisco (25 mi. N Ocampo), 1586 m., 1 (KU); 3) 4.7 mi. W Ocampo, 1464 m., 18 (TCWC); 4) 8.6 mi. W Ocampo, 1586 m., 21 (TCWC); 5) 14.2 mi. W Ocampo, 1708 m., 12 (TCWC); 6) 15.2 mi. W Ocampo, 1708 m., 73 (TCWC); 7) 21 mi. S, 2.5 mi. W Ocampo, 1068 m., 5 (KU), 1 (UIMNH); 8) 8 mi. N, 25 mi. W Cuatro Cienegas, 1220 m., 1 (KU); 9) 21 mi. S, 11 mi. E Australia, 1342 m., 1 (KU); 10) Carneros, 2074 m., 2 (USNM); 11) Sierra Encarnación, 2288 m., 1 (USNM); 12) El Gorrión, 4 (UIMNH); 13) 1.2 mi. S, 1 mi. W El Gorrión, 3 (TCWC). *Zacatecas*: 14) 0.5 mi. S Coahuila-Zacatecas border, Hwy. 54, 9 (TCWC).

External, cranial, and dental morphology.—Sixteen measurements of the skin and skull were recorded for all museum specimens. External measurements were taken from skin labels.

Cranial measurements, taken with dial calipers to the nearest 0.1 millimeter, are listed in Table 4. All measurements are in millimeters; weights, in grams.

Nongeographic variation was assessed in a series of 90 *P. hooperi* collected in the Ocampo region. Specimens were assigned to one of six age categories according to the criteria of Schmidly (1972, 1973) and Cornely *et al.* (1981). Geographic variation was analyzed using adult specimens of *P. hooperi* from 10 of the 14 localities. Specimens were grouped into four samples as follows (the localities included in each sample are numbered as listed above): *sample 1* (Acebuches), two individuals from localities 1 and 2; *sample 2* (Ocampo), 45 individuals from localities 3-6; *sample 3* (Cuatro Cienegas), three individuals from localities 7 and 8; and *sample 4* (El Gorrión), eight individuals from localities 13 and 14.

Interspecific comparisons were made using a sample of 59 adult *P. hooperi*, 45 adult *P. eremicus*, and 27 adult *P. pectoralis* from areas of sympatry and near sympatry in Coahuila. Each species was compared with respect to the external and cranial measurements previously listed as well as several qualitative features of the pelage, skull, and phallus. These characters and their character states are discussed and illustrated beyond.

Univariate analyses of the data were performed using two subroutines (Procedure Means and Procedure Anova) of the Statistical Analysis System (SAS). Procedure Means generates standard statistics (mean, range, standard deviation, standard error of the mean, variance, and coefficient of variation). When comparing two or more groups, Procedure Anova tests for significance differences ($P \leq .05$) among the means of the groups by employing a single classification analysis of variance. If significant differences are found, Duncan's Multiple Range Mean Test is used to determine the maximally nonsignificant subsets.

Three multivariate statistical techniques were employed. A multivariate analysis of variance (Manova) program in SAS, employing Wilks' criterion, was used to test the hypotheses of no overall sex or species effect. Discriminant function analysis was performed using the BMDO4 program of the BMD Biomedical Computer Programs (Dixon, 1976) to determine the extent to which reference samples of *P. eremicus*, and *P. hooperi* could be distinguished from one another. The principal components analysis routine of the SAS system was used to summarize as much of the geographic variation as possible among individuals of *P. hooperi* from different localities.

Structural details of four teeth, the opposing upper and lower first and second molars on the right side, were examined and coded for each species according to the scheme proposed by Hooper (1957) and Hershkovitz (1962). Primary attention was given to the lophs (lophids) and styles (stylids), which, when present, are situated in enamel valleys between the principal cusps. According to Hooper (1957), these are the structures most responsible for the complexities in dental topography in *Peromyscus*. When these structures are present and fully developed, the tooth is complex and elaborate in pattern; when they are lacking, the dental pattern is simple.

Male accessory glands.—The reproductive tracts of five adult males (TCWC 31684, 31685, 40478, 40481, 31715), all with scrotal testes, were dissected from fluid-preserved carcasses and stored in 70 per cent ethanol. The penis was removed from selected standard museum and fluid-preserved specimens of each species, cleared, stained, and preserved, following the technique outlined by Lidicker (1968). Six measurements of the penis were recorded (as defined by Hooper, 1958): length of distal tract, length of glans, length of protractile tip, diameter of glans, length of baculum, and length of cartilage.

Karyology.—Bone marrow mitoses were prepared according to the techniques of Lee (1969) and Lee and Elder (1977). All animals received the yeast pretreatment as outlined by Lee and Elder (1980); G and C-bands were induced by methods cited in that report. Cell cultures from two individuals were initiated and used for localization of nucleolus organizer regions (NORs). For visualizing NORs the method of Bloom and Goodpasture (1976), as modified by Lee and Martin (1980), was used. The chromosomes were numbered according to the Standardized Karyotype for *Peromyscus* (Committee for Standardization of Chromosomes of *Peromyscus*, 1977). Ten animals processed for marrow mitoses (including two for cell cultures) were from localities 6 (8 individuals) and 13 (2).

Electrophoresis.—Blood samples and homogenates of kidney and liver were prepared for electrophoresis from freshly killed individuals according to the methods described by Selander *et al.* (1971) and Kilpatrick and Zimmerman (1975). Proteins encoded at 18 loci were examined as follows: lactate dehydrogenase (LDH-1, LDH-2, LDH-3); 6-phosphogluconate dehydrogenase (6PGD-1); glutamate oxaloacetate transaminase (GOT-1, GOT-2); malate dehydrogenase (MDH-1, MDH-2); malic enzyme (ME-1); indolphenol oxidase (IPO-1); serum albumin (ALB-1); transferrin (TRF-1); three esterases (ES-1, ES-5, ES-6); and hemoglobin (HB-

1, HB-2, HB-3). The normalized identity (I) between species was calculated for all pair-wise combinations using the genic identity of Nei (1978). Species were clustered using the unweighted pair-group method. Heterozygosity (H) was calculated by direct count.

Growth and development.—Observations were recorded from 33 individuals comprising 13 laboratory-reared litters. A lab colony was established from one male and two females collected at locality 6 and maintained for over 3 years. Body weight and measurements were recorded daily for young from the day of birth until 30 days of age, and thereafter at 10 or 30 day intervals. Vaginal smears, following the technique of Clark (1936), were taken to determine the age of first estrus. Gestation period was estimated from postpartum litters born to lactating females. The number of vocalizations emitted during a 3-minute period was recorded daily during the first week after birth by restraining individual neonates in a small cardboard box. The remaining growth and developmental parameters were monitored in the manner described by Layne (1968) and Svihla (1932).

Ecology

Description of the Ocampo Area

Ocampo is a small town near the western edge of an intermontane basin, Llano de Ocampo, in central Coahuila (27° 22′N, 102° 36′W). The town, elevation 1099 meters, is situated in the foothills at the junction of the low lying Sierra la Madera and the Sierra El Fuste ranges (Fig. 3). The Sierra la Madera, to the southwest of Ocampo, attains elevations of at least 2745 meters and the higher slopes support pine forest (Baker, 1956:140).

Precipitation is scanty in the Ocampo region and is confined largely to sporadic heavy thunderstorms from July to October. The area has a mean annual precipitation of less than 200 millimeters (Shreve, 1944). In summer, air temperatures exceed 44°C during the day; however, nights are relatively cool. Winter temperatures may fall below 0°C at night.

An unimproved road extends westward from Ocampo through a pass separating the Fuste and Madera mountain ranges. For about 15 kilometers the road roughly parallels a narrow, rocky arroyo and gradually ascends a gently sloping rocky pediment. The vegetation from Ocampo up to about 1403 meters falls within the Chihuahuan Desert Scrub floral zone (this and all other vegetative descriptions taken from Muller, 1947). As the road increases in elevation, Grassland Transition vegetation is encountered at the

upper limits of the Desert Scrub along the foothills of the flats and bajadas. The road then gradually traverses the Grassland Transition zone to 1708 meters at the summit and continues downward and westward into the Bolson de Mapimi.

Habitat and Interspecific Relationships

We collected small mammals at several stations along the road west of Ocampo. Collecting results and habitat descriptions for these sites, which may be arranged into three groups according to vegetation and topography, are as follows:

1. Succulent Desert Scrub sites (1.0, 1.6, 2.7, 3.5, and 3.9 mi. W Ocampo, 1190 to 1403 m.) were located on rocky slopes of shallow soils and in the arroyo at the lower elevations along the road (Fig. 1A). The dominant plants at these sites included creosotebush (*Larrea divaricata*), blackbrush acacia (*Acacia rigidula*), Spanish dagger (*Yucca torreyi*), prickly pear (*Opuntia* sp.), ocotillo (*Fouquieria splendens*), lechuguilla (*Agave lecheguilla*), leatherstem (*Jatropha dioica*), and strawberry cactus (*Echinocereus* sp.).

A total of 624 trapnights at these localities produced 38 *Perognathus nelsoni*, 2 *Perognathus flavus*, 17 *Dipodomys merriami*, 2 *Dipodomys nelsoni*, 1 *Onychomys torridus*, 1 *Neotoma albigula*, 15 *Peromyscus pectoralis*, and 19 *Peromyscus eremicus*.

2. A mixture of Desert Scrub and Grassland Transition vegetation appears at slightly higher elevations farther west along the road at two sites (4.7 and 8.6 mi. W Ocampo, 1464 to 1563 m.; Fig. 1B). Here, Desert Scrub, with prickly pear and lechuguilla as well as the other dominants listed for the previous localities, typifies the upper reaches of the arroyo where shallow and stony soils of igneous origin predominate. Vegetation of the Grassland Transition type, dominated by bear grass (*Nolina* sp.), giant dagger (*Yucca carnerosana*), sotol (*Dasylirion* sp.), and gramma grass (*Bouteloua* sp.), occupies the limestone slopes adjacent to the arroyo.

Trap lines in the arroyo proper (423 trapnights) produced 34 *Perognathus nelsoni*, 1 *Perognathus flavus*, 15 *Dipodomys merriami*, 1 *Reithrodontomys fulvescens*, 5 *Neotoma albigula*, 8 *Peromyscus pectoralis*, 29 *Peromyscus eremicus*, and 4 *Peromyscus hooperi*.

Trap lines on the adjacent slopes (724 trapnights) produced 4 *Perognathus nelsoni*, 2 *Perognathus flavus*, 10 *Dipodomys merriami*, 7 *Dipodomys nelsoni*, 3 *Reithrodontomys fulvescens*, 2

Neotoma albigula, 8 *Peromyscus eremicus*, and 31 *Peromyscus hooperi*.

