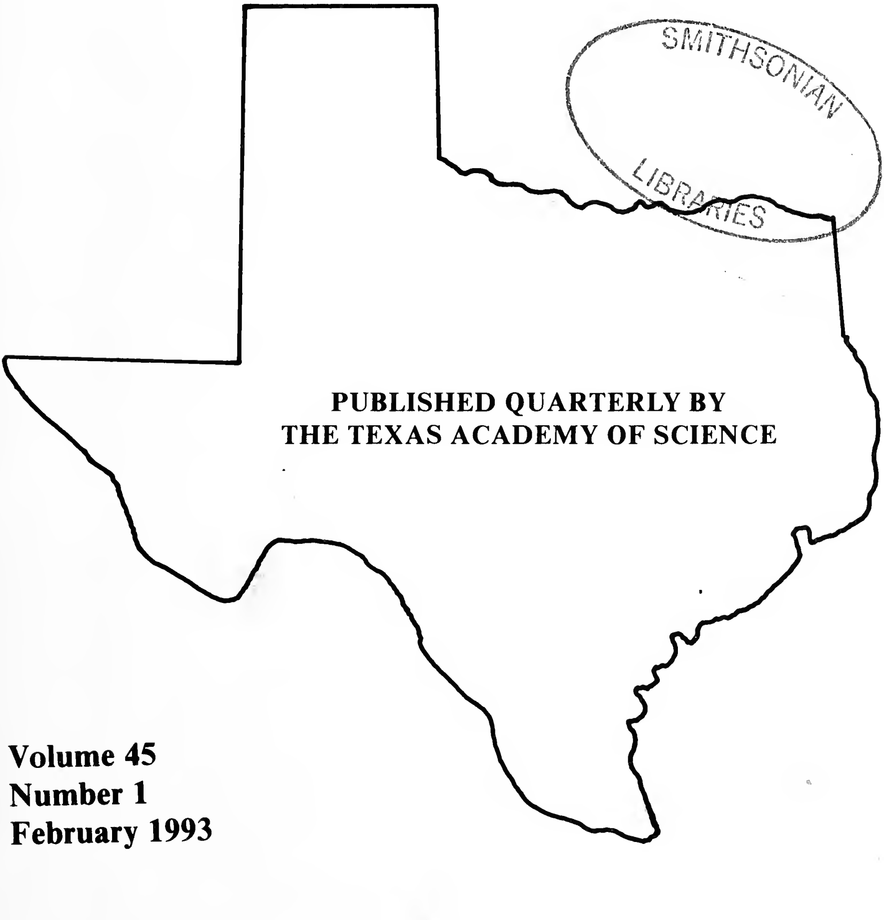
THE TEXAS JOURNAL OF SCIENCE



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THE TEXAS ACADEMY OF SCIENCE MOURNS THE DEATH OF

Dr. J. Knox Jones, Jr.

Dr. J. Knox Jones, Jr., Horn Professor of Biological Sciences at Texas Tech University, died on 15 November 1992. Dr. Jones was recognized as the Academy's Distinguished Texas Scientist in 1992 and he was Editor of the **Texas Journal of Science** from 1986 until his death. A full obituary will appear in a forthcoming issue of the journal.

I will not attempt to fill Knox's shoes, but I hope to carefully follow the trail that he blazed.

Frank W. Judd
Editor

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General Notes

Scholarly papers in any field of science, technology, or science education will be considered for publication in *The Texas Journal of Science.* Instructions to authors are published one or more times each year in the *Journal* on a space-available basis, and also are available from the Editor (The University of Texas—Pan American, Coastal Studies Laboratory, Box 2591, South Padre Island, Texas 78597, (210) 761-2644).

