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## SYSTEMATICS OF THE SOUTHERN RACES OF TWO SPECIES OF KANGAROO RATS (DIPODOMYS COMPACTUS AND D. ORDII)

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Populations of kangaroo rats (Rodentia: Heteromyidae: Dipodomys) occur in the southern portion of Texas, south of a line from Del Rio to San Antonio to Aransas Pass, and on the adjacent barrier islands of Texas and Tamaulipas, México. These populations, as arranged taxonomically by Hall and Kelson (1959), comprise four subspecies of the wide ranging species Dipodomys ordii. However, recent genetic and phenetic evidence (Johnson and Selander, 1971; Brownlee, 1973; Best and Schnell, 1974; and Stock, 1974) suggests that kangaroo rats from the barrier islands of Texas and México (referred to Dipodomys compactus) are specifically distinct from populations on the South Texas mainland (referred to Dipodomys ordii), Schmidly and Hendricks (1976) found compactus to differ markedly from adjacent races of ordii in certain cranial features. More importantly, they discovered that both species occur on the South Texas mainland, apparently without interbreeding. These authors found the two species within 15 miles of one another in Willacy County, and all trenchant morphological and chromosomal differences were maintained.

Subsequently, we have located three additional sites of sympatry in Zapata and Jim Hogg counties. The purpose of this paper is to assess morphological differentiation between *compactus* and *ordii* with particular reference to these sympatric sites. Variation within and among populations of *compatus* as well as southern populations (Texas and México) of ordii is reviewed also in order to allocate South Texas specimens to recognized subspecific taxa. Schmidly and Hendricks (1976) recognized four subspecies of D. compactus, namely, D. c. compactus, from Padre Island; D. c. largus from Mustang Island; D. c. parvabullatus from the barrier islands of Tamaulipas; and D. c. sennetti from the South Texas mainland. These authors referred South Texas samples of ordii to D. o. durranti, although this assignment was tentative because they had not examined specimens of all adjacent subspecies.

## METHODS AND MATERIALS

We examined 629 specimens, recording external measurements from specimen labels (TL, total length; TAL, tail length; HFL, hind foot length) as well as the following cranial measurements (abbreviations before each character are used hereafter): GSL, greatest skull length; MW, maxillary width; LIW, least interorbital width; GSW, greatest skull width; RW, rostral width; NL, nasal length: LMTR, length maxillary toothrow: LSW, least supraoccipital width: LMB, length mastoid bulla; WMB, width mastoid bulla; SD, skull depth; WSP, width supraoccipital at suture; and WI, width interparietal at suture. Cranial measurements were taken according to Desha (1967), with a few exceptions, and skull depth was recorded as described by Hooper (1952:10). Width of the supraoccipital (WSP) was taken across this bone from one junction of the supraoccipito-parietal suture and the mastoid bulla to the other. Width of the interparietal (WI) was measured from one junction of this bone and the supraoccipito-parietal suture to the other. Specimens were aged according to the method outlined by Desha (1967), and only adults were used in statistical analyses.

Specimens were examined from 205 localities. These were plotted on a map and subsequently combined into 63 samples (Figs. 1, 2), each having enough specimens to yield meaningful statistics and small enough in aerial extent to include potentially interbreeding populations in a relatively homogenous environment. Both *compactus* and *ordii* occur sympatrically at three sites (41-42, 44-45, and 48-49), and at these each species was considered a separate sample. The locality for each specimen included in a sample group is given in specimens analyzed.

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 statis-



FIG. 1.—Geographic localities of *Dipodomys compactus* (squares) and *D. ordii* (dots) from Texas and México. Grouped samples used in the statistical analyses are outlined and numbered.

tics (mean, range, standard deviation, standard error of the mean, variance, and coefficient of variation—CV). When comparing two or more groups, Procedure Anova tests for significant differences ( $P \leq 0.05$ ) among the means of the groups by employing a single classification analysis of variance.



FIG. 2.—Geographic localities of *Dipodomys compactus* (squares) and *D. ordii* (dots) in South Texas. Triangles represent localities where both species were collected. The northern boundary of the Rio Grande Plain is depicted as a broad line along the northern and eastern edge of the area.

Several multivariate statistical techniques were employed. The Numerical Taxonomy Programs (NT-SYS) of Rohlf and Kishpaugh (1972) were used to cluster samples according to phenetic affinity (using average taxonomic distance as a measure of similarity and the UPGMA cluster option). Matrices were generated from both the standardized character means and the unstandardized canonical variable means for those vectors that accounted for a significant amount of variation (characteristic roots  $\geq 1$ ). Higher cophenetic correlation values were obtained from distance phenograms generated with the unstandardized canonical variable means, and only these phenograms are illustrated and discussed. Canonical means were derived from a multivariate analysis of variance (MANOVA) program in SAS.

A MANOVA-canonical analysis also was used to assess the degree of divergence among samples. Discriminant function analysis was used to determine the extent to which reference samples of two different comparisons (South Texas ordii and compactus; mainland compactus and island compactus) could be distinguished from one another. Detailed explanations of these statistical techniques are given in Schmidly and Hendricks (1976), Yates and Schmidly (1977), Honeycutt and Schmidly (1979), and Wilkins and Schmidly (1979).

## NONGEOGRAPHIC VARIATION

Sexual variation.—No consistent sexual dimorphism was found in any of the characters analyzed at 13 separate localities. Width of the mastoid bulla showed the greatest difference between sexes but it was significantly different (ANOVA:  $P \leq .05$ ) at only three of the 13 localities. Males of *compactus* were slightly larger than females in external measurements, but females were larger in most cranial features. Males of *ordii* were only slightly larger than females. Because differences between males and females were not statistically significant in most characters, sexes were combined for subsequent statistical analyses.

These results do not agree with those of Desha (1967), Schmidly (1971), and Kennedy and Schnell (1978) who reported extensive sexual dimorphism in samples of *D. ordii*. However, those three studies were limited either to a few populations (Desha, 1967; Schmidly, 1971) or covered geographic areas not considered in this study (Kennedy and Schnell, 1978). Schmidly and Hendricks (1976) included both males and females in an analysis of geographic variation and noted only limited sexual dimorphism in cranial and external measurements of kangaroo rats from South Texas and México.