3. The Grassland Transition vegetation reaches its maximum development in this region at two sites (14.2 and 15.2 mi. W Ocampo, 1708 m.) where the road crosses the summit (Fig. 2). Here, among the limestone hills, clumps of standing and fallen giant dagger are interspersed with dense stands of sotol, bear grass, agave (*Agave scabra*), false-agave (*Hectia* sp.), mariola (*Parthenium incanum*), desert privet (*Forestiera* sp.), candelilla (*Euphorbia antisyphilitica*), ephedra (*Ephedra* sp.), evergreen sumac (*Rhus varians*), agarita (*Berberis* sp.), and white-thorn acacia (*Acacia constricta*). The dominant grasses are gramma and threeawn (*Aristida* sp.), and the area is overgrazed. Creosotebush, ocotillo, prickly pear, and lechuguilla are uncommon at these sites.

A total of 834 trap nights produced 17 *Perognathus nelsoni*, 11 *Dipodomys merriami*, 12 *Dipodomys nelsoni*, 4 *Peromyscus eremicus*, and 66 *Peromyscus hooperi*.

Based on those collections, the optimum habitat for *P. hooperi* is most abundant where the Grassland Transition vegetation reaches its fullest development along the flanks and crests of the mountains between 1400 and 1700 meters. In such places, standing and fallen giant daggers are dominant along with several succulent desert plants and grassy cover is relatively abundant (Fig. 2). *P. hooperi* was not found at lower elevations on the rocky hills nor on the desert plain where Chihuahuan Desert Scrub vegetation dominates (Fig. 1A); *P. eremicus* and *P. pectoralis* are the dominant species of *Peromyscus* in that habitat. At its lowest extension, the Grassland Transition vegetative zone meets and interdigitates with the succulent desert vegetation characteristic of the rocky arroyos and limestone hillsides. In those situations, *P. hooperi* is confined to the slopes or areas where giant dagger, bear grass, and sotol dominate, whereas *P. eremicus* and *P. pectoralis* occur mainly in the rocky outcrops and arroyos that support desert scrub habitat (Fig. 1B). *P. eremicus* occurs as a "straggler" in the higher elevations of the Grassland Transition zone, but there it clearly is numerically subordinate to *P. hooperi*.

We also trapped *P. hooperi* at two localities in extreme southern Coahuila and adjacent Zacatecas. On 22 March 1978, 108 Sherman live traps placed in a sotol-giant dagger-agave association 1.2 mi. S, 1 mi. W El Gorrión produced 3 *Peromyscus hooperi*, 3 *Peromyscus melanophrys*, 2 *Neotoma albigula*, 1 *Neotoma goldmani*, 1 *Perognathus nelsoni*, and 1 *Peromyscus pectoralis*. On

FIG. 2.—Habitats along dirt road traveling westward from Ocampo. **A.** Collecting site 14.2 mi. W Ocampo where *P. hooperi* was abundant. **B.** Collecting site 15.2 mi. W Ocampo showing standing and fallen giant daggers where *P. hooperi* was numerous.

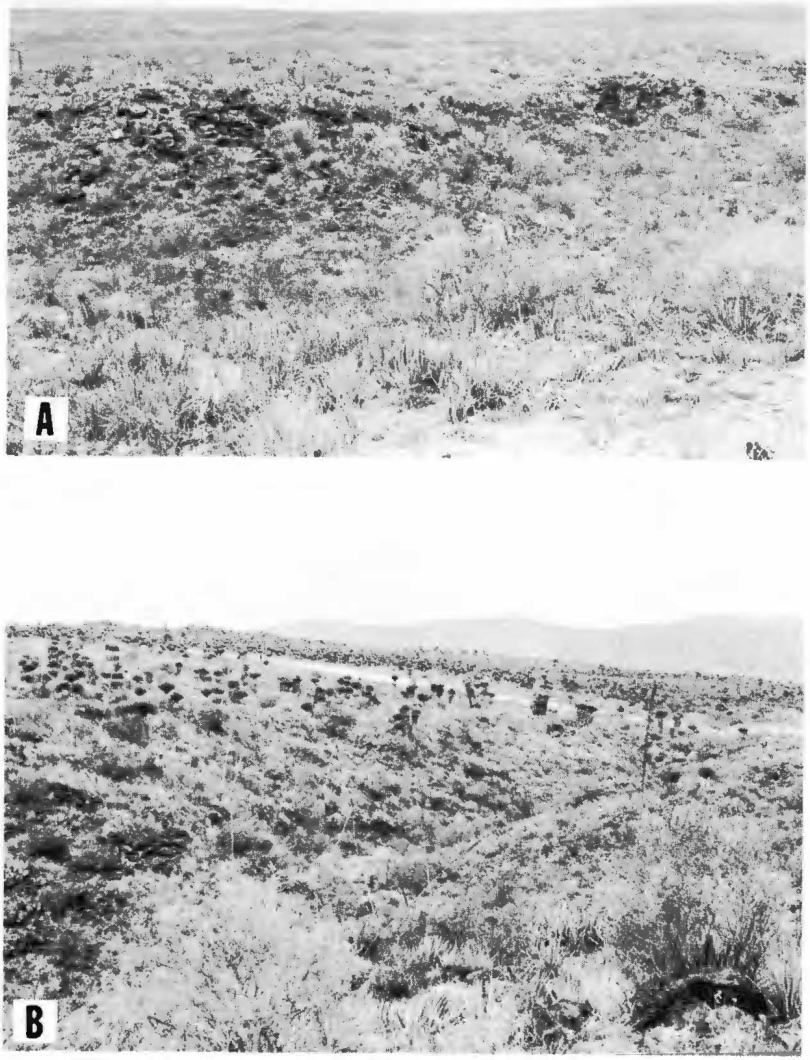

FIG. 1.—Habitats along dirt road traveling westward from Ocampo. **A.** Collecting site 1 mi. W Ocampo where *P. eremicus* and *P. pectoralis* were taken. **B.** Collecting site 4.7 mi. W Ocampo; *P. hooperi* was taken on the bajadas where giant dagger and sotol are dominant; and *P. eremicus* and *P. pectoralis* were obtained in the rocky arroyo.

the same night, 128 Shermans placed in a yucca-sotol-giant dagger association along a rocky hillside 0.5 mi. S of the Coahuila-Zacatecas border on highway 54 produced 9 *Peromyscus hooperi*, 8 *Peromyscus pectoralis*, 1 *Peromyscus melanophrys*, and 1 *Neotoma goldmani*.

These results corroborate our conclusions from trapping *P. hooperi* in the Ocampo region, namely, that the species has extremely narrow habitat preferences, occurring only in Grassland Transition vegetation where sotol, beargrass, various kinds of yucca (especially giant dagger), agave, and gramma, are the dominant plants.

Distribution

P. hooperi has been recorded from 13 localities in Coahuila and one from extreme northeastern Zacatecas (Fig. 3). These 14 localities are aligned in a nearly straight line extending from north-northwest to south-southeast through central Coahuila and just entering northern Zacatecas. In north-central Coahuila, localities correspond to the location of a continuous chain of mountains beginning with the Sierra El Pino in the north and continuing southeastward with the Sierra El Fuste, Sierra la Madera, Sierra la Fraqua, and the Sierra la Paila, respectively. The records from extreme southeastern Coahuila are in the Sierra Playa Madera and Sierra Encarnación ranges, which form a west to east axis across the southern part of the state and connect this region with the Sierra Madre Occidental of Durango and the Sierra Madre Oriental of Nuevo León (Muller, 1947). Insofar as can be ascertained from field notes and by visiting several of these localities, all are situated on the eastern or southeastern facing slopes of the aforementioned ranges in Grassland Transition vegetation.

Two other major montane axes traverse Coahuila in a north to south directional arrangement (Muller, 1947). Along the western border of the state, the Sierra Mojada, Sierra Almagre, and Sierra Hechiceros run northward almost to the valley of the Rio Grande. The Sierra El Carmen axis, which includes numerous smaller ranges, extends from extreme northern Coahuila along the eastern flanks of the state to the Sierra Madre Oriental in southeastern Coahuila. Significantly, *P. hooperi* has not been recorded from either one of those north-south montane axes, although Grassland Transition vegetation occurs in the foothills of each of them.

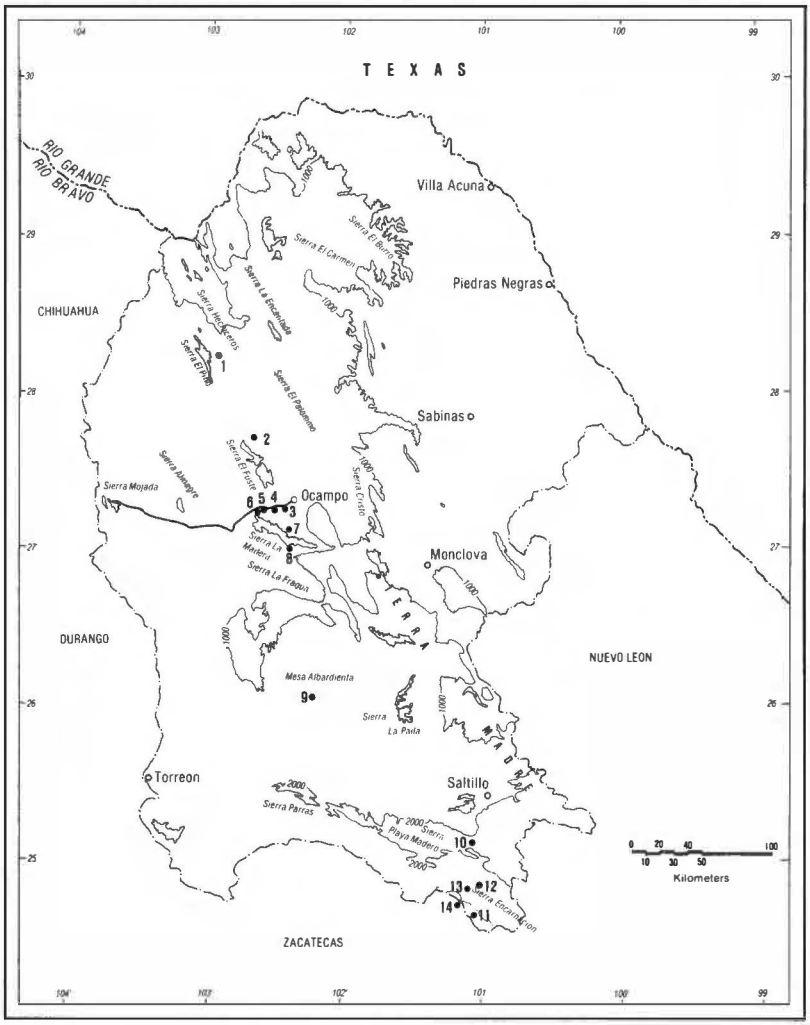

FIG. 3.—Distribution of *Peromyscus hooperi* in northern México. Numbers identify localities mentioned in the text. The 1000 and 2000-meter contours are shown and the mountain ranges are named according to México (1983).