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SYSTEMATIC STATUS OF THE DEER MOUSE, *PEROMYSCUS MANICULATUS*, ON THE LLANO ESTACADO AND IN ADJACENT AREAS

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Abstract.—Geographic and nongeographic variation of deer mice, *Peromyscus maniculatus*, were statistically analyzed to determine the systematic status of populations of this species on the Llano Estacado and in adjacent areas of Texas. Four external and 12 cranial measurements were analyzed. Museum specimens were classified as juveniles, subadults, young adults, adults, or old adults based on tooth wear and pelage characteristics. Only individuals categorized as adults of one age or another were used in statistical analyses. A MANOVA was used to test for sexual dimorphism, which resulted in a nonsignificant ($P = 0.083$) value, allowing the sexes to be combined. ANOVAs and discriminant function analysis also were used to define taxonomic affinities. From this analysis, it was concluded that *P. m. pallescens* extends from south-central Texas northward and westward, intergrading with *P. m. luteus* in the Lubbock area and perhaps elsewhere in the southeastern part of the Llano. Mice clearly referable to *Peromyscus maniculatus luteus* as currently recognized appear to occupy all other areas of the Llano Estacado. *Key words*: deer mouse; *Peromyscus maniculatus*; distribution; systematics; Llano Estacado, Texas.

The deer mouse, *Peromyscus maniculatus*, with more than 60 recognized subspecies (Hall, 1981), occurs from British Columbia east to Labrador and southward through most of the United States into Mexico as far as Oaxaca. It occupies a wide variety of habitats across this broad range, with some subspecies being more habitat specified than others.

The Llano Estacado is the southernmost extension of the Great Plains. It is an immense plateau lying south of the Canadian River in eastern New Mexico and western Texas (Lotspeich and Coover, 1962). Caprock cliffs delimit its northern and eastern margins and, to a lesser extent, the western edge (Mescalero Ridge). To the south, the Llano merges without sharp contrast with the Monahans Sandhills and adjacent areas. Lacking significant topographic features, the Llano has a relatively uniform climate (Judd, 1970).

The taxonomic status of *Peromyscus maniculatus* on the Llano Estacado has long been the subject of speculation (Blair, 1954b; Judd, 1970); according to Hall (1981), five subspecies occupy the Llano and areas immediately adjacent to it. Several species of *Peromyscus* often live together in a relatively small geographic area (Thompson and Conley, 1983), and identification of specimens sometimes poses problems (Cornely et al., 1981); differentiation at the subspecific level also can be problematic. The paucity of investigations addressing intergradation between subspecies of *P. maniculatus* that utilize similar habitats contributes to the complexity of the problem (Caire and Zimmerman, 1975). A circuitous pattern of gene exchange may take place between adjacent populations, with little or no direct interbreeding (Blair, 1953), thus adding to the problems surrounding the relationships among, and identity of, subspecies. Blair (1954a) found no evidence of reproductive isolation among *P. m. pallescens*, *P. m. blandus*, and *P. m. rufinus*. Although more is known about population dynamics and geographic variation in *Peromyscus maniculatus* than any other species of small mammal (Blair, 1953), its taxonomic status is still uncertain over parts of its distribution, including the Llano Estacado. The only apparent distinct geographic feature that might provide a barrier to gene flow between or among subspecies in the vicinity of the Llano is the edge of the caprock, which is evident to a greater or lesser degree along all but the southern part of the region.

The deer mouse is generally distributed over the Llano Estacado, but rarely is locally common. It is much less abundant overall, for example, than its relative, *Peromyscus leucopus*. Most often, *P. maniculatus* has been taken in mesquite grassland, in grassy areas having a sandy substrate, such as on the Muleshoe Sandhills, and along overgrown grassy-woody fence rows.

Judd (1970) examined 145 specimens from the Llano and assigned them to the subspecies *P. m. luteus*. The relative scarcity of *P. maniculatus* on the Llano Estacado (Blair, 1954b; Judd, 1970; Jones et al., 1988) has made it difficult to assemble representative groups of specimens to determine their taxonomic status. New collections have been acquired since Judd's work, however, and multivariate statistical techniques have come into general use. The goal of research resulting in this paper was to better define the systematic affinities of *Peromyscus maniculatus* on the Llano and in adjacent areas through use of multivariate morphometeric analysis.