Individual variation.—Coefficients of variation (CV) for external measurements of compactus (sample 51) ranged from 1.82 (HFL, male) to 5.49 (TL, male); for cranial measurements, from 1.34 (GSL, female) to 15.32 (WI, male). CVs for external measurements of *D. ordii* (sample 35) ranged from 3.38 (HFL, male) to 6.55 (TL, male); for cranial measurements from 1.40 (NL, female) to 22.3 (WI, male). Males of both *compactus* (mean CV=5.28) and *ordii* (mean CV=6.44) are slightly more variable than females (mean CV=3.59 and 5.05, respectively).

The characters LSW, WSP, and WI exhibited high CVs. This could result from a lack of refinement in taking these measurements or from the influence of bullar inflation, which reduces these cranial elements from two directions (Lidicker, 1960). Although the reliability of characters involving the supraoccipital and interparietal bones has been questioned by several authors (Lidicker, 1960; Schmidly, 1971), some acceptable measurement of these features is useful in determining the extent of bullar inflation. CVs of these measurements are near the upper limits of those considered acceptable for taxonomic studies by Long (1968). For *compactus*, LSW exhibits the lowest mean CV (9.94); for *ordii*, WSP (mean CV=11.34) has the lowest value.

Pelage variation.—Island populations of compactus exhibit intrapopulational variation in color. Two distinct color phases have been recorded in samples of this species, namely Light Ochraceous-Buff (red) and Cartridge Buff (gray) (Setzer, 1949). The frequency of these two color phases in four island populations is as follows (per cent incidence of gray phase followed by per cent incidence of red): Mustang Island, 17.2, 82.8; N Padre Island, 65.3, 34.7; S Padre Island, 93.3, 6.7; and Tamaulipas, 5.6, 94.4.

## **GEOGRAPHIC VARIATION**

## Univariate Analysis

To investigate the distinctness of *compactus* with respect to *ordii* a west to east transect was constructed for five characters (GSL, GSW, LMB, WMB, WSP) among 14 samples from mainland South Texas (Fig. 3). Characters that reflect the width of the supraoccipital (WSP) and the size and inflation of the auditory bulla (GSW, LMB, WMB) separated the samples into two groups, a *compactus* group (samples 49, 41, 44, 43, 51, 53, 46, 54) and an *ordii* group (50, 48, 42, 45, 47, 52). Differences were reinforced by comparisons made between samples where the two species occur sympatrically—the characters GSW, LMB, and WMB differed significantly between groups at these localities. Only GSL showed general overlap among all samples.

Patterns of univariate variation among samples of *D. compac*tus were examined along a transect proceeding from Mustang Island, Texas, south to the barrier islands of Tamaulipas, México,



FIG. 3.—Univariate variation, expressed by Dice-Leraas diagrams of selected characters, among samples of *Dipodomys compactus* (stippled closed rectangles) and *D. ordii* (dark closed rectangles) along a transect in South Texas. Sample designation (Loc) and size (N) appear along the left margin (if N varies, the different N appears to the right of the diagram). See Fig. 1 for location of samples. The horizontal line represents the range; vertical line, the mean; open rectangle, one standard deviation; and closed rectangle, two standard errors of the mean.

and thence northwest across mainland South Texas to Jim Hogg County. The Dice-Leraas diagrams do not reveal a uniform pattern of geographic variation among island samples (Fig. 4). Specimens from south Padre Island (59) are the largest while those from Tamaulipas (22) are the smallest. To the northwest, along the mainland, size increases slightly; mainland samples are slightly larger than island forms in three characters (GSW, LMB, WMB), although these differences are not statistically significant.

Patterns of univariate variation among samples of *D. ordii* were examined for five characters (GSL, MW, LMB, WMB, SD) along a transect extending from Oklahoma southwest to Chihuahua, and thence southeast to San Luis Potosí (Fig. 5). Proceeding along this transect, a reduction in size is evident in all characters. A distinct break separates samples from Oklahoma and northern Texas (1, 2, 5), which are significantly larger in all characters except WMB and LMB from southern samples of *ordii*. Size gradually decreased beginning with samples from Trans-Pecos, Texas, on into southern Chihuahua. Continuing southeastward into northern San Luis Potosí, size remained fairly constant (GSL, MW, SD) or increased slightly (LMB, WMB). Proceeding southward from here, a general decrease in size was evident. A second transect encompassing samples from South Texas and moving westward



F1G. 4.—Geographic variation of *Dipodomys compactus*, expressed by Dice-Leraas diagrams of selected characters, along a transect through its range. See Figs. 1 and 2 for location of samples and Fig. 3 for an explanation of the diagrams.

into central México (35, 42, 47, 15, 18, 21) also was analyzed, but the Dice-Leraas diagrams showed little significant variation and, for that reason, were not illustrated. Samples from South Texas are similar to those in southwestern Coahuila.

## Multivariate Analyses

Cluster analysis.—A distance phenogram using all samples was generated, which showed two major groupings (cophenetic correlation coefficient, 0.926). Cluster A corresponded to samples of *compactus* and cluster B to samples of *ordii*. Within the *ordii* cluster, samples 1-5 (from Oklahoma and northern Texas) formed



FIG. 5.—Geographic variation in *Dipodomys ordii*, expressed by Dice-Leraas diagrams of selected characters, along a transect from Oklahoma to central México. See Fig. 1 for location of samples and Fig. 3 for an explanation of the diagrams.

a separate and distinct subgroup. Samples of *compactus* (41, 44, 49) and *ordii* (42, 45, 48) from the three sites of sympatry in Jim Hogg and Zapata counties fell within their proper species grouping but were clustered together at fourth and third order levels, respectively.

To elucidate patterns of variation within the *compactus* and *ordii* clusters, each was subjected to separate cluster analysis (excluding samples 1-5 of *ordii*). The *compactus* samples (Fig. 6A) are arranged in two clusters. Cluster A includes those samples from the barrier islands plus mainland sample 58; cluster B represents all samples from the South Texas mainland except 58.

The phenogram for *ordii* (Fig. 6B) also separates into two groups (C and D), with the exception of sample 55 (Willacy County, Texas), which segregates by itself. Group (C) consists of specimens from West Texas (sample 6) and adjacent Chihuahua, México (9, 11). Group (D) contains the remaining samples of *ordii* and can be further divided into subgroups I and II. Subgroup I includes samples from western Texas (7), southern Texas (32), northern México (12), and southern México (26). Subgroup II consists of the remaining samples from the Big Bend Basin and Rio Grande Plain of Texas and the Mexican Plateau. This subgroup separates into northern and southern divisions, *a* and *b*, respectively. The northern division represents samples from the Mesa del Norte of México (10, 13-20), the Big Bend Basin (8), and all South Texas *ordii*, whereas southern division includes samples from the Mesa Central of México (21, 23-25, and 27).