The presently known geographic distribution of *P. hooperi* is enigmatic. Our records show this species to be confined not only to the Grassland Transition Vegetative Association but in a peculiar north-northwest to south-southeast line. There is no apparent explanation why the species should not be found at other localities, at least in Coahuila, where this vegetative association occurs.

Extensive collecting throughout the state by personnel from the University of Kansas (Baker, 1956) did not yield specimens outside this range (we have examined all relevant specimens at Kansas). No physiographic or biotic factors known to us suggest a hypothesis for explaining the distribution of *P. hooperi*.

Because we found this species only in the Grassland Transition habitat and because this habitat and, we assume, populations of *P. hooperi* are disjunct, we regard its present distribution as relict. That is, we think its present occurence is reduced from some former, at least continuous (if not more extensive) distribution. We have no way of estimating the extent of such former distribution. Certainly, intensive collecting in this habitat throughout Coahuila is encouraged.

Identification

P. hooperi can be distinguished from *P. eremicus* and *P. pectoralis*, where it occurs sympatrically with these latter two species in Coahuila, by using a suite of morphological and cytological characters (Table 1).

Peromyscus hooperi *compared with* P. eremicus

Distinguishing these two species is difficult using conventional measurements. In their original description, Lee and Schmidly (1977) had only five adult specimens of *P. hooperi*, which they compared with 14 specimens of *P. eremicus*. None of the latter specimens was from an area of sympatry of the two species. Those authors reported an absolute difference in size between the two species, with no overlap in five of seven measurements. Critical examination of a large series of specimens of both species from the Ocampo region, however, has revealed that the degree of difference between them is not so great as originally suggested by the authors (Table 2). Slight morphological overlap is evident in all external and cranial measurements, making positive identification difficult. Nevertheless, *P. hooperi* and *P. eremicus* fall into nonoverlapping subsets in the Duncan's analysis for all characters except length of hind foot, length of maxillary toothbrow, and length of the auditory bulla (Table 2), indicating that the two species do differ significantly in most external and cranial measurements.

Multivariate analyses also revealed a statistically significant difference between most mensural characters of the two species.

TABLE 1.—*Morphologic comparisons of three species of* Peromyscus *from Coahuila.*

Attribute	*P. hooperi*	*P. eremicus*	*P. pectoralis*
Hind foot	Hairy on proximal one-fourth to calcaneum	Naked to the end of the calcaneum	Hairy on proximal one-fourth to calcaneum
Mammary glands	Pectoral (1-1) and inguinal (2-2) mammae present	Only inguinal (2-2) mammae present	Pectoral (1-1) and inguinal (2-2) mammae present
Molars	Low frequency of occurrence of styles and lophs	Low frequency of occurrence of styles and lophs	High frequency of occurrence of styles and lophs
Phallus	Medium with protractile tip; glans with two dorsal and one ventral flap (not as distinct as lappets)	Short and broad; vase-shaped with no protractile tip; no dorsal lappets	Long and slender with protractile tip; glans with two dorsal lappets separated by a cleft and a single ventral lappet
Baculum	Medium and slender with rounded base; cartilaginous tip medium, conical	Short and gross with squarish base; cartilaginous tip very small, diffuse	Long and slender with rounded base; cartilaginous tip large, conical
Shelf of bony palate	No bony protuberance on posterior margin	Posterior margin with short bony protuberance	Usually without bony protuberance on posterior margin
Nasal bones	Posterior ends tapered in a V-shaped fashion	Posterior ends truncate or flat	Posterior ends truncate or V-shaped
Premaxillaries	Variable: either subequal to or extending beyond margin of nasals	Distinctly extending beyond level of nasals	Variable: either subequal to or extending beyond margin of nasals
Chromosomes (2n=48 in all species)	Three pairs of biarmed autosomes; 20 pairs of acrocentrics	All biarmed autosomes	Six pairs of biarmed autosomes; 17 pairs of acrocentrics

TABLE 2.—*Variation among three species of* Peromyscus (*H* = hooperi, *E* = eremicus, *P* = pectoralis) *from Coahuila in four external, 12 cranial, and five phallic measurements. Species are listed in decreasing order of means. Vertical lines in the column marked Duncan's indicate nonsignificant subsets for groups of means that were significantly different at the 0.05 level using Anova. Groups of means that were found to be not significantly different at the 0.05 level are marked ns. Characters that could not be measured for a species are marked NA.*

Species	N	Mean (Range) ± 1 SD	CV	Duncan's
		Total Length		
H	59	201.80 (172-218) ± 10.16	4.76	|
P	27	201.00 (186-232) ± 10.14	5.05	|
E	45	185.49 (161-205) ± 9.84	5.28	|
		Length of Tail		
P	27	110.30 (92-132) ± 7.53	6.84	|
H	59	108.75 (86-123) ± 7.28	6.41	|
E	45	95.47 (79-105) ± 7.65	7.94	|
		Length of Hind Foot		
P	27	21.33 (19-23) ± 1.14	5.37	|
H	59	21.15 (20-23) ± 0.83	3.88	|
E	45	20.29 (18-24) ± 1.15	6.66	|
		Length of Ear		
H	59	19.22 (17-22) ± 1.06	5.44	|
P	27	18.59 (17-20) ± 1.01	5.42	|
E	45	18.33 (17-21) ± 1.61	8.38	|
		Greatest Length of Skull		
H	59	26.48 (25.75-27.50) ± 0.41	1.52	|
P	27	26.16 (25.00-27.35) ± 0.62	2.38	|
E	45	25.95 (24.00-26.00) ± 0.61	2.50	|
		Basilar Length		
H	59	21.45 (20.55-22.90) ± 0.50	2.30	|
P	27	20.77 (19.20-22.45) ± 0.66	3.16	|
E	45	20.24 (18.95-21.80) ± 0.67	3.21	|
		Length of Nasals		
H	59	9.97 (9.25-10.65) ± 0.30	2.96	|
P	27	9.73 (9.15-10.50) ± 0.32	3.29	|
E	45	8.89 (8.25-10.20) ± 0.50	5.48	|
		Length of Rostrum		
P	27	9.90 (9.25-10.55) ± 0.33	3.32	|
H	59	9.75 (9.30-10.35) ± 0.24	2.46	|
E	45	8.83 (8.25-9.65) ± 0.37	4.32	|

TABLE 2.—*Continued.*

		Mastoid Breadth		
H	59	11.74 (11.30-13.10) ± 0.25	2.04	|
E	45	11.12 (10.55-11.55) ± 0.24	2.24	|
P	27	10.90 (10.40-11.50) ± 0.30	2.78	|
		Zygomatic Breadth		
H	59	13.12 (11.60-13.70) ± 0.34	2.56	|
P	27	12.78 (12.30-13.45) ± 0.34	2.64	|
E	45	12.75 (12.10-13.45) ± 0.35	2.49	|
		Skull Depth		
H	59	9.16 (8.60-9.90) ± 0.31	3.37	|
P	27	8.99 (8.35-9.50) ± 0.24	2.70	|
E	45	8.86 (8.10-9.20) ± 0.26	3.27	|
		Length of Bony Palate		
H	59	3.96 (3.60-4.25) ± 0.15	3.84	|
P	27	3.76 (3.50-4.05) ± 0.13	3.47	|
E	45	3.74 (3.30-4.20) ± 0.19	5.35	|
		Length of Incisive Foramen		
H	59	4.59 (4.10-5.00) ± 0.22	4.77	|
P	27	4.51 (3.95-4.85) ± 0.24	5.38	|
E	45	4.27 (3.80-4.55) ± 0.23	6.93	|
		Length of Maxillary Toothrow		
H	59	3.96 (3.75-4.15) ± 0.08	2.18	
P	27	3.95 (3.70-4.20) ± 0.15	3.79	ns
E	45	3.91 (3.80-4.10) ± 0.09	3.07	
		Length of Auditory Bulla		
H	59	4.93 (4.70-5.30) ± 0.13	2.64	|
E	45	4.92 (4.35-5.30) ± 0.18	3.80	|
P	27	4.50 (4.00-5.10) ± 0.36	7.83	|
		Breadth of Auditory Bulla		
H	59	3.80 (3.30-4.00) ± 0.14	3.64	|
E	45	3.70 (3.40-4.20) ± 0.18	5.11	|
P	27	3.25 (2.90-3.85) ± 0.25	7.75	|
		Length of Distal Tract		
P	7	15.25 (14.08-16.11) ± 0.84	5.54	|
H	16	12.67 (11.73-13.87) ± 0.52	3.99	|
E	12	9.88 (8.75-10.45) ± 0.48	4.87	|

TABLE 2.—*Continued.*

		Length of Glans		
P	7	10.90 (10.03-11.73) ± 0.74	6.76	|
H	16	8.51 (7.79-9.28) ± 0.46	5.39	|
E	12	6.46 (5.76-7.36) ± 0.52	8.12	|
		Length of Protractile Tip		
P	7	3.38 (2.99-3.84) ± 0.32	9.56	|
H	16	2.53 (2.13-2.88) ± 0.21	8.27	|
E	12	NA		
		Diameter of Glans		
E	12	4.01 (3.73-4.48) ± 0.26	6.41	|
H	16	3.19 (2.45-3.73) ± 0.35	10.97	|
P	7	3.12 (2.67-3.52) ± 0.36	11.23	|
		Length of Baculum		
P	7	12.80 (11.95-13.55) ± 0.62	4.88	|
H	16	10.91 (10.03-11.73) ± 0.37	3.44	|
E	12	7.92 (6.93-8.85) ± 0.52	6.50	|
		Length of Cartilaginous Tip		
P	7	0.79 (0.75-0.85) ± 0.05	6.74	|
H	16	0.44 (0.32-0.53) ± 0.07	7.73	|
E	12	NA		

Wilks' Criterion produced a highly significant *F*-value ($P \leq 0.001$) for a multivariate analysis of variance between *P. hooperi* and *P. eremicus*. Similarly, discriminant function analysis resulted in a histogram that clearly revealed two distinct groupings with no intermediate specimens. The Mahalanobis D^2 value for this comparison ($D^2 = 21.83$; $F_{12,74} = 32.03$; $P \leq 0.0001$) is similar to that reported by Wilkins and Schmidly (1979) for comparisons between three species of pocket mice (*Perognathus*) from West Texas. The measurements that contributed most significantly to the discrimination between *P. hooperi* and *P. eremicus* were greatest length of skull, mastoid breadth, length of nasals, and length of incisive foramen. *P. hooperi* averages larger than *P. eremicus* in all of those features.