HISTORICAL TAXONOMY

Osgood (1905) described *Peromyscus luteus*, with type locality at Kennedy, Cherry County, Nebraska. Later, he (1909) relegated *luteus* to subspecific status under *P. maniculatus*, and assigned 10 specimens from Washburn, Armstrong Co., Texas, to *P. m. nebrascensis* [= *luteus*] (see Jones, 1958, for the proper use of the subspecific name *nebrascensis*). Hall (1981) mapped five subspecies converging in the geographic region on or near the Llano Estacado, but the exact borders of the ranges of these races was unclear. They are listed below, based on Hall's distributional scheme.

Peromyscus maniculatus blandus Osgood, 1904, was mapped as occurring from southern Coahuila and Chihuahua northward to a latitude of approximately 34° north. In the United States, *P. m. blandus* is found in the lower Sonoran life-zone of western Texas, north to southern New Mexico (Osgood, 1909). This race evidently occurs throughout the southern Pecos River drainage, an area directly adjacent to the southwestern and western edges of the Llano Estacado.

Peromyscus maniculatus luteus Osgood, 1905, was shown to range from South Dakota southward to the southern edge of the Llano Estacado. Osgood (1909) associated *luteus* primarily with the sandhill region of western Nebraska and adjacent areas.

Peromyscus maniculatus nebrascensis (Coues, 1877) was reported as extending from southeastern Alberta and southern Saskatchewan, south through the western parts of the Dakotas and Nebraska to the Oklahoma Panhandle, and westward to include the southeastern part of Montana and the eastern parts of Wyoming and Colorado. Hall (1981) even mapped an extension of the distribution of this race into the Texas Panhandle, although no specimens were referenced from that area. Osgood (1909) associated the subspecies now known as *nebrascensis* with the plains and foothill regions of the Rocky Mountains.

Peromyscus maniculatus pallescens J. A. Allen, 1896, occurs throughout central Texas and approaches the Llano from the southeast. It also has been recorded from Hardeman County, Texas, by Hall (1981), but this was an extrapolation of a county record referenced only to species by Davis (1974). Jones et al. (1987), however, listed *P. m. pallescens* as a subspecies that might be present in northwestern Texas.

Peromyscus maniculatus rufinus (Merriam, 1890) is distributed from western Colorado southward through the southeastern corner of Utah into most of eastern Arizona and western New Mexico. Hall (1981) illustrated the eastern extent of the range of this subspecies as entering the extreme northwestern edge of the Texas Panhandle, although no specimen records were cited from there. *P. m. rufinus* inhabits areas of transition and boreal vegetation in the southern Rocky Mountains (Osgood, 1909; Wilson, 1968). Wilson found it to be the dominant small mammal of mixed conifer forests above 8500 feet. Dalquest et al. (1990) reported that *P. m. rufinus* and *P. m. luteus* intergrade in Union County, New Mexico. Judd (1970) opined that habitat limitations prevent *P. m. rufinus* from entering the Llano Estacado. We concur that *P. m. rufinus* is not found on the Llano, and it is included here for comparative purposes only. As an aside having no relationship to the present study, Hoffmeister (1986) regarded *rufinus* as a synonym of *P. m. sonoriensis.*

METHODS AND MATERIALS

Four external measurements (total length, length of tail vertebrae, length of hind foot, length of ear) were obtained from original specimen labels. Weights of pregnant females were removed from the data set. No weights were recorded for specimens of *P. m. pallescens* from Hill County, and that subspecies thus could not be compared with the other groups for that parameter. Inconsistency in recording weight and problems associated with missing values prompted removal of that measure from the analysis. Furthermore, because missing values did not allow us to maintain reasonable sample sizes, external measurements were not used in tests involving multivariate techniques.

Judd (1970) noted considerable variation in pelage color within samples taken from the Llano Estacado, and remarked that many deer mice from that region appeared to be intermediate in color between *P. m. pallescens* and *P. m. nebrascensis*, but that some resembled *P. m. luteus*. Although qualitative observations of pelage were made, quantitative pelage characteristics were not assessed in this study.

Twelve cranial measurements were taken (by Cooper) with Fowler digital calipers to the nearest 0.01 mm. These were selected based on other studies of *Peromyscus* (Osgood, 1909; Fox, 1948; Cockrum, 1954; Judd, 1970; Schmidly, 1973; Cornely et al., 1981; Koh and Peterson, 1983). Description of cranial measurements follows:

Greatest length of skull.—Length from anterior margin of nasal bone to posterior projecting margin of occiput.