FIG. 6.—Distance phenograms of the cluster analyses for samples of *Dipodomys* compactus (A) and D. ordii (B) analyzed separately. The cophenetic correlation coefficient for the compactus cluster is 0.889; for ordii, 0.857.

MANOVA-canonical analysis.—Four different criteria (Hotelling-Lawley's Trace, Pilla's Trace, Wilks' Criterion, and Roy's Maximum Root Criterion) were used to test the hypothesis of no overall locality effect, that is, no significant morphological difference among samples, following a multivariate analysis of variance of all samples. All four criteria gave highly significant *F*-values ( $P \le 0.0001$ ), indicating that significant morphological differences exist among samples.

For the MANOVA of all samples, Vectors I to IV were significant and accounted for 65.21, 10.28, 5.92, and 4.69 per cent (total 86.10 per cent) of the variation, respectively. In the *D. compactus* MANOVA, Vectors I and II accounted for 70.76 per cent of the variation (53.48 and 17.28 per cent, respectively). Vectors I, II, and III of the *D. ordii* MANOVA explained 63.23 per cent of the variation (26.93, 22.51, and 13.79 per cent, respectively).

Canonical analysis using all samples (Fig. 7) depicts two groups (A and B) which are comparable to the two clusters shown in Fig. 6. Group A includes samples of *D. compactus*. As in previous analyses, samples from the zone of sympatry separate readily from one another. The major separation between the two groups occurs along Vector I. Several cranial features (GSL, GSW, LMB, and WMB) exert a high influence on this vector as does the external character TAL (Table 1). Except for GSL, in which there is general overlap in both species, these characters are consistently larger in *ordii* than in *compactus* (Fig. 3). Samples of *ordii* are distinguished from one another along the second vector; GSL and WMB are again important as is SD.

Samples 1-5 separate from other samples of *ordii*, as they did in the cluster analysis. Sample 2 (Oklahoma), because of its less inflated mastoid bulla and wider supraoccipital and interparietal bones, is somewhat intermediate between samples of *ordii* from northern Texas (1, 3-5) and those of *compactus*. However, this intermediacy is not thought to represent phenotypic affinity toward *compactus*.

Canonical analysis for samples of *D. compactus* (Fig. 8) delineates two groups, island and mainland, which are identical to the two groups in the cluster analysis. Sample 58 again shows affinity with the island form, although it is somewhat intermediate between the two groups. The separation along Vector I is most heavily influenced by the characters TAL, HFL, GSL, LMB, WMB, and SD. Little differentiation occurs along Vector II.

Canonical analysis of *D. ordii* samples (excluding 1-5) reveals a segregation of samples into three geographic groups (Fig. 9). The



FIG. 7.—Projections of the first two canonical vectors for all samples of *Dipodomys compactus* (A) and *D. ordii* (B). For each locality, the cross is positioned near the mean value for each sample in the character space; the ellipse surrounding each cross represents one standard deviation around the mean. See Figs. 1 and 2 for location of samples.

western group (A) is composed of specimens from Trans-Pecos, Texas, (samples 6, 7) and northern Chihuahua, México (9, 11, 12). Sample 26 (Aguascalientes, México), which is not geographically proximal, is associated with this group, but samples 8 (Big Bend Basin, Texas) and 10 (Samalayuca, Chihuahua, México), which are geographically close, are not. The second, or Mesa del Norte group (B), consists of samples from northern México (except 9, 11, 12), sample 8, and all samples of south Texas ordii. The third group (C) is comprised of samples from the Mesa Central of México (21, 23, 24, 25, 27), and this group is identical to the Mesa Central division of the cluster analysis. The western group segregates from the others along Vector I, with the characters TAL, GSL, NL, LMB, and WMB having the highest per cent influence. The Mesa del Norte and Mesa Central groups segregate along Vector II, with TL, TAL, HFL, GSL, GSW, and NL exerting the highest influence.

TABLE 1.—Eigenvalues for the first two canonical variates and the percentage influence of each character in distinguishing samples of Dipodomys compactus and D. ordii from Texas and México. The relative importance of each original variable to a particular canonical variate is computed by multiplying the eigenvalue by the median value of the dependent variable, summing all values for a particular vector, and then computing the per cent of relative importance of each variable per vector.

Character	Median	Canonical Variate I		Canonical Variate II	
		Eigenvalue	Per cent influence	Eigenvalue	Per cent influence
TL	238.18	-0.0010111	6.84	0.0004682	2.36
TAL	131.67	0.0035409	13.23	-0.0016785	4.65
HFL	37.21	-0.0013423	1.42	0.0081740	6.40
GSL	37.36	-0.0146814	15.56	0.0291253	22.90
MW	20.19	0.0012186	0.71	-0.0002819	0.13
LIW	12.87	0.0099736	3.64	-0.0219979	5.96
GSW	23.54	0.0139852	9.34	-0.0019678	0.97
RW	3.60	-0.0485440	4.97	0.0288871	2.19
NL	13.60	-0.0181189	6.99	-0.0298818	8.54
LMTR	4.87	-0.0410823	5.68	0.0623567	6.40
LSW	2.28	-0.0369883	2.38	0.0207834	0.99
LMB	15.36	0.0310106	13.52	-0.0240858	7.79
WMB	10.18	0.0398195	11.50	0.0692352	14.84
SD	13.31	0.0111129	4.22	0.0567317	15.89

Discriminant function analysis.—The histogram for the discriminant function scores of the compactus-ordii comparison clearly shows two distinct groupings (A and B) with no intermediate specimens (Fig. 10). The Mahalanobis  $D^2$  value for this comparison ( $D^2=107.9$ ;  $F_{15,167}=298.8$ ;  $P \le 0.001$ ) is well above that reported by Wilkins and Schmidly (1979) for comparisons between three species of pocket mice from west Texas. This indicates that compactus and ordii may be distinguished without ambiguity from one another by using morphological features. Furthermore, there is no indication of hybridization or morphological intermediacy between compactus and ordii where their ranges overlap.