Two qualitative characters of the skull (shape of the posterior ends of the nasal bones and presence of a palatine spur) also are useful in differentiating the two species (Fig. 4). The posterior ends of the nasal bones are tapered in a V-shaped pattern in *P. hooperi*

and not truncate or flat, as they are in *P. eremicus*. This character provided separation of 91 per cent of the specimens examined. The posteromedial margin of the palate in *P. eremicus* has a short bony protuberance (unlike *P. hooperi*) in 85.8 per cent of our specimens. Use of these characters in combination allowed positive identification of all specimens from Coahuila regardless of age. Although they are not diagnostic, there are some differences between *P. hooperi* and *P. eremicus* in the frequency of occurrence of styles and lophs on the molar teeth (Fig. 5). The former has a greater proportion of mesolophs and mesostyles on M2 and a much greater proportion of mesostylids on m2.

The phalli of the two species are strikingly different. The glans penis of *P. eremicus* is vase-shaped, broad with respect to length, and strongly flared distally; there is no protractile tip (Fig. 6). The glans of *P. hooperi* is small but relatively wide, with a long, narrow protractile tip. There are also marked differences in the bacula of the two species, with that of *P. eremicus* being shorter (Table 2), heavier, and having a much broader base than that of *P. hooperi* (Fig. 6). Additionally, the baculum of *P. eremicus* terminates in a minute cap of cartilage rather than a distinct cartilaginous cone, as in *P. hooperi.*

There are differences in external features between the two species. Pectoral mammae are absent in *P. eremicus*, but present in *P. hooperi.* Lee and Schmidly (1977), using dry museum specimens, erroneously reported only axillary mammae in *P. hooperi.* In *P. eremicus*, the soles of the hind feet are naked to the end of the calcaneum (occasionally they are naked in a narrow area or covered medially by ends of the lateral root hairs on the tarsus between the ends of the metatarsals and the end of the calcaneum); in *P. hooperi*, the soles of the hind feet are hairy on the proximal fourth to the calcaneum.

Chromosomally, the two species are markedly different. In *P. eremicus* (2n=48, AN=92) all of the autosomes (46) are biarmed, whereas *P. hooperi* (2n=48, AN=52) has only three pairs of biarmed autosomes (1, 22, 23).

Peromyscus hooperi *compared with* P. pectoralis

Although there are no diagnostic external or cranial measurements that separate these two species, they fall into nonoverlapping subsets in the Duncan's analysis (Table 2) for all but four measurements (total length, length of tail, length of hind

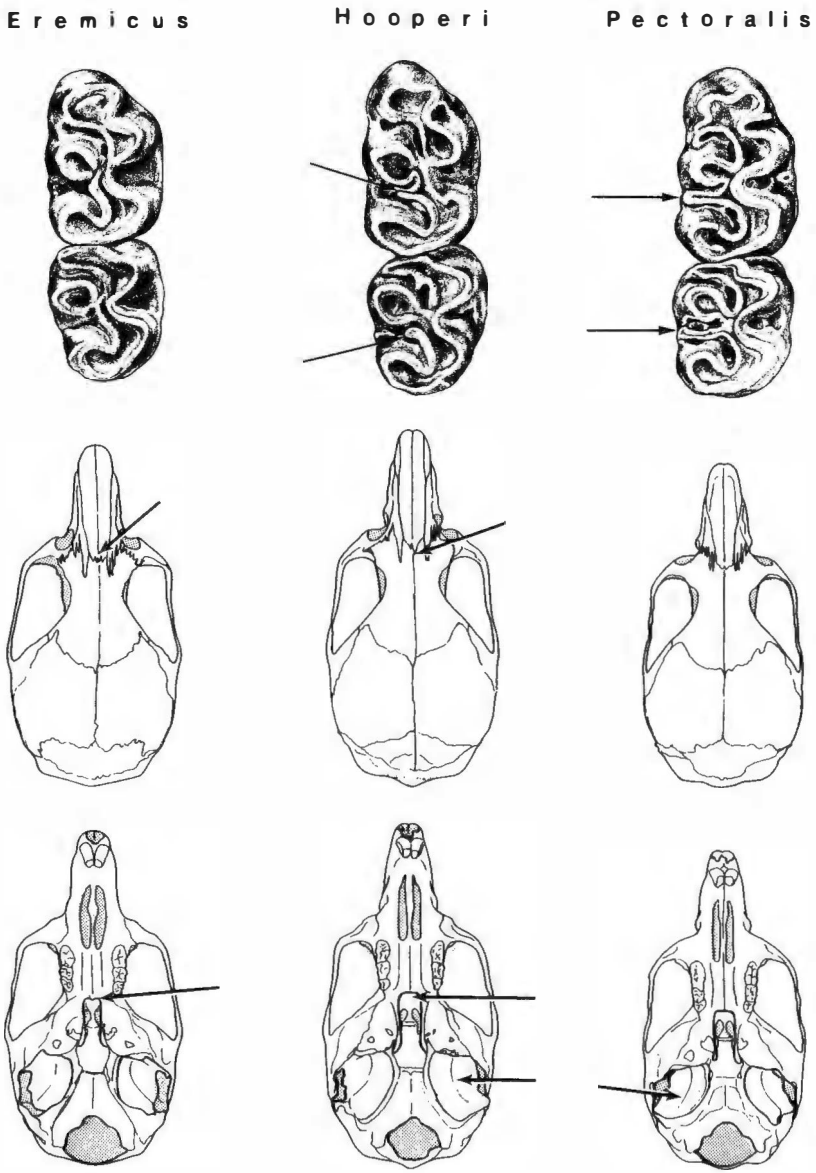

FIG. 4.—Qualitative morphological differences among *P. hooperi*, *P. eremicus*, and *P. pectoralis*. **Top**. Occlusal view of teeth (M1 and M2) illustrating molar complexity. **Middle**. Position of nasals and shape of posterior margin of nasals. **Bottom**. Ventral view of skull showing degree of inflation of auditory bulla and development of spur on the posterior margin of the bony palate.

foot, and length of incisive foramen). In all cranial measurements except length of rostrum and length of incisive foramen, *P. hooperi* is significantly larger than *P. pectoralis*. Another cranial difference between the two species is the size of the auditory bulla, which is significantly larger and more inflated in *P. hooperi* than in *P. pectoralis*. This difference is reflected in the measurements of bulla length and breadth, both of which have significantly larger means in *P. hooperi* than in *P. pectoralis*.

Dental differences clearly distinguish the two species. The molars of *P. pectoralis* are complex with distinct enamel ridges (called mesolophs) arising out of the mure of M2 and projecting to the labial side of the tooth where they terminate in raised projections called styles (Fig. 4). The lower molars (m2) typically have mesostylids and ectostylids but not mesolophids or ectolophids. Additionally, an anteroloph arises from the procingulum of M1. *P. hooperi* has a much simpler dentition, with a lower frequency of mesolophs and never with an anteroloph (Fig. 5). Furthermore, in those specimens of *P. hooperi* with a mesoloph, this structure never extends more than one-quarter of the distance between the mure of the tooth and its labial edge.

Differences in the phalli of *P. hooperi* and *P. pectoralis* are not so marked as those noted between *P. hooperi* and *P. eremicus*. Both species, in contrast to *P. eremicus*, have a glans penis composed of a main body of dense tissues and a tapered, protractile tip. The bacula of both are small in diameter, relatively long, and end in a cartilaginous spine (Fig. 6). There are, however, several diagnostic differences between them, with the baculum and the cartilaginous spine being longer in *P. pectoralis* than in *P. hooperi* (Table 2). Compared to *P. pectoralis*, the main body of the glans of *P. hooperi* is shorter and relatively broader, and the protractile tip is much shorter and more delicate. The proximal two-thirds of the surface of the glans of *P. hooperi* is invested with short spines or tubercles, and there are slight longitudinal furrows on the surface of the glans. The glans of *P. pectoralis* is comparatively smoother, with only weakly developed spines over the proximal one-third of its length and no evidence of furrows. The distal margin of the glans in *P. hooperi* has two dorsal lobelike flaps separated by a cleft and a rounded ventral flap. These flaps are differently shaped and less pronounced than the lappets on the phallus of *P. pectoralis*, although the two structures are probably homologous.

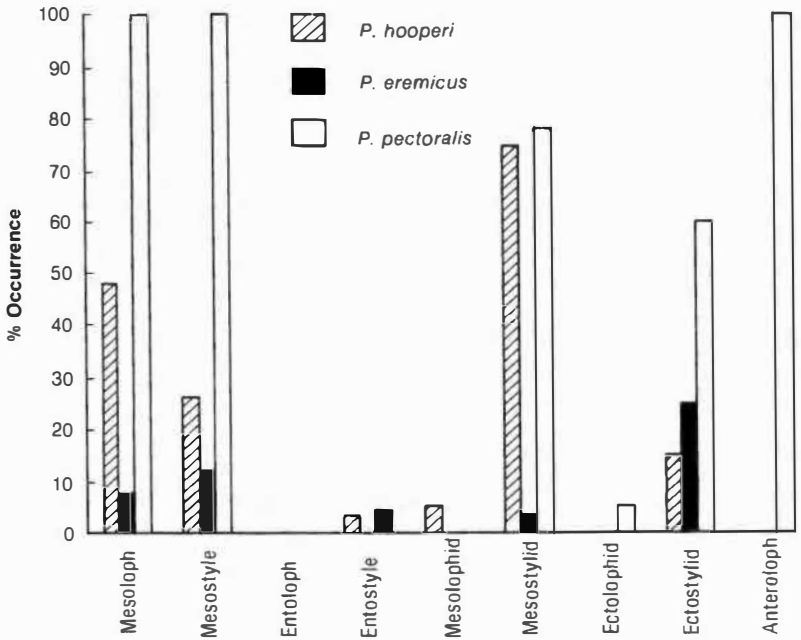

FIG. 5.—Frequencies of styles (stylids) and lophs (lophids) among three species of *Peromyscus* from Coahuila.