Breath of braincase.— Greatest width of braincase measured perpendicular to long axis of skull between posterior margins of zygomatic arches.

Zygomatic breadth.—Greatest distance perpendicular to long axis of skull across the zygomatic arches.

Interorbital constriction.—Least width across frontal bones (that is, least constriction in interorbital region).

Length of rostrum.—Distance from anteriormost projection of nasal bone to lateral junction of lacrimal and maxilla.

Occipital depth.—Distance from ventral plane of auditory bullae to dorsalmost projection of parietals.

Breadth of rostrum.—Greatest distance across rostrum anterior to zygomatic arches.

Condylobasal length.—Greatest distance from posteriormost projection of occipital condyle to anteriormost projection of premaxilla.

Breadth of upper molars.—Greatest distance across outer buccal margins of upper molars.

Length of maxillary toothrow.—Greatest length of alveolar space of the upper molar toothrow.

Length of diastama.—Shortest distance between posterior alveolus of incisor and alveolar space at anterior margin of upper molar row.

Length of palate.—Shortest distance from anteriormost point at posterior border of palate to posterior lip of alveolus of incisor.

All statistical tests were made using SPSS/PC + statistical package (SPSS, Inc., 1986) for IBM compatible personal computers. Specified tests are discussed in greater detail in the following sections on nongeographic and geographic variation.

Nongeographic Variation

Subspecies of *Peromyscus maniculatus* have been extensively studied with regard to growth rates and development (see, for example, Svihla, 1934, 1935; Dice, 1936, 1937; Dice and Bradley, 1942). In order to minimize the effects of variation in external and cranial dimensions associated with normal development, we initially excluded juveniles and subadults from our evaluations. Dice (1936) found that mice in laboratory populations of *P. m. gracilis* had demonstrable growth in both external and cranial dimensions after the second year of life, although individuals rarely live that long in the wild. Fox (1948), however, found no significant age variation in adult specimens that possessed at least slight wear on the last molar. We assigned specimens of *P. maniculatus* to one of five age classes based on criteria developed by Koh and Peterson (1983).

Juvenile.—Specimens with grayish pelage, M3 not reaching the height of M1 and M2.

Subadult.—Specimens with drab brownish subadult pelage or in the process of molting to or from that pelage, with little or no tooth wear evident.

Young adult.—Specimens with new adult pelage, with some wear on cusps of upper molars.

Adult.—Specimens in adult pelage, with noticeable wear on cusps of upper molars.

Old adult.—Specimens in adult pelage, with substantial wear on upper molars (cusps obliterated).

To assess the amount of morphological variation that was attributable to sexual variation, a sample from Lubbock County was analyzed for secondary sexual dimorphism. Comprised of 32 specimens (17 males and 15 females, all young adults and adults), the Lubbock sample represents the largest available from a single locality. A one-way multivariate analysis of variance was performed, using the program MANOVA from SPSS (SPSS, Inc., 1986) with sex as the main factor. The effect of sex was nonsignificant ($P = 0.083$), and the sexes thus were combined for subsequent analyses.

A one-way multivariate analysis of variance was performed on the same Lubbock sample, using the program MANOVA with age as the main factor (entire sample made up of young adults and adults). Nonsignificant ($P = 0.330$) results were obtained for the effect of age, and animals from these two age groups (and old adults) thus were combined in all subsequent analyses.

GEOGRAPHIC VARIATION

In order to obtain acceptable sample sizes for statistical treatment, mice from some localities were pooled. In forming *a priori* groups, however, caution was taken not to cross biogeographic barriers in pooling specimens (Thorpe, 1976; Hollander, 1990). In one case, however, the grouped sample representing *P. m. blandus* crossed such a barrier in that the Pecos River divided localities from which specimens were selected from Pecos and Winkler counties. Individuals we examined from possible areas of intergradation between subspecies were not grouped, but were treated as "unknowns." The small available sample of *P. m. nebrascensis* precluded it from the statistical analysis. A listing of the resulting eight *a priori* groups follows (see Table 1 for a summary of statistics): group 1—Lubbock County, Texas; group 2—Sherman and Moore counties, Texas; group 3—Lamb and Bailey counties, Texas; group 4—Randall and Castro counties, Texas; group 5—Cherry and

TABLE 1. Summary statistics including sample size (N), mean, standarrd deviation (SD), standard error (SE), and minimum and maximum values.