The frequency histogram of the Z-scores for the comparison between island and mainland populations of *D. compactus* shows a general segregation into two groups (C and D), although there is some overlap between them. There are four instances of a specimen being assigned to a group other than the one to which it belongs geographically. Once again specimens from locality 58 show more affinity to the island than to the mainland samples. Two specimens of 58 combine with the island group, one is intermediate between island and mainland groups, and one separates with the mainland samples. One other mainland specimen (from locality 53) combines with the island group, whereas one island specimen (from locality 59) combines with the mainland rats. The  $D^2$  value for this comparison is 10.3 ( $F_{15,138}=23.8$ ;  $P \leq 0.001$ ).

## **TAXONOMIC CONCLUSIONS**

Utilizing univariate and multivariate statistical techniques, samples of *Dipodomys compactus* and *D. ordii* from South Texas are distinct from one another without evidence of hybridization. This agrees with results of studies by Johnson and Selander (1971), Brownlee (1973), Best and Schnell (1974), Stock (1974), and Schmidly and Hendricks (1976). In South Texas, the two species appear to be confined to the Rio Grande Plain (Fig. 2). *D. compactus* occurs on the eastern two-thirds of the mainland, whereas *D. ordii* inhabits the western two-thirds. Their ranges narrowly overlap throughout central south Texas, and three sites of sympatry have been identified in Jim Hogg and Zapata counties.

Two subspecies are recognized within D. compactus (Fig. 11). D. c. compactus, comprising populations formerly referred to the subspecies compactus, largus, and parvabullatus, occurs on Mustang and Padre Islands of Texas and the barrier islands of Tamaulipas, México. D. c. sennetti inhabits the eastern two-thirds of the South Texas mainland. Sample 58 exhibits marked affinity for the island subspecies. All other mainland samples exhibit more affinity for one another than for island samples.

D. ordii from the southern portion of the range in Texas and México are aligned herein into eight subspecies (Fig. 12; excluding D. o. pullus which was not examined). The subspecies extractus, medius, oklahomae, ordii, and richardsoni were studied only for comparison with the more southern races. Except for extractus, no evidence to contradict the current taxonomic arrangement of these subspecies was found. D. o. extractus exhibits intermediacy between D. o. ordii and D. o. obscurus, which raises questions

FIG. 8.—Projections of the first two canonical vectors for samples of *Dipodomys* compactus. Group A represents samples of island compactus and group B samples of mainland compactus. See Fig. 7 for an explanation of symbols.

FIG. 9.—Projections of the first two canonical vectors for samples of *Dipodomys* ordii. These groups represent samples from: A, west Texas and north Chihuahua, México; B, Big Bend Basin and Rio Grande Plain of Texas and Mesa del Norte, México; and C, Mesa Central, México. See Fig. 7 for an explanation of symbols.





ordii, group B; below: island compactus, group C, versus mainland compactus, group D).



Fig. 11.—Geographic distributions of the subspecies of *Dipodomys compactus*: 1, *D. c. compactus*; and 2, *D. c. sennetti*.

as to its status, although no change is recommended here. For a further discussion, see Anderson (1972) and Baumgardner (1979).

D. ordii from south Texas was assigned to the subspecies durranti by Schmidly and Hendricks (1976). However, in both univariate and multivariate analyses, south Texas ordii consistently group with samples from northern México and the Big Bend region of Texas (Figs. 6B, 9). This combined group, which is referred herein to D. o. obscurus, includes the previously recognized subspecies attenuatus, idoneus, and obscurus as well as northern samples of durranti. Its range includes the Mesa del Norte of México and the adjacent regions of the Big Bend Basin and Rio Grande Plain of Texas.

The remaining subspecies of *D. ordii* occur on the Mesa Central of México. *D. o. durranti* occupies the extreme northern portion of this region in Nuevo Leon, Coahuila, San Luis Potosí, Tamaulipas, and Zacatecus. *D. o. palmeri* inhabits the remainder of this region south to Hidalgo. As noted by Schmidly and Hendricks



FIG. 12.—Geographic distributions of the subspecies of Dipodomys ordii: 1, D. o. durranti; 2, D. o. extractus; 3, D. o. medius; 4, D. o. obscurus; 5, D. o. oklahomae; 6, D. o. ordii; 7, D. o. palmeri; and 8, D. o. richardsoni.

(1976), the distinctiveness of these two subspecies is questionable. They group closely together in the multivariate analyses (Fig. 6B, 9), although there are significant differences between them in three of the five characters examined in the univariate analysis (Fig. 5).

## Systematic Accounts

Only specimens used in statistical analyses are listed in the accounts beyond. Additional specimens, consisting of non-adults, skin or skull only specimens, or unmeasured specimens, are listed in Baumgardner (1979). The number in parenthesis preceding a locality is its sample number. The number of specimens from a locality and the abbreviation of the institution of deposition follows each locality.

#### Dipodomys compactus True

- 1889. Dipodomys compactus True, Proc. U.S. Nat. Mus., 11:160, January 5.
- 1891. Dipodops sennetti J. A. Allen, Bull. Amer. Mus. Nat. Hist., 3:226, April 29, type from near Brownsville, Cameron Co., Texas (part, specimens from the eastern two-thirds of the South Texas mainland).
- 1942. Dipodomys ordii, Davis, J. Mamm., 23:332, August 14.
- 1976. Dipodomys compactus, Schmidly and Hendricks, Bull. Southern California Acad. Sci., 75:235, November.

Holotype.—None designated, but Poole and Schantz (1942:406) assumed it to be a female, USNM 19665/35227; Padre Island, Cameron Co., Texas; 3 April 1888; obtained from C. K. Worthen.

Distribution.—The barrier islands of Tamaulipas, México, Mustang and Padre islands of South Texas, and the adjacent twothirds of the mainland east from Zapata County and south from Bexar and Gonzales counties.

Comparisons.—See account of D. ordii.