The standard karyotype of *P. hooperi* differs from that of *P. pectoralis* in having 52 instead of 58 autosomal arms (latter number reported by Lee *et al.*, 1972).

MORPHOLOGICAL VARIATION

Nongeographic

Three aspects of morphological variation (age, secondary sexual, and individual) were analyzed. These reveal the phenotypic and to some extent the genetic variability within the species and understanding them is basic to the study of geographic variation.

Age variation.—Age variation was studied to ascertain 1) the degree of difference relating to growth that occurred among the six age categories and 2) which individuals had terminated growth, or nearly so, and could be termed adults. Mice of age group I were not represented in our sample of *P. hooperi* and only a single individual of age group II was present.

Of the four external and 12 cranial measurements tested, only two (skull depth and length of maxillary toothrow) revealed no significant differences among the means of the five age categories

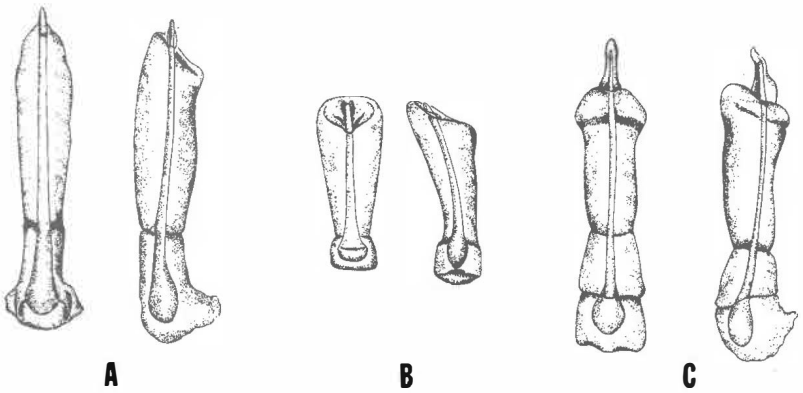

FIG. 6.—Lateral and dorsal view of the penis showing degree of development of protrusible tip on glans and baculum: **A**, *pectoralis*, **B**, *eremicus*; **C**, *hooperi*.

(Table 3). One measurement (basilar length) exhibited five nonoverlapping subsets, and another measurement (length of nasals) had four such subsets (VI-V, IV, III, II). Three nonoverlapping subsets (VI-IV, III, II) were found for mastoid breadth, zygomatic breadth, and length of auditory bulla, and two nonoverlapping subsets (VI-III, II) resulted for breadth of auditory bulla.

All remaining measurements exhibited some overlapping of maximal nonsignificant subsets (Table 3). Two of these measurements had means that fell into two subsets. One age category (V) is shared between the two subsets for length of bony palate, and two age categories (V and IV) are shared between the two subsets for hind foot length. Three measurements exhibited three overlapping subsets. Tail length was divided VI-V, V-IV, and III-II; ear length was arranged in subsets of VI-V, V-III, and IV-II; and length of the incisive foramen was arranged in subsets of VI-IV, V-III, and II. Four measurements were divided into four nonsignificant subsets. Three of these (total length, greatest length of skull, and length of rostrum) exhibited the following pattern of subsets: VI-V, V-IV, III, and II. Subsets of VI-V, IV, III, and II were found for length of nasals.

Based upon this analysis, the most parsimonious grouping of categories is: II (smallest individuals), III (medium-sized mice), and IV-V-VI (largest individuals). Members of age categories IV, V, or VI were found to have the largest mean for all measurements except skull depth, length of maxillary toothrow, and breadth of auditory bulla. For all measurments except length of maxillary toothrow,

TABLE 3.—*Variation with age in four external and 12 cranial measurements of* Peromyscus hooperi *from Coahuila, México. Age categories are listed in decreasing order of means. Groups of means that were significantly different at the 0.05 level using single classification analysis of variance were tested with Duncan's Procedure to find the maximally nonsignificant subsets, which are indicated by vertical lines in the column marked Duncan. Age categories are defined in text.*

Age	N	Mean ± 1 SD	CV	Duncan's
		Total Length		
6	13	207.85 ± 8.51	4.10	|
5	14	203.57 ± 11.12	5.46	|
4	32	197.50 ± 8.84	4.48	|
3	28	185.86 ± 12.54	5.75	|
2	1	156.00		|
		Tail Length		
6	13	114.00 ± 6.42	5.63	|
5	14	108.43 ± 9.12	8.41	|
4	32	107.09 ± 5.82	5.44	|
3	28	100.32 ± 9.15	9.12	|
2	1	93.00		|
		Hind Foot		
6	13	21.54 ± 0.88	4.07	|
5	14	21.28 ± 0.47	2.20	|
4	33	21.00 ± 0.90	4.29	|
3	30	20.83 ± 1.08	5.21	|
2	1	20.00		|
		Ear Length		
6	12	19.75 ± 1.14	5.76	|
5	14	19.36 ± 0.74	3.85	|
4	33	19.00 ± 1.09	5.74	|
3	29	18.86 ± 0.99	5.25	|
2	1	17.00		|
		Greatest Length of Skull		
6	15	26.91 ± 0.26	0.97	|
5	13	26.60 ± 0.49	1.83	|
4	29	26.37 ± 0.32	1.23	|
3	28	25.64 ± 0.52	2.04	|
2	1	23.80		|

TABLE 3.—*Continued.*

		Basilar Length		
6	15	21.91 ± 0.32	1.45	
5	13	21.55 ± 0.55	2.57	
4	32	21.22 ± 0.38	1.82	
3	28	20.57 ± 0.48	2.33	
2	1	18.55		
		Length of Nasals		
6	15	10.13 ± 0.35	3.45	
5	14	10.10 ± 0.24	2.41	
4	32	9.90 ± 0.26	2.65	
3	29	9.51 ± 0.33	3.52	
2	1	8.60		
		Length of Rostrum		
6	15	9.92 ± 0.16	1.65	
5	14	9.79 ± 0.24	2.48	
4	32	9.70 ± 0.24	2.51	
3	29	9.32 ± 0.35	3.73	
2	1	8.00		
		Mastoid Breadth		
6	15	11.82 ± 0.17	1.46	
5	14	11.75 ± 0.19	1.63	
4	32	11.74 ± 0.30	2.58	
3	28	11.52 ± 0.30	2.57	
2	1	10.60		
		Zygomatic Breadth		
6	14	13.24 ± 0.18	1.32	
5	14	13.21 ± 0.32	2.41	
4	34	13.07 ± 0.38	2.94	
3	30	12.74 ± 0.33	2.59	
2	1	11.55		
		Skull Depth		
6	15	9.24 ± 0.24	2.62	
4	32	9.14 ± 0.30	3.28	
3	29	9.07 ± 0.39	4.30	
5	13	9.06 ± 0.38	4.15	
2	1	8.60		

TABLE 3.—*Continued.*

		Length of Bony Palate	
6	15	4.01 ± 0.14	3.37
4	34	3.94 ± 0.16	4.07
5	14	3.92 ± 0.15	3.77
3	30	3.85 ± 0.16	4.06
2	1	3.60	
		Length Incisive Foramen	
6	14	4.65 ± 0.21	4.59
5	15	4.58 ± 0.22	4.91
4	34	4.52 ± 0.21	4.71
3	30	4.46 ± 0.23	5.23
2	1	3.80	
		Length Maxillary Toothrow	
2	1	4.00	
6	15	3.97 ± 0.11	2.81
4	34	3.95 ± 0.08	2.03
5	14	3.93 ± 0.07	1.70
3	30	3.90 ± 0.09	2.24
		Length Auditory Bulla	
6	15	4.96 ± 0.13	2.62
5	14	4.94 ± 0.12	2.33
4	34	4.93 ± 0.14	2.80
3	29	4.82 ± 0.12	2.45
2	1	4.30	
		Breadth Auditory Bulla	
5	14	3.80 ± 0.12	3.20
4	34	3.78 ± 0.14	3.66
3	29	3.76 ± 0.14	3.88
6	15	3.74 ± 0.15	3.91
2	1	2.85	

age category II had the smallest mean. We have termed the three groups mentioned above as juvenile, subadult, and adult, respectively, and use this terminology throughout the remainder of this paper.

Secondary sexual variation.—Adult males were tested against adult females to determine if means for the 16 measurements were significantly different between them. There was a significant

TABLE 4.—*Secondary sexual variation in four external and 12 cranial measurements of adult* Peromyscus hooperi *from vicinity of or near Ocampo, Coahuila, México. Means for males and females that are significantly different* ($P<0.05$) *are indicated by an asterisk.*

	Males (36)		Females (27)			
	$\bar{X} \pm 1$ SD	CV	$\bar{X} \pm 1$ SD	CV	*F*-value	*P*
Total length	199.56±11.53	5.78	203.48±7.59	3.73	2.08	0.16
Tail length	108.59±8.38	7.72	109.40±5.58	5.10	0.42	0.52
Hind foot length	21.20±0.91	4.31	21.15±0.73	3.46	0.04	0.84
Ear length	19.32±1.12	5.80	19.12±0.97	5.08	0.79	0.38
Greatest skull length	26.48±0.40	1.52	26.69±0.41	1.52	3.19	0.08
Basilar length	21.37±0.48	2.24	21.59±0.51	2.35	4.50	0.04*
Length of nasals	9.98±0.31	3.14	10.03±0.28	2.79	1.24	0.27
Length of rostrum	9.72±0.21	2.16	9.84±0.27	2.76	3.00	0.09
Mastoid Breadth	11.68±0.20	1.68	11.86±0.28	2.39	8.38	0.01*
Skull depth	9.16±0.31	3.39	9.14±0.30	3.35	0.00	0.98
Length of bony palate	3.93±0.15	3.94	3.98±0.15	3.73	0.22	0.64
Length incisive foramen	4.53±0.22	4.77	4.60±0.22	4.77	1.76	0.19
Length maxillary toothrow	3.94±0.07	1.77	3.96±0.10	2.59	0.42	0.52
Length auditory bulla	4.92±0.12	2.52	4.96±0.14	2.77	2.45	0.12
Breadth auditory bulla	3.76±0.12	3.20	3.80±0.16	4.08	5.07	0.03*
Zygomatic breadth	13.08±0.29	2.23	13.22±0.38	2.88	2.18	0.14

difference (ANOVA; $P \leq 0.05$) between the sexes in three measurements (basilar length, mastoid breadth, and breadth of the auditory bulla), with females being larger than males (Table 4). In the remaining 13 measurements, females averaged larger than males, but not significantly, in all but three measurements (hind foot length, ear length, and skull depth).