Group	Mean	SE	SD	Minimum	Maximum	*N*
Breadth of braincase						
GLOC 1	10.84	.06	.35	9.72	11.56	32
GLOC 2	11.13	.04	.20	10.75	11.54	30
GLOC 2	11.12	.05	.23	10.67	11.58	17
GLOC 4	11.15	.09	.32	10.52	11.70	13
GLOC 5	11.35	.06	.26	10.78	11.83	22
GLOC 6	11.49	.05	.26	10.87	11.91	28
GLOC 7	11.50	.07	.33	10.97	12.20	23
GLOC 8	11.05	.08	.44	10.00	11.51	28
Breadth across upper molars						
GLOC 1	4.58	.03	.16	4.24	4.94	32
GLOC 2	4.74	.03	.15	4.41	5.09	30
GLOC 3	4.76	.04	.17	4.47	5.09	17
GLOC 4	4.75	.04	.16	4.50	4.98	13
GLOC 5	4.69	.04	.21	4.01	5.13	23
GLOC 6	4.81	.03	.16	4.41	5.03	28
GLOC 7	4.85	.03	.16	4.62	5.24	25
GLOC 8	4.58	.03	.16	4.25	4.89	29
Condylobasal length						
GLOC 1	21.72	.14	.80	20.04	23.19	32
GLOC 2	22.59	.11	.62	21.12	23.75	30
GLOC 3	22.51	.16	.67	20.96	23.59	17
GLOC 4	22.81	.13	.48	22.08	23.79	13
GLOC 5	22.22	.16	.76	20.49	24.08	22
GLOC 6	23.11	.12	.64	21.68	24.97	28
GLOC 7	23.38	.18	.89	21.47	25.15	25
GLOC 8	21.42	.16	.85	19.26	22.62	27
Length of diastama						
GLOC 1	6.27	.06	.36	5.52	7.00	32
GLOC 2	6.51	.11	.60	3.57	7.06	30
GLOC 3	6.52	.09	.38	5.83	7.24	17
GLOC 4	6.66	.08	.28	6.34	7.36	13
GLOC 5	6.52	.08	.40	5.51	7.32	23
GLOC 6	6.88	.06	.32	6.37	7.52	28
GLOC 7	6.67	.08	.41	6.00	7.68	25
GLOC 8	5.93	.06	.31	4.94	6.34	29
Occipital depth						
GLOC 1	8.77	.07	.38	8.02	9.59	31
GLOC 2	9.06	.07	.38	8.29	9.82	30
GLOC 3	9.03	.07	.28	8.61	9.51	17
GLOC 4	9.17	.09	.33	8.61	9.84	13
GLOC 5	9.22	.07	.32	8.44	9.68	22
GLOC 6	9.34	.05	.29	8.70	9.79	28