## Dipodomys compactus compactus True

- 1889. Dipodomys compactus True, Proc. U.S. Nat. Mus., 11:160, January 5.
- 1942. Dipodomys ordii compactus, Davis, J. Mamm., 23:332, August 14.
- 1951. Dipodomys ordii parvabullatus Hall, Univ. Kansas Publ., Mus. Nat. Hist., 5:38, October 1; type from 88 mi. S, 10 mi. W Matamoros, Tamaulipas, México.
- 1951. Dipodomys ordii largus Hall, Univ. Kansas Publ., Mus. Nat. Hist., 5:40, October 1; type from Mustang Island, 14 mi. SW Port Aransas, Aransas Co., Texas.
- 1976. Dipodomys compactus compactus, Schmidly and Hendricks, Bull. Southern California Acad. Sci., 75:235, November.
- 1976. Dipodomys compactus largus, Schmidly and Hendricks, Bull. Southern California Acad. Sci., 75:235, November.
- 1976. Dipodomys compactus parvabullatus, Schmidly and Hendricks, Bull. Southern California Acad. Sci., 75:235, November.

Holotype.—See account of D. compactus.

Distribution.—Mustang and Padre Islands of South Texas and the barrier islands of Tamaulipas, México.

Comparisons.—From D. c. sennetti, D. c. compactus differs in having less inflated mastoid bullae, a slightly narrower skull with wider supraoccipital and interparietal bones. Also, compactus exhibits two dorsal pelage color phases (red and gray), whereas sennetti has only the red phase.

Specimens analyzed (71).-MEXICO: TAMAULIPAS: (22) 88-90 mi. S, 10 mi. W Matamoros, 5 (KU); (22) 90 mi. S, 10 mi. W Matamoros, 1 (USNM). TEXAS: CAMERON CO.: (59) 2 mi. E, 6.5 mi. N Port Isabel, 2 (UIMNH); (59) Padre Island, 2 mi. E, 6 mi. N Port Isabel, 2 (UIMNH); (59) Padre Island, 3 mi. E, 6 mi. N Port Isabel, 12 (TCWC); (59) 2 mi. E, 5 mi. N Port Isabel, 8 (UIMNH). KLEBERG CO.: (38) Padre Island, 10 (1 MWU, 9 USNM). NUECES CO.: (33) Mustang Island, SW Port Aransas, 3 (TCWC); (33) Mustang Island, 1 mi. S Port Aransas, 3 (TNHC); (33) 14 mi. SW Port Aransas, 5 (KU); (33) 15 mi. SW Port Aransas, Mustang Island, 2 (TCWC); (33) 19 mi. S Port Aransas, Mustang Island, 16 (7 MVZ, 9 TCWC); (36) 3.6 mi. S Bob Hall Pier on Padre Island, 1 (TAIU); (36) 23 mi. S Port Aransas, 1 (TCWC).

#### Dipodomys compactus sennetti (J. A. Allen)

- 1891. Dipodops sennetti J. A. Allen, Bull. Amer. Mus. Nat. Hist., 3:226, April 29 (part, specimens from eastern two-thirds of the South Texas mainland).
- 1942. Dipodomys ordii sennetti, Davis, J. Mamm., 23:332, August 14 (part, specimens from the eastern two-thirds of the South Texas mainland).
- 1976. Dipodomys compactus sennetti, Schmidly and Hendricks, Bull. Southern California Acad. Sci., 75:235, November.

Holotype. — Male, AMNH 3478/2733; near Brownsville, Cameron Co., Texas; 9 March 1888; obtained by J. M. Priour; type locality reported by Bailey (1905:45) as Santa Rosa, 85 mi. SW Corpus Christi.

Distribution.—The eastern two-thirds of the South Texas mainland, east of Zapata County and south of Bexar and Gonzales counties.

Comparisons.—See account of D. c. compactus.

*Remarks.*—Topotypes of this subspecies are the most atypical of the mainland specimens and show affinity to the island subspecies.

Specimens analyzed (83).—TEXAS: ATASCOSA CO.: (28) 7 mi. E Lytle, 1 (TNHC). BROOKS CO.: (53) Encino Division, King Ranch, near Encino, 2 (TCWC). CAMERON CO.: (58) near Santa Rosa, 4 (USNM). HIDALGO CO.: (53) 13.2 mi. S Encino (Brooks Co.), Hwy. 281, 1 (TCWC); (53) 4.4 mi. N Linn, Hwy. 281, 1 (TCWC). JIM HOGG CO.: (43) 1 mi. E, 1.2 mi. S Hebbronville, Hwy. 1017, 1 (TCWC); (43) 2 mi. S, 3.7 mi. W Hebbronville, 4 (TCWC); (41) 13.4 mi. SSE Mirando City (Webb Co.), Hwy. 649, 21 (TCWC); (43) 7.2 mi. S Hebbronville, Hwy. 1017, 1 (TCWC); (44) 18.5 mi. SSE Mirando City (Webb Co.), Hwy. 649, 1 (TCWC); (43) 1 mi. E, 12.5 mi. S Hebbronville, Hwy. 1017, 1 (TCWC); (51) 20 mi. S Hebbronville, 14 (TNHC); (51) 23.6 mi. S Hebbronville, Hwy. 1017, 3 (TCWC); (51) 28.7 mi. S Hebbronville, Hwy. 1017, 2 (TCWC). KENEDY CO.: (46) 2.2 mi. S Miflin, U.S. 77, 1 (TAIU); (46) 12 mi. S Sarita, 1 (TCWC); (54) 6 mi. S Norias, Hwy 77, 1 (TCWC); (54) 1 mi. E Rudolf, Norias Division, King Ranch, 2 (TCWC); (54) 7 mi. E Rudolf, Norias Division, King Ranch, 1 (TCWC); (54) 8.6 mi. S Norias, Hwy. 77, 2 (TCWC). KLEBERG CO.: (46) 2 mi. S Riviera, 7 (TCWC). STARR CO.: (51) 11.7 mi. E, 27.5 mi. N Rio Grande City, Hwy. 1017, 2 (TCWC). WEBB CO.: (37) 4 mi. WNW Bruni, Hwy. 359, 1 (TCWC); (40) 9.1 mi. S Mirando City, Hwy. 649, 1 (TCWC). WILLACY CO.: (54) 6.2 mi. N Raymondville, Hwy. 77, 1 (TCWC); (56) Red Fish Bay, 28 mi. E Raymondville, 2 (TCWC); (56) Sauz Ranch, 2 (USNM). ZAPATA CO.: (49) 2 mi.NE Bustamante, Hwy. 16, 2 (TCWC).

#### Dipodomys ordii Woodhouse

1853. ' D[ipodomys] ordii Woodhouse, Proc. Acad. Nat. Sci. Philadelphia, 6:224.

Holotype.—None designated. Species characterized from specimens obtained at El Paso, Texas, by Dr. Woodhouse.