The extent of sexual dimorphism in *P. hooperi* is slightly greater than that reported for other species of *Peromyscus*. Cockrum (1954), Fox (1948), Schmidly (1973), and Legg (1978) noted sexual differences in only one cranial measurement for *P. leucopus*, *P. maniculatus*, *P. boylii*, and *P. eremicus*, respectively. Schmidly (1972) reported significant differences between the sexes in two measurements from a sample of *P. pectoralis*. Although there is a slight amount of secondary sexual dimorphism between males and females in the Ocampo sample of *P. hooperi*, we have combined

values for the sexes in analyzing geographic variation. An overall test for the effect of sex, using multivariate analysis of variance, indicated that the sexes were not significantly different (Wilks' Criterion; $F_{16,33} = 1.52$; $P \leq 0.15$).

Individual variation.—Coefficients of variation (CV) for dimensions of adult males and females are given in Table 4. As expected, coefficients for external measurements average considerably higher than those for cranial features. Length of tail has the highest coefficient of the 16 measurements tested for both males and females. Only four other measurements for males (total length, hind foot length, ear length, and length of incisive foramen) and three for females (ear length, length of incisive foramen, and breadth of the auditory bulla) have coefficients of variation of 4.0 or more. Males have higher coefficients in seven measurements, and females have higher values in seven; there are two measurements with the same coefficient for both sexes. The average CV for measurements of *P. hooperi* (3.42), as presented in Table 2, is considerably lower than those for *P. eremicus* (4.75) and *P. pectoralis* (4.42). This low average CV value for *P. hooperi* corresponds to the low mean value of genetic heterozygosity in this species (see *Protein Variation*).

Geographic

There is little geographic variation in morphological features among the four samples of *P. hooperi*. Mice from the southern part of the species range (samples 3 and 4) are slightly darker in dorsal coloration than those from northern samples (1 and 2), but these differences are not striking. Analysis of variance revealed only four measurements (greatest length of skull, skull depth, length of incisive foramen, and maxillary toothrow length) with a significant *F*-value ($P \leq .05$) among the four samples. With the exception of skull depth, which formed two nonoverlapping subsets (samples 3-1 and 4-2), the samples for these measurements in the Duncan's analysis fell into two significantly different but overlapping subsets of three samples each. The two subsets for greatest length of skull consisted of samples 1-3-2 and 3-2-4; for length of incisive foramen, 3-4-1 and 4-1-2; and for length of maxillary toothrow, 4-2-3 and 2-3-1. These groupings reflect some differentiation between northern and southern samples of *P. hooperi*, but the pattern is not concordant among all measurements.

A plot of the first two principal components extracted from the matrix of correlation among characters revealed no clear differentiation among the individuals of the four samples. Specimens from sample 2 (Ocampo) were dispersed throughout the plot and overlapped all specimens of the other three samples except for a single individual from sample 4 (El Gorrión) and one from sample 3 (Cuatro Cienegas). Principal component I accounted for 35 per cent of the variation among individuals; principal component II, 10 per cent. All characters exhibited high positive loadings in component I, suggesting this represents a general size factor. Component II contrasted cranial measurements, most of which had high positive loadings, against external measurements, all of which had negative loadings.

Karyology

The karyotype of *Peromyscus hooperi* is comprised of three pairs of biarmed autosomes (nos. 1, 22, and 23) and 20 pairs of acrocentric autosomes (all others). The X is a large subtelocentric, and the Y is a small metacentric (2n = 48; FN = 52). Except for identification of the Y and the numerical designations, this description is the same as that originally given by Lee and Schmidly (1977) based on standard chromosomes. The G-banded karyotype of *P. hooperi* (Fig. 7A) is thus identical to the standard for *Peromyscus* (Committee, 1977). All autosomes and the X bear centromeric heterochromatin and one pair of arms of the Y is heterochromatic as identified by C-bands (Fig. 7B). Three nucleolus organizers (NORs) are located near the telomeres of short arms on pairs 1, 22, and 23 (Fig. 8). No karyotypic variation was found among the 10 specimens examined.

Most karyological characteristics (2n, FN, G-bands, and C-bands) of *P. hooperi* agree closely with those of *P. banderanus*, *P. crinitus*, *P. simulus*, and at least the northern populations of *P. boylii* (Greenbaum and Baker, 1978; Yates *et al.*, 1979; Committee, 1977; Robbins and Baker, 1981; Carleton *et al.*, 1982; unpubl. data). The autosomal component of this karyotype has been postulated as ancestral in the genus *Peromyscus* (see above references as well as Lee and Schmidly, 1977, and Lee and Elder, 1977). Details of any differences among these species in the sex chromosomes and number and location of NORs have not yet been described. The number and location of NORs is the same in *P. hooperi* and *P. crinitus* (nos. 1, 22, and 23; unpubl. data). In contrast, populations of *P. boylii* from southern Arizona have at least five pairs of NORs

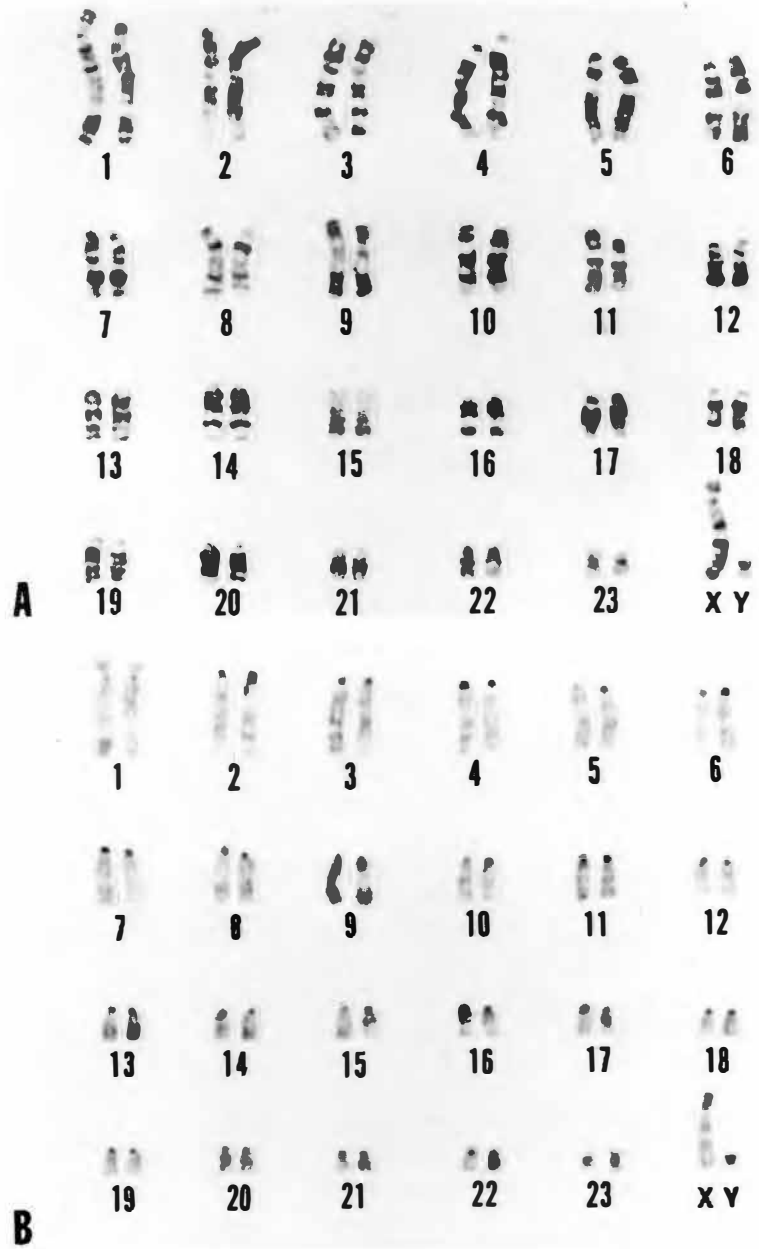

FIG. 7.—G-banded (**A**) and C-banded (**B**) karyotype of *P. hooperi* (male, from 15.2 mi. W Ocampo, Coahuila). Some pairings in B are conjectural.

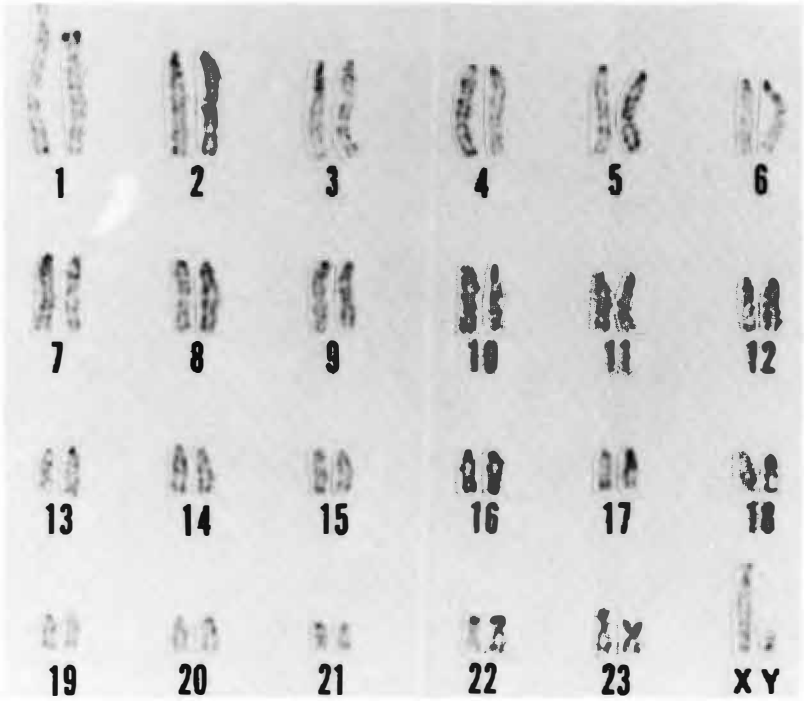

FIG. 8.—Silver stained karyotype of *P. hooperi* (male, same locality as Fig. 7). Note Ag-NORs on pairs 1, 22, 23. Some pairings are conjectural.

(specific chromosomes not known; unpubl. data). The karyotype of *P. simulus*, for which G and C-bands are as yet unknown, will almost certainly demonstrate this same ancestral G and C-band pattern. The general similarity between the G-banded euchromatin of *Peromyscus* and *Baiomys*, *Peromyscus* and *Onychomys*, *Peromyscus* and *Reithrodontomys fulvescens*, and *Peromyscus* and *Nyctomys* (unpubl. data) strongly supports the antiquity of this karyotype.