Table 1. Continued

GLOC 7	9.36	.06	.31	8.77	10.04	24
GLOC 8	8.73	.09	.46	7.74	9.50	28
			Greatest length of skull			
GLOC 1	23.73	.14	.77	21.48	24.89	31
GLOC 2	24.69	.10	.56	23.83	25.86	29
GLOC 3	24.47	.13	.52	23.40	25.44	17
GLOC 4	24.86	.15	.53	24.10	25.63	13
GLOC 5	24.57	.17	.80	22.84	26.22	21
GLOC 6	25.53	.16	.79	24.18	27.87	25
GLOC 7	25.72	.22	1.06	23.58	27.82	24
GLOC 8	23.67	.18	.93	21.39	25.03	28
			Length of rostrum			
GLOC 1	8.86	.09	.46	8.05	10.10	28
GLOC 2	9.29	.06	.32	8.79	9.90	29
GLOC 3	9.16	.08	.35	8.48	9.69	17
GLOC 4	9.40	.07	.25	8.89	9.90	13
GLOC 5	9.24	.12	.55	8.27	10.59	22
GLOC 6	9.92	.07	.37	9.23	10.72	25
GLOC 7	9.82	.11	.54	8.83	10.61	25
GLOC 8	8.83	.09	.50	7.79	9.66	28
			Length of maxillary toothrow			
GLOC 1	3.61	.03	.16	3.26	3.98	32
GLOC 2	3.75	.03	.14	3.47	4.04	30
GLOC 3	3.74	.04	.18	3.40	4.0	17
GLOC 4	3.76	.05	.20	3.39	4.0	13
GLOC 5	3.69	.04	.17	3.18	4.04	23
GLOC 6	3.91	.03	.15	3.60	4.28	28
GLOC 7	3.89	.03	.17	3.69	4.44	25
GLOC 8	3.60	.03	.17	3.23	3.96	29
			Length of palate			
GLOC 1	9.84	.07	.41	9.14	10.63	32
GLOC 2	10.05	.06	.30	9.54	10.64	30
GLOC 3	9.97	.09	.37	9.07	10.37	17
GLOC 4	10.37	.09	.33	9.87	10.85	13
GLOC 5	10.01	.11	53	8.75	11.31	23
GLOC 6	10.51	.07	.36	9.78	11.39	28
GLOC 7	10.36	.08	.40	9.63	11.29	25
GLOC 8	9.50	.08	.44	8.44	10.39	29
			Interorbital constriction			
GLOC 1	3.76	.03	.16	3.45	4.13	32
GLOC 2	3.93	.03	.14	3.67	4.26	30
GLOC 3	3.86	.02	.10	3.73	4.05	17
GLOC 4	3.91	.03	.11	3.67	4.08	13
GLOC 5	3.94	.04	.17	3.70	4.35	23

Table 1. Continued

GLOC 6	3.94	.05	.27	2.95	4.30	28
GLOC 7	4.01	.03	.14	3.64	4.27	25
GLOC 8	3.88	.04	.23	3.28	4.20	28
			Breadth of rostrum			
GLOC 1	4.34	.05	.27	3.58	4.81	32
GLOC 2	4.49	.03	.18	4.18	5.01	30
GLOC 3	4.58	.05	.21	4.12	4.80	17
GLOC 4	4.58	.06	.22	4.29	4.96	13
GLOC 5	4.54	.05	.23	4.12	5.12	22
GLOC 6	4.46	.03	.17	4.10	4.85	27
GLOC 7	4.59	.06	.30	3.87	5.11	25
GLOC 8	4.40	.04	.22	3.76	4.90	29
			Zygomatic breadth			
GLOC 1	12.34	.10	.53	10.95	13.19	32
GLOC 2	12.84	.07	.37	12.13	13.91	30
GLOC 3	13.01	.07	.29	12.57	13.51	16
GLOC 4	12.99	.07	.25	12.50	13.33	11
GLOC 5	13.03	.09	.44	12.28	13.75	22
GLOC 6	13.00	.08	.41	12.15	13.84	28
GLOC 7	13.40	.09	.42	12.47	14.15	24
GLOC 8	12.43	.10	.47	11.05	13.22	20

Thomas counties, Nebraska; group 6—Lincoln and Otero counties, New Mexico; group 7—Winkler and Pecos counties, Texas; group 8—Hill County, Texas.

Groups 1, 3, and 4 are from the Llano Estacado. Group 2 represents a sample from north of the Canadian River in an area were mice possibly could be assignable to *P. m. nebrascensis* according to Hall (1981). Group 5 represents topotypic material of *P. m. luteus* from the sandhill region of Nebraska. All specimens of group 6 are from mountainous areas of New Mexico and represent *P. m. rufinus*. Animals in group 7 represent *P. m. blandus* from just beyond the southern edge of the Llano. *Peromyscus maniculatus pallescens* was represented by group 8—specimens from Hill County, Texas.