Distribution.—From southern Canada to the southern edge of the Mexican Central Plateau and from the eastern boundry of the Rocky Mountains to the eastern limits of the Great Plains of the United States (Hall and Kelson, 1959).

Comparison.—In the southern range of D. ordii, compactus is the only other five-toed kangaroo rat of comparable size. Externally ordii differs from compactus in having a longer, bushier, and slightly more crested tail. Also the ventral pencil is darker, less broken, and extends to the tip of the tail. The pelage of ordii is longer and silkier. In areas of proximity, the pelage of ordii tends toward brownish hues whereas that of compactus has an orange cast.

Cranially the two differ in the inflation of the mastoid bullae. That of *ordii* exhibits greater inflation, giving the skull a more triangular appearance. This inflation causes the intermediate supraoccipital and interparietal elements to be narrower. Also, the interparietal of *ordii* comes to a finer point posteriorly and is more triangular in shape than that of *compactus*, which is rectangular to roundish in shape.

#### Dipodomys ordii durranti Setzer

- 1949. Dipodomys ordii fuscus Setzer, Univ. Kansas Publ., Mus. Nat. Hist., 1:555, December 27.
- 1952. Dipodomys ordii durranti Setzer, J. Washington Acad. Sci., 42:391, December 17.

Holotype. —Adult, male, USNM 93886; Jaumave, Tamaulipas, México; 3 June 1898; obtained by E. W. Nelson and E. A. Goldman.

Distribution. — The northern half of the Mesa Central of México in southern Nuevo Leon and the adjacent regions of the states of Coahuila, San Luis Potosí, Tamaulipas, and Zacatecus.

Comparisons. - See Setzer (1949).

*Remarks.*—Although previous authors have included specimens from northern Tamaulipas and Coahuila, México (Setzer, 1949) and southern Texas (Schmidly and Hendricks, 1976) in this subspecies, our analyses indicate these samples should be referred to *D. o. obscurus.* 

Specimens analyzed (83).—MEXICO: COAHUILA: (21) 7 mi. S, 4 mi. E Bella Union, 7200 ft., 28 (KU); (21) 12 mi. W San Antonio de las Alazanas, 6500 ft., 2 (KU); (23) 8 mi. N La Ventura, 5500 ft., 3 (KU); (23) San Juan Neponuceno, 5 mi. N La Ventura, 4 (MVZ); (23) La Ventura, 6 (USNM). NUEVO LEON: (24) Dr. Arroyo, 1 (USNM). SAN LUIS POTOSI: (24) 7.6 mi. S Matehuala, 2 (MVZ). TAMAULIPAS: (25) Miquihuana, 10 (6 USNM, 4 KU); (24) Nicolas, 56 km. NW Tula, 5500 ft., 6 (KU); (25) Juamave, 8 (USNM); (25) 8 mi. N Tula, 4500 ft., 2 (KU); (23) 3 mi. N Lulu, 3 (MVZ); (23) Lulu, 8 (MVZ).

#### Dipodomys ordii obscurus (J. A. Allen)

- 1891. Dipodops sennetti J. A. Allen, Bull. Amer. Mus. Nat. Hist., 3:226, April 29 (part, specimens from western two-thirds of the South Texas mainland).
- 1903. Perodipus obscurus J. A. Allen, Bull. Amer. Mus. Nat. Hist., 19:603, November 12.
- 1921. Dipodomys ordii obscurus, Grinnell, J. Mamm., 2:96, May 2.
- 1939. Dipodomys ordii attenuatus Bryant, Occas. Papers, Mus. Zool., Louisiana State Univ., 5:65, November 10, type from Mouth of Santa Helena Canyon, 2146 ft., Big Bend of Rio Grande, Brewster Co., Texas.
- 1942. Dipodomys ordii sennetti, Davis, J. Mamm., 23:332, August 14 (part, specimens from the western two-thirds of the South Texas mainland).
- 1949. Dipodomys ordii idoneus Setzer, Univ. Kansas Publ., Mus. Nat. Hist., 1:546, December 27, type from San Juan, 12 mi. W Lerdo, 3800 ft., Durango, México.
- 1976. Dipodomys ordii durranti, Schmidly and Hendricks, Bull. Southern California Acad. Sci., 75:235, November (part, specimens from northern Tamaulipas and Coahuila, México, and South Texas).

Holotype.—Adult, male AMNH 20957; Rio Sestin, northwestern Durango, México; 13 April 1903; obtained by J. H. Batty.

Distribution.—Northern portion of the Mexican Plateau above southern Coahuila, known as the Mesa del Norte, and the adjoining regions of the Big Bend Basin and Rio Grande Plain of Texas.

Comparisons.—From D. o. durranti, D. o. obscurus differs in having a slightly wider maxillary width and less inflated mastoid bullae.

From D. o. extractus, obscurus differs in having a slightly smaller skull length, maxillary width, and less inflated mastoid bullae.

From D. o. ordii, obscurus differs in having a shorter skull, narrower and shorter mastoid bullae, lesser skull depth, and a slightly narrower maxillary width.

From *D. o. palmeri, obscurus* differs in having a greater skull length, maxillary width, and skull depth as well as a slightly longer and narrower bullae.