PROTEIN VARIATION

Genetic variation in samples of *P. hooperi* from localities 3, 13, and 14 was assessed from an analysis of 18 loci. Variation in *P. hooperi* was compared with that of 26 species of *Peromyscus* representing members of the subgenera *Peromyscus*, *Haplomylomys*, *Osgoodomys*, and *Megadontomys* (sensu Hooper and Musser, 1964). Representatives of the seven species groups of the subgenus *Peromyscus* (Hooper, 1968) were also included in our samples.

P. hooperi is fixed for electromorphs that are also fixed in the other 26 species at the HB-3, MDH-1, MDH-2, ME-1, LDH-2, and IPO-1 loci. Electromorphs at the ALB-1, LDH-1, LDH-3, GOT-2, 6PGD-1, ES-1, ES-5, ES-6, and TRF-1 loci vary extensively among and within most species examined. *P. hooperi*, however, is variable only at ALB-1 and TRF-1. Genetic variation in our samples is, therefore, relatively low with heterozygosity values (H) from 0.015 to 0.049 ($\bar{H} = 0.028$) and polymorphism (P) from 0.056 to 0.111 ($\bar{P} = 0.074$).

P. hooperi has a unique allele at the TRF-1 locus that is fixed in two of our samples. This species also is fixed for an allele at the ES-1 locus that occurs at a low frequency in only five other species (*P. gratus*, see Modi and Lee, 1984; *P. nasutus*; *P. difficilis*; *P. leucopus*; and *P. melanophrys*).

The most striking similarity in shared alleles of *P. hooperi* is with members of the subgenus *Haplomylomys*, with common alleles at three loci: HB-1, HB-2 and GOT-1. Except for *P. maniculatus*, which has the same allele at the HB-2 locus, none of these three alleles occurs in other *Peromyscus*. The electrophoretic expression of these alleles at the hemoglobin loci results in a single-banded pattern in *P. hooperi*, *P. eremicus*, and *P. merriami*. All other species of *Peromyscus* have a double-banded hemoglobin pattern.

Nei's (1978) genic identity over all loci further exemplifies the foregoing allelic comparisons. Mean genic identities between *P. hooperi* and members of four subgenera are: *Haplomylomys*, 0.629; *Osgoodomys*, 0.625; *Megadontomys*, 0.630; *Peromyscus*, 0.577. A phenogram (Fig. 9) constructed from the original matrix indicates that *P. hooperi* is allied to members of the subgenus *Haplomylomys*. The similarity, however, is notably weak and heavily weighted by the unique hemoglobin pattern shared by *P. hooperi*, *P. eremicus*, and *P. merriami*, and the shared fixed allele at the GOT-1 locus.

Male Accessory Glands

The male genital tract of *P. hooperi* (Fig. 10) is essentially similar to those of *P. eremicus* and *P. leucopus*, as described by Linzey and Layne (1969), with the following differences: 1) preputial glands absent (macroscopically) as in *P. leucopus* and in contrast with their presence in *P. eremicus*; 2) bulbourethrals much larger and shaped like the head of a golf-club; 3) vesiculars relatively smaller but extending more laterally from the urethra and with

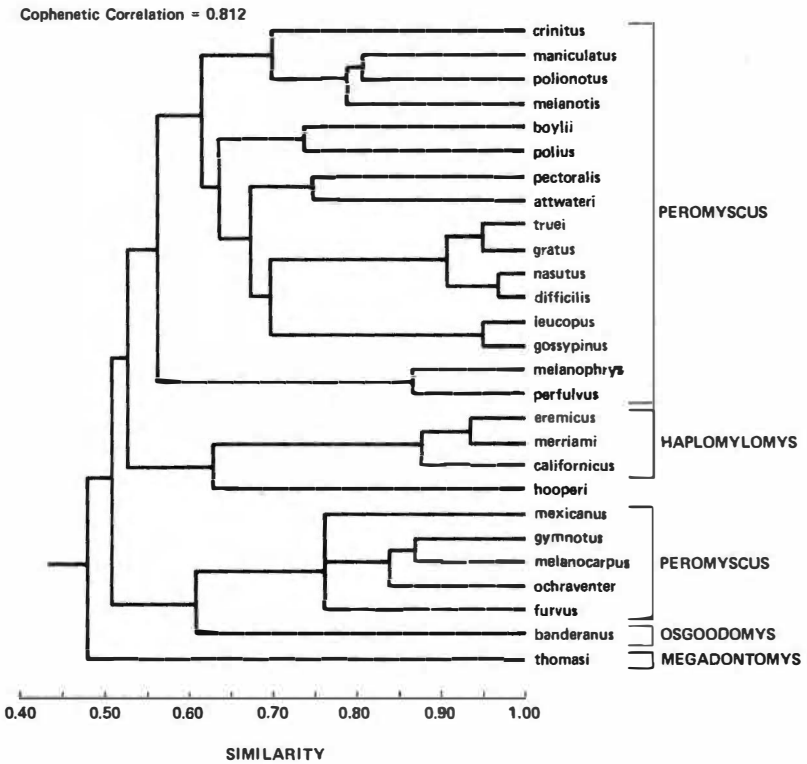

FIG. 9.—Phenogram (derived from the UPGMA clustering routine) of Nei's genic identity values for 26 species representing four subgenera of *Peromyscus*.

a relatively larger subterminal flexure, 4) anterior prostates somewhat smaller; 5) dorsal prostates larger and with a medial lobe visible in ventral view; and 6) testes actually and relatively larger.

Average measurements of five male *P. hooperi* are: testes, 11.7 × 7.4; length of deferent duct, 15.0; length of urethra, 19.5; ampullary gland 2.4 × 2.4; vesicular gland, 7.9 × 2.8; anterior prostate gland, 3.2 × 1.9; dorsal prostate gland, 4.5 × 2.0; ventral prostate gland, 4.8 × 2.8; bulbourethral gland, 3.3 × 4.0.

Of the differences listed above, the absence of preputials and presence of the median lobe of the dorsal prostates represent substantial departures from the glandular complement of *P. eremicus*. With the exception of the medial lobe of the dorsal prostates, the differences between *hooperi* and *P. leucopus* are only in the relative sizes of individual glands. The degree of development of the lateral lobes and medial lobes of the dorsal prostates varies

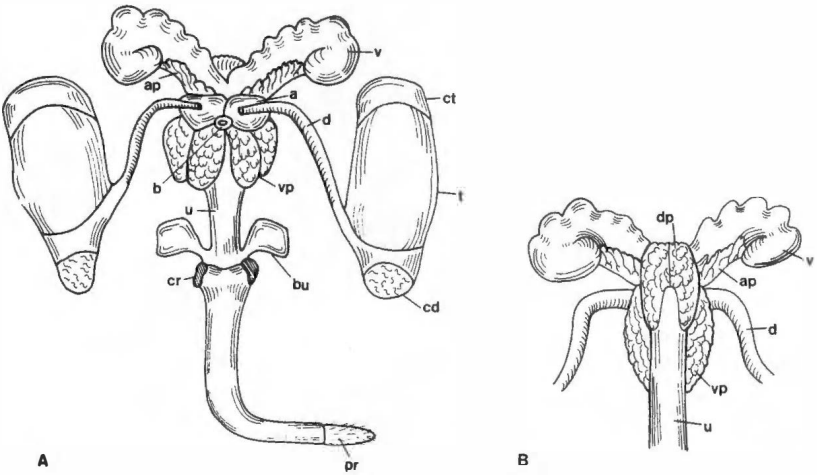

FIG. 10.—Ventral (**A**) and dorsal (**B**) views of the male genital tract of *P. hooperi*. Abbreviations: a, ampullary gland; ap, anterior prostate gland; b, bulb of penis; bu, bulbo-urethral gland; cd, cauda epididymis; cr, crus penis; ct, caput epididymis; d, deferent duct; dp, dorsal prostate gland; pr, prepuce; t, testis; u, urethra; v, vesicular gland; vp, ventral prostate gland.

individually in *P. hooperi*, although the medial lobe was present in all specimens examined. Linzey and Layne (1969) did not mention or figure a medial lobe of this gland in any species of *Peromyscus*, but Voss and Linzey (1981) noted it to be fairly common (and intraspecifically variable) in South American cricetines.

GROWTH, DEVELOPMENT, AND REPRODUCTION

Breeding Season and Sex Ratio

Births of 13 litters, reared in the laboratory, occurred during the following months: June (3), July (1), August (1), September (2), October (2), November (3), and December (1). No births occurred from January through May. Due to maternal infanticide, litter size was determined from only 10 litters that produced 29 individuals. The mean litter size of 2.9 (Table 5) is approximately equal to the generic mean of 3.0 (Modi, 1984). The sex ratio among 30 laboratory-born individuals (13 males:17 females) and 145 wild-caught individuals (79 males:66 females) is not significantly different (Chi-square test; $P > 0.1$). In the wild, pregnant females ($N = 4$) have been recorded in March, April, and May with an average of 3.5 embryos.

TABLE 5.—*Standard univariate statistics for eight growth and reproductive parameters. Following mean litter size, in parentheses, is modal litter size. N refers to the number of individuals (parameters 1-7), or the number of trials (parameter 8).*

Characteristics	N	Mean	SD	Range
Erection of pinnae (days)	11	3.45	0.93	2-5
Eruption of lower incisors (days)	13	7.31	0.75	6-8
Eye opening (days)	9	13.33	1.00	12-15
Age at weaning (days)	3	22.67	2.89	21-26
Gestation period (days)	2	33.50	0.71	33-34
Age at first estrus (days)	3	69.00	6.99	62-76
Litter size	10	2.90(3)	0.57	2-4
Vocalizations (no./3 min.)	25	383.33	53.44	195-513

The average gestation period, while lactating, for laboratory-reared individuals (33.5 days) in within the range (30 to 40 days) reported for other species of *Peromyscus* (Layne, 1968:155; Modi, 1984). The average age at first estrus (69.0 days) is slightly greater than for most other species in the genus (Layne, 1968; Modi, 1984).

Postnatal Growth and Development

The dorsal regions of the head and body of newborns are slightly pigmented, but the venter, legs, elbows, thighs, ankles, and feet are unpigmented. Mystacial vibrissae are the only body hairs present. Tail annulations, plantar tubercles, and claws are present but inconspicuous. The eyeball under the skin and the eye suture are faintly detectable. All digits are fused, and the pinnae are firmly pressed against the head. Newborns are moderately vocal, producing high-pitched squeaks when handled; otherwise, they remain quiet. They rest on their sides, and teat clinging is not highly developed. These observations are generally similar to those recorded for other members of the genus (Layne, 1968).