The presence of significant geographic variation among groups was tested using multivariate analysis of variance (program MANOVA, SPSS, Inc., 1986). Significant results were obtained ($P < 0.001$) indicating morphometeric differentiation among at least some groups. The 12 cranial and four external measurements then were tested using one-way ANOVAs with the *a priori* groups as the main effect. If significant differences were detected, the character then was subjected to a Student-Neuman-Keuls multiple range test. All characters displayed significant results ($P < 0.05$), indicating some morphometeric differentiation between or among some *a priori* groups for every character. All characters, except length of hind foot ($P = 0.0178$) were significant at $P < 0.001$. The Student-Neuman-Keuls test was selected to delineate nonoverlapping subsets among the *a priori* groups. Student-Neuman-Keuls procedure is computationally identical to Welsch's set-up procedure, except that a different table of critical values is associated with each test (Sokal and Rohlf, 1981). The summarized results of the Student-Neuman-Keuls multiple range test appear in Table 2. Grouped locality (Gloc) 8 and Gloc 1 were placed in the same subset for 10 of the 16 parameters. Glocc 1 and 5 formed subsets for only three of 16 characters. Gloc 6 and Gloc 7 were grouped in subsets for 14 of 16 characters.

A discriminant function analysis (DFA—program Discriminant, SPSS, Inc., 1986) then was employed to test how well individuals within grouped localities could be distinguished. Because any missing value would result in removal of the entire specimen from analysis, only cranial characters were included in the DFA (Table 3). The resulting 60.37 percent of grouped cases correctly classified indicated that the *a priori* groups did not particularly well reflect potential biological groupings in the region. If all of the Llano Estacado specimens are grouped with *P. m. luteus* and analyzed by DFA, the percentage of correctly classified specimens increases to a respectable 77.44 percent. However, in this grouping strategy there are only four samples, which somewhat restricts the resolution capability of the test.

Discussion

Results of the multiple range tests lead us to conclude that most *P. maniculatus* on the Llano Estacado clearly should be assigned to *P. m. luteus*. Grouped localities 2, 3, and 4 all formed subsets with Gloc 5, for 15 of the 16 characters tested. The strong affinity with the *luteus* material reaffirms the existing taxonomic status for *P. maniculatus* from the northern and central Llano Estacado.

However, mice from the immediate vicinity of Lubbock are intergrades between *P. m. pallescens*, based on cranial measurements and qualitative pelage characteristics, and some mice with relatively dark pelage occur even farther westward, in Hale and Lamb Counties. Specimens from the Lubbock County sample formed subsets with Gloc 5 for only three of the 16 characters tested, but this group formed subsets with Gloc 8 for 12 of the 16 characters. Seven of the 16 characters formed nonoverlapping subsets, indicating a significant difference between the subsets at ($P < 0.05$). The Lubbock mice also have pelage characteristics that resemble *pallescens* more than *luteus*, exhibiting a distinctive dorsal stripe similar to *pallescens*. Few Lubbock specimens exhibited the pale buffy pelage of topotypic *luteus* material, but many specimens assigned to *luteus* from the northern Llano Estacado generally had a darker brown coat than

TABLE 2. Results of the one-way ANOVAs on 12 cranial and four external characters with the grouped localities (GLOC) as the main effect. Also the results of Student-Newman-Keuls multiple range test (MRT). Asterisks in a column indicate nonsignificant subsets.