Specimens analyzed (203).-MEXICO: CHIHUAHUA: (14) Las Arenosos, 4050 ft., 6 (KU); (14) Sierra Almagre, 5300 ft., 12 mi. S Jaco, 6 (KU); (17) 15 mi. ESE Boquilla, 4700 ft., 2 (KU); (17) 19 mi. N, 7 mi. E Parral, 1 (KU); (17) 2 mi. E La Parrena, 5000 ft., 1 (KU); (17) 5 km. S Jiminez, 2 (KU); (17) 5 mi. E Parral, 5700 ft., 7 (KU). COAHUILA: (13) 11 mi. W Hcda. San Miguel, 2200 ft., 1 (KU); (18) 3 mi. NE Sierra Mojada, 4100 ft., 1 (KU); (16) 1 mi. S Hermanas, 1 (KU); (18) 4 mi. N Acatita, 3600 ft., 2 (KU); (18) 1 mi. SW San Pedro de las Colonias, 3700 ft., 3 (KU); (18) 8 mi. SE San Pedro de las Colonias, 3700 ft., 1 (KU); (18) 10 mi. E Torreon, 3600 ft., 6 (KU); (18) 1 mi. N San Lorenzo, 4200 ft., 3 (KU); (20) N foot Sierra Guadalupe, 6200 ft., 9 mi. S, 5 mi. W General Cepeda, 7 (KU). DURANGO: (19) Rio de Bocas, 7 (AMNH); (18) 1 mi. WSW Mapimi, 3800 ft., 3 (KU); (19) Rosario, 4 (AMNH); (18) 5 mi. SE Lerdo, 3800 ft., 5 (KU); (19) 6 mi. NW Rodeo, 4200 ft., 1 (KU). TAMAULIPAS: (15) NUEVO Laredo, 3 (USNM). TEXAS: BREWSTER Co.: (8) Cooper's Well, 47 mi. S Marathon, 2450 ft., 3 (MVZ); (8) Big Bend National Park (BBNP), 10 mi. NE Panther Junction, 2820 ft., 4 (SWTSUMC); (8) BBNP, Upper Tornillo Creek Bridge, 1 (SWTSUMC); (8) Upper Tornillo Creek Bridge, BBNP, 8 mi. NNE Panther Junction, 14 (TCWC); (8) Lower Tornillo Creek Bridge, BBNP, 15 mi. SE Panther Junction, 1 (TCWC); (8) Mouth Santa Helena Canyon, 2146 ft., Rio Grande, 2 (1 TCWC, 1 MVZ). DIMMIT Co.: (30) 2 mi. NE Carrizo Spring along Nueces River, 1 (TCWC); (30) 10 mi. SW Carrizo Springs, 1 (TCWC); (30) 2 mi. SW Asherton, Hwy. 1916, 2 (TCWC). HIDALGO CO.: (57) 17 mi. NW Edinburg, 1 (TNHC). JIM HOGG Co.: (42) 13.4 mi. SSE Mirando City (Webb Co.), Hwy. 649, 11 (TCWC); (42) 14 mi. SSE Mirando City (Webb Co.), Hwy. 649, 1 (TCWC); (42) 14.3 mi. SSE Mirando City (Webb Co.), Hwy. 649, 1 (TCWC); (42) 14.7 mi. SSE Mirando City (Webb Co.), Hwy. 649, 3 (TCWC); (42) 16.1 mi. SSE Mirando City (Webb Co.), Hwy. 649, 2 (TCWC); (45) 18.1 mi. SSE Mirando City (Webb Co.), Hwy. 649, 1 (TCWC); (45) 18.7 mi. SSE Mirando City (Webb Co.), Hwy. 649, 2 (TCWC); (45) 19.4 mi. SSE Mirando City (Webb Co.), Hwy. 649, 4 (TCWC); (45) 20 mi. SSE Mirando City (Webb Co.), Hwy. 649, 2 (TCWC); (45) 20.3 mi. SSE Mirando City (Webb Co.), Hwy. 649, 3 (TCWC); (47) 22.5 mi. SSE Mirando City (Webb Co.), Hwy. 649, 1 (TCWC); (47) 23.7 mi. SSE Mirando City (Webb Co.), Hwy. 649, 1 (TCWC); (47) 25.6 mi. SSE Mirando City (Webb Co.), Hwy. 649, 2 (TCWC); (47) 14 mi. N, 3 mi. W Guerra, Hwy. 649, 1 (TCWC); (47) 26 mi. SW Hebbronville, Hwy. 16, 4 (TCWC); (47) 23 mi. S. Hebbronville, Hwy. 16, 1 (TCWC); (47) 18 mi. SW Hebbronville, Hwy. 16, 2 (TCWC); (47) 22 mi. SW Hebbronville, Hwy. 16, 1 (TCWC); (47) 20.5 mi. SW Hebbronville, Hwy. 16, 3 (TCWC); (47) 13.7 mi. N Guerra, Hwy. 649, 2 (TCWC); (52) 0.9 mi. N Guerra, Hwy. 649, 1 (TCWC); (52) 2.8 mi.S Guerra, Hwy. 649, 1 (TCWC). McMullen Co.: (29) 15 mi. NE Tilden, 1 (TCWC). WEBB Co.: (32) 40 mi. SW Catarina, on Rio

Grande, 2 (TNHC); (35) 21 mi. NE Laredo city limits, 1 (USFWS); (34) 21.1 mi. N Bruni, Hwy. 2050, 2 (TCWC); (35) 13 mi. NE Laredo city limits, 2 (USFWS); (35) 12 mi. NE Laredo city limits, 1 (USFWS); (34) 15 mi. N Aguilares, Hwy. 2895, 1 (TCWC); (35) 11 mi. NE Laredo city limits, 2 (USFWS); (35) 8 mi. NNE Laredo city limits, 1 (USFWS); (35) 10 mi. NE Laredo city limits, 1 (USFWS); (35) 6.5 mi. NNE Laredo city limits, 3 (USFWS); (35) 5 mi. NE Laredo city limits, 1 (USFWS); (35) 4 mi. ENE Laredo city limits, 1 (USFWS); (35) 5 mi. E Laredo city limits, 1 (USFWS); (35) 8 mi. E Laredo city limits, 1 (USFWS); (35) 10 mi. E Laredo city limits, 1 (USFWS); (39) 2 mi. N Aguilares, Hwy. 2895, 1 (TCWC); (39) 4.5 mi. SSE Mirando City, Hwy. 649, 2 (TCWC); (39) 5.6 mi. SSE Mirando City, Hwy. 649, 1 (TCWC); (39) 6.6 mi. SSE Mirando City, Hwy. 649, 2 (TCWC). WILLACY Co.: (55) 10 mi. NW Raymondville, 5 (TNHC). ZAPATA Co.: (48) 10.9 mi. NE Bustamante, Hwy. 16, 2 (TCWC); (48) 9.8 mi. NE Bustamante, Hwy. 16, 2 (TCWC); (48) 7.6 mi. NE Bustamante, Hwy. 16, 1 (TCWC); (48) 2 mi. NE Bustamante, Hwy. 16, 3 (TCWC); (50) 5 mi. N Zapata, 1 (TNHC); (50) 3 mi. SW Bustamante, Hwy. 16, 3 (TCWC); (50) 4 mi. SW Bustamante, Hwy. 16, 1 (TCWC); (50) 3.5 mi. NE Zapata, 4 (TNHC).