By the second day, the young begin to grip the teats more strongly, and faint hairs appear on the head and dorsum. By the third to fourth day dorsal pigmentation is darker, epidermal scales are evident, and the pinnae become erect (Table 5). At five days, feeble locomotory capacities are developed as evidenced by limited abilities to right, grasp, and crawl. By the seventh day, the lower incisors have erupted, teats are apparent on some females, and ventral hairs are visible. The digits of the forefeet are separate, and the upper incisors have erupted by day nine. After 13 days, the eyes have opened, and the external auditory meatus is patent. Less

TABLE 6.—*Increases in body weight, total length, tail length, and hind foot length as a function of age. Sample size, mean, and percentage of adult value are given for each characteristic at each age.*

	Weight			Total			Tail			Foot		
Days	*N*	Mean	%	*N*	Mean	%	*N*	Mean	%	*N*	Mean	%
0	16	2.62	13	13	48.85	27	13	13.46	15	13	6.85	32
3	14	3.40	16	11	57.91	31	11	17.36	19	11	8.46	39
6	14	4.46	21	14	69.93	38	14	23.93	26	14	11.36	52
9	15	5.45	26	15	82.60	45	15	30.53	33	15	13.47	62
12	14	6.56	32	14	97.79	53	14	38.64	42	14	15.93	73
15	11	7.84	38	11	112.64	61	11	48.00	52	11	18.09	83
15	7	9.01	43	7	125.57	68	7	57.00	61	7	18.86	87
21	8	9.53	46	8	133.75	73	8	63.13	68	8	19.25	89
24	14	10.07	48	14	140.86	77	14	67.43	73	14	20.21	93
27	9	12.47	60	9	151.67	82	9	74.11	80	9	20.89	96
30	17	12.63	61	17	153.82	84	17	75.06	81	17	20.65	95
40	17	15.99	77	17	164.77	90	17	81.82	88	17	21.18	98
60	17	18.63	90	17	176.06	96	17	88.60	96	17	21.65	100
90	16	19.11	92	16	180.63	98	16	90.94	98	16	21.69	100
120	15	20.35	98	15	183.20	100	15	91.20	98	15	21.67	100
150	14	20.81	100	14	183.86	100	14	92.71	100	14	21.71	100

time is spent on the teats by day 16, and the mice appear to be weaned by day 23, as evidenced by activity and foraging patterns.

Increases in body weight and proportions as a function of age are given in Table 6. These measurements increase rapidly at first and then decrease as an asymptote is approached. This pattern of growth is similar to that reported for other species of *Peromyscus* (Layne, 1968). Approximate age at one-half growth of adult weight is about 26 days for *P. hooperi* compared to a mean of 27.39 days for other species in the genus. The relative body weight at birth for *P. hooperi* (12.58%) is slightly greater than the mean for the genus (9.0%; Modi, 1984).

Parental Behavior

In captivity, adults constructed compact, dome-shaped nests using cotton. The males spent time in and out of the nest while in the cage with the females and young, but never exhibited any form of guardian behavior. Young were transported by females either by teat-clinging or mouth carrying (Svihla, 1932). Only rarely did females attempt to bite the experimenter when the young were removed for examination. Copulation and parturition were not observed.

Our behavioral observations of *P. hooperi* coincide closely with the generalizations of Layne (1968) for the genus *Peromyscus*. Of special interest is the apparent tolerance behavior exhibited by females toward young of former litters, young of new litters, and males. This also has been observed for two species in the subgenus *Haplomylomys*, *P. californicus* (Eisenburg, 1962, 1963; McCabe and Blanchard, 1950) and *P. eremicus* (Eisenburg, 1963).

Maturational and Seasonal Molts

All species of *Peromyscus* studied to date undergo two sequential developmental molts—postjuvenile and postsubadult (Layne, 1968). For *P. hooperi*, a ventral postjuvenile molt occurs between 35 to 40 days of age. During this molt, a soft white pelage, proceeding from the anterior end, replaces the former gray fur. However, no dorsal postjuvenile molt was detected. A dorsal postsubadult molt occurs between 10 to 20 weeks of age and lasts about five weeks.

During the postsubadult molt, the subadult dorsal gray fur is replaced by adult brown pelage. Buffy patches first appear midlaterally, move dorsally, and finally meet middorsally forming a saddle. The subadult pelage on the dorsum is then replaced anteriorly and posteriorly such that the head and rump are the last areas in which hair replacement occurs. This molting pattern is consistent with that reported for other species of *Peromyscus*.

Distinct summer and winter pelages are discernable in adult specimens of *P. hooperi*. Specimens taken in December, January, and February are typically gray (Lee and Schmidly, 1977). During the period from March to May, brownish pelage replaces gray pelage, beginning posteriorly and proceeding anteriorly. Specimens examined from June through September are pale brown, and molt lines are often apparent.

Adaptive Significance

Modi (1984) analyzed the reproductive tactics for 18 species and subspecies of *Peromyscus* (including *P. hooperi*), with respect to nine growth, developmental, and reproductive parameters. In six of the nine characteristics (adult mass, litter size, relative mass of the conceptus, gestation period, age at weaning, and growth rate) the values reported herein for *P. hooperi* are relatively consistent with those from other members of a temperate pastoral species assemblage in this genus (Modi, 1984). These features were interpreted as general r-type life history tactics.

With respect to three characteristics (higher relative birth mass, earlier age at eye opening, and late age at first estrus), *P. hooperi* differs somewhat from other species in the genus. *P. hooperi* seems to possess a reproductive strategy that is adaptive for inhabiting an arid desert habitat where resource availability is unpredictable. Under conditions of food or water scarcity, breeding females might be energetically strained during late gestation and lactation. *P. hooperi* could have responded to such pressures by evolving a rather high relative birth mass, which Tuomi (1980) suggested is an adaptation for increasing juvenile survival. Also, the early age at eye opening in *P. hooperi* indicates that young can avoid predators and begin feeding by themselves at an earlier age, thereby reducing the female's energic costs during lactation (Eisenberg, 1981:324).

P. hooperi also evolved a rather advanced age at first estrus. It is unknown exactly why this might be adaptive, but delayed breeding could be advantageous if early breeders suffer higher mortality due to increased predation risks or a lack of food availability.

Young *P. hooperi* are vocal during the first few days of life and after a week or so become quiet. This characteristic is also well documented in other species of *Peromyscus* (Layne, 1968). A mother-neonate communication system of this sort might be adaptive when nestlings require maternal attention, or if they become separated by predatory attempts or adverse environmental conditions.

Summary and Conclusions

In our judgement, *P. hooperi* is a relict, monotypic species without close living relatives. The slight, but discordant geographic variation in morphology, pelage coloration, and allozymes does not warrant formal taxonomic subdivisions within the species.

Ecologically, it is strictly confined to certain localities in the Grassland Transition vegetative association. Data from field observations plus the geographic occurrence of this habitat indicate that the species consists of numerous disjunct populations separated by Chihuahuan Desert. The present fragmented and restricted distribution almost certainly was formerly more widespread. From our observations, the tenuous conditions of this habitat in central Coahuila, as a result of overgrazing, seriously jeopardizes the continued survival of *P. hooperi*.

In cranial and external morphology, *P. hooperi* is most similar to populations of *P. eremicus* and *P. pectoralis*, with which it is

sympatric. Several statistical analyses clearly demonstrate, however, the distinctness of these three species, and we suggest that similarities among them are the result of homoplasy. The simplicity of the occlusal surfaces of the molars (reduction in, or lack of, styles and lophs) resembles these features in *P. eremicus* and implies a kinship with members of the subgenus *Haplomylomys*. The extent of fur on the plantar surfaces resembles that seen in the subgenus *Peromyscus*.

Certain phallic characters of *P. hooperi* resemble those in both the subgenus *Peromyscus* (protractile tip, proportions of baculum) and the subgenus *Haplomylomys* (proportions of glans). There are, though, a number of distinctive features of the phallus (actual size of glans, dorsal flaps on distal margin of glans). All features considered, the phallus of *P. hooperi* is unique and does not fit well with either of those subgenera. The absence of preputial glands links *P. hooperi* with the subgenus *Peromyscus*, whereas the large dorsal prostate glands are distinctive. Number and placement of mammae (one pair pectoral, two pairs inguinal) are like those in the subgenus *Peromyscus*.

P. hooperi, together with *P. banderanus*, *P. boylii*, *P. crinitus*, and *P. simulus*, possesses the primitive autosomal karyotype of the genus *Peromyscus*. The systematic position of *P. hooperi* thus is not clarified by this symplesiomorphic feature.

Electrophoretically, *P. hooperi* is not closely related to any of the 26 species of *Peromyscus* used in this comparison. The genic identities (Nei) between *P. hooperi* and each of these 26 species are all below 0.66. Although *P. hooperi* is genically closest to members of the subgenus *Haplomylomys*, the identity value is very low (0.63). The allozymic data, although providing no strong indication of the systematic relationships of *P. hooperi*, do support the distinctive position of this species.

In a recent paper, Fuller *et al.* (1984) provided data showing that the albumin of *P. hooperi*, as tested by microcomplement fixation, is about equally distant from members of the subgenera *Peromyscus* and *Haplomylomys* (immunological distance or ID-values of 13 and 12, respectively). The ID-value between *P. leucopus* and *P. merriami* is 9. [Paragraph added in press.]

Characteristics of reproduction and postnatal development provide no information regarding the relationships of *P. hooperi*. In *Peromyscus* reproductive tactics are correlated more with general habitat-niche requirements rather than with phylogenetic relationships.

Our analyses of the various biological attributes of *P. hooperi*, summarized above, do not provide an unambiguous conclusion regarding its systematic status. In several significant characters, *P. hooperi* serves to bridge the subgenera *Haplomylomys* and *Peromyscus*. In our opinion, however, *P. hooperi* shares more features in common with the subgenus *Peromyscus*, and we suggest this as the appropriate systematic placement. Furthermore, inasmuch as no species of the genus shows close relationships with *P. hooperi* it should occupy its own species group.

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Addresses of authors: D. J. SCHMIDLY, *Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843-2258*; M. R. LEE AND W. S. MODI, *Department of Ecology, Ethology, and Evolution, University of Illinois, Urbana, Illinois 61801*; E. G. ZIMMERMAN, *Department of Biology, North Texas State University, Denton, Texas 76203*. Present address for MODI: *Laboratory of Viral Carcinogenesis, National Cancer Institute, Frederick, Maryland* 21701.