#### Dipodomys ordii palmeri (J. A. Allen)

1881. Dipodops ordii palmeri J. A. Allen, Bull. Mus. Comp. Zool., 8:187, March. 1921. Dipodomys ordii palmeri, Grinnell, J. Mamm., 2:96, May 2.

Syntypes.—Two adult males, MCZ 5886 and 5887; San Luis Potosí, México; 1 May 1878 and 1 September 1878, respectively; obtained by Dr. Edward Palmer.

Distribution.—Southern portion of the Central Plateau of México from northern San Luis Potosí and Zacatecus south to Hidalgo.

Comparisons. - See Setzer (1949).

*Remarks.*—D. o. palmeri differs from durranti in three of the five univariate characters examined with Dice-Leraas diagrams; however, these two subspecies group together consistently in the multivariate analyses. For this reason, their subspecific distinctness is questionable, and additional study may show they are similar enough to be placed under the single subspecies palmeri, which has priority over the name durranti.

Specimens analyzed (24).—MEXICO: AGUASCALIENTES: (26) 1 mi. N Chicalote, 2 (MVZ). SAN LUIS POTOSI: (27) 2 mi. NW San Luis Potosí, 2 (MVZ); (27) Jesús María, 18 (USNM). ZACATECUS: (26) 4 km. E Morelos, 2 (MWU).

#### **OTHER SUBSPECIES**

Subspecies accounts are not included for D. o. oklahomae, D. o. richardsoni, D. o. medius, D. o. extractus, and D. o. ordii. Information presented in this study does not alter the accounts, descriptions, and distributions of these taxa as provided by Setzer (1949). Specimens analyzed for these subspecies are as follows:

D. o. oklahomae (10).—OKLAHOMA: CLEVELAND CO.: (2) 2.5 mi. S Norman, 10 (KU).

D. o. richardsoni (16).—TEXAS: FLOYD CO.: (3) 24 mi. E Floydada, 1 (TCWC). HARTLEY CO.: (1) 1 mi. SW Dalhart, 1 (TCWC); (1) 2 mi. SW Dalhart, 4000 ft., 2 (TCWC). HEMPHILL CO.: Gene Howe Wildlife Management Area: (1) Persimmon Gap, on creek, 10 mi. NE Canadian, 2 (TCWC); (1) 7.5 mi. NE Canadian, 1 (TCWC); (1) 7 mi. NE Canadian, 2 (TCWC); (1) 5 mi. NE Canadian, 1 (TCWC); (1) 6 mi. ENE Canadian, 2 (TCWC). POTTER CO.: (1) 2 mi. W Lake Meredith, 2700 ft., 2 (TCWC); (1) 18 mi. N Amarillo, 3500 ft., 1 (TCWC). WHEELER CO.: (1) Wallace Ranch, SW Wheeler, 1 (TCWC).

D. o. medius (28).—TEXAS: ANDREWS CO.: (5) 15 mi. SW Andrews, 3000 ft., 1 (TCWC). GAINES CO.: (4) Cedar Lake, 20 mi. ENE Seminole, 3 (TCWC). WARD CO.: (5) 2 mi. NE Monahans, 3 (MWU); (5) 11 mi. W Monahans, 2 (MWU). WINKLER CO.: (5) 3.5 mi. S Kermit, 19 (TCWC).

D. o. ordii (85).—MEXICO: CHIHUAHUA: (9) 10 mi. SE Zaragosa, 3700 ft., 5 (KU); (11) 1 mi. S Kilo, 4185 ft., 2 (KU); (11) 8 mi. E Villa Ahumada, 4000 ft., 2 (KU); (12) 11 mi. NNW San Buenaventura, 1 (KU); (12) 1 mi. N Arados, 1540 m., 1 (KU); (12) 2 mi. W Parrita, 2 (KU). TEXAS: CULBERSON CO.: (7) 16 (TCWC). EL PASO CO.: (6) 3 mi. NE El Paso city limits, 8 (MVZ); (6) 7.5 mi. E El Paso City Hall, 4000 ft., 12 (KU); (6) 12 mi. E, 1 mi. S El Paso City Hall, 4000 ft., 4 (KU); (6) 18 mi. E, 3 mi. S El Paso City Hall, 4000 ft., 8 (KU); (6) 11 mi. SE El Paso City Hall, 2 (KU). HUDSPETH CO.: (6) Fort Hancock, 6 (MWU). JEFF DAVIS CO.: (7) Limpia Creek, 16 mi. NE Fort Davis, 1 (KU). PRESIDIO CO.: (7) 2 mi. S Paisano, 9 (TCWC); (7) 1 mi. W Plata, 2 (MWU); (7) Bandera Mesa, 2 (MWU); (7) 3 mi. E Presidio, 1 (MWU). REEVES CO.: (7) 20 mi. S Pecos, 1 (KU).

D. o. extractus (15).—MEXICO: CHIHUAHUA: (10) 8 mi. NE Samalayuca, 4300 ft., 2 (KU); (10) 1 mi. E Samalayuca, 4500 ft., 13 (MVZ).

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Institutions from which specimens were examined together with institutional abbreviations used in the lists of specimens follow (curators given in parenthesis): AMNH, American Museum of Natural History (Syndey Anderson); KU, Museum of Natural History, The University of Kansas (Robert S. Hoffmann); MCZ, Museum of Comparative Zoology, Harvard University (Barbara Lawrence); MVZ, Museum of Vertebrate Zoology, University of California (William Z. Lidicker, Jr.); MWU, Department of Biology, Midwestern University (Walter W. Dalquest); SWTSUMC, Southwest Texas State University Mammal Collection, Southwest Texas State University (John T. Baccus); TAIU, Department of Biology, Texas A&I University (Allan H. Chaney); TCWC, Texas Cooperative Wildlife Collection, Texas A&M University (David J. Schmidly); TNHC, Texas Natural History Collection, Texas Memorial Museum, University of Texas at Austin (Robert F. Martin); UIMNH, Museum of Natural History, University of Illinois (Donald F. Hoffmeister); USNM, National Museum of Natural History, Bird and Mammal Laboratories, U.S. Bureau of Sports Fisheries and Wildlife, Washington, D.C. (Clyde Jones and Charles O. Handley); USFWS, U.S. Bureau of Sport Fisheries and Wildlife, Denver Collection of the Bird and Mammal Laboratories (Robert B. Finley). We are especially grateful to these individuals who loaned us specimens or allowed us to study material under their care.

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