Group	MRT				Mean	Range	*N*	P
					Breadth of braincase			
GLOC 1	*				10.84	9.72-11.56	32	<0.001
GLOC 8		*			11.05	10.00-11.51	28	
GLOC 3		*			11.12	10.67-11.58	17	
GLOC 2		*			11.13	10.75-11.54	30	
GLOC 4		*	*		11.15	10.52-11.70	13	
GLOC 5			*	*	11.35	10.78-11.83	22	
GLOC 6				*	11.49	10.87-11.91	28	
GLOC 7				*	11.50	10.97-12.20	23	
					Breadth across upper molars			
GLOC 8	*				4.58	4.25-4.89	29	<0.001
GLOC 1	*				4.58	4.24-4.94	32	
GLOC 5		*			4.69	4.01-5.13	23	
GLOC 2		*	*		4.74	4.41-5.09	30	
GLOC 4		*	*		4.75	4.50-4.98	13	
GLOC 3		*	*		4.76	4.47-5.09	17	
GLOC 6		*	*		4.81	4.41-5.03	28	
GLOC 7			*		4.85	4.62-5.24	25	
					Condylobasal length			
GLOC 8	*				21.42	19.26-22.62	27	<0.001
GLOC 1	*				21.72	20.04-23.19	32	
GLOC 5		*			22.22	20.49-24.08	22	
GLOC 3		*			22.51	20.96-23.59	17	
GLOC 2		*			22.59	21.12-23.75	30	
GLOC 4		*	*		22.81	22.08-23.79	13	
GLOC 6			*		23.11	21.68-24.97	28	
GLOC 7			*		23.38	21.47-25.15	25	
					Length of diastama			
GLOC 8	*				5.93	4.94-6.34	29	<0.001
GLOC 1		*			6.27	5.52-7.00	32	
GLOC 2			*		6.51	3.57-7.06	30	
GLOC 5			*		6.52	5.51-7.32	23	
GLOC 3			*		6.52	5.83-7.24	17	
GLOC 4			*		6.66	6.34-7.36	13	
GLOC 6			*		6.88	6.37-7.52	28	
GLOC 7			*		6.67	6.00-7.68	25	
					Occipital depth			
GLOC 8	*				8.73	7.74-9.50	28	<0.001
GLOC 1	*				8.77	8.02-9.59	31	
GLOC 3		*			9.03	8.61-9.51	17	
GLOC 2		*			9.06	8.29-9.82	30	
GLOC 4		*	*		9.17	8.61-9.84	13	
GLOC 5		*	*		9.22	8.44-9.68	22	

Table 2. Continued

GLOC 6			*	9.34	8.70-9.79	28	
GLOC 7			*	9.36	8.77-0.04	24	
				Greatest length of skull			
GLOC 8	*			23.16	21.39-25.03	28	<0.001
GLOC 1	*			23.73	21.48-24.89	31	
GLOC 3		*		24.47	23.40-25.44	17	
GLOC 5		*		24.57	22.84-26.22	21	
GLOC 2		*		24.69	23.83-25.86	29	
GLOC 4		*		24.86	24.10-25.63	13	
GLOC 6			*	25.53	24.18-27.87	25	
GLOC 7			*	25.72	23.58-27.82	24	
				Length of rostrum			
GLOC 8	*			8.83	7.79-9.66	28	<0.001
GLOC 1	*			8.86	8.05-10.10	28	
GLOC 3		*		9.16	8.48-9.69	17	
GLOC 5		*		9.24	8.27-10.59	22	
GLOC 2		*		9.29	8.79-9.90	29	
GLOC 4		*		9.40	8.89-9.90	13	
GLOC 7			*	9.82	8.53-10.61	25	
GLOC 6			*	9.92	9.23-10.72	25	
				Length of maxillary toothrow			
GLOC 8	*			3.60	3.23-3.96	29	<0.001
GLOC 1	*			3.61	3.26-3.98	32	
GLOC 5	*	*		3.69	3.18-4.04	23	
GLOC 3		*		3.74	3.40-4.10	17	
GLOC 2		*		3.75	3.47-4.04	30	
GLOC 4		*		3.89	3.69-4.10	13	
GLOC 7			*	3.89	3.69-4.44	25	
GLOC 6			*	3.91	3.60-4.28	28	
				Length of palate			
GLOC 8	*			9.50	8.44-10.39	29	<0.001
GLOC 1		*		9.84	9.14-10.63	32	
GLOC 3		*		9.97	9.07-10.37	17	
GLOC 5		*		10.01	8.75-11.31	23	
GLOC 2		*		10.05	9.54-10.64	30	
GLOC 7			*	10.36	9.63-11.29	25	
GLOC 4			*	10.37	9.87-10.85	13	
GLOC 6			*	10.51	9.78-11.39	28	
				Interorbital constriction			
GLOC 1	*			3.76	3.45-4.13	32	<0.001
GLOC 3	*	*		3.86	3.28-4.20	28	
GLOC 8		*		3.88	3.28-4.20	28	
GLOC 4		*		3.91	3.67-4.08	13	
GLOC 2		*		3.93	3.67-4.26	30	
GLOC 6		*		3.94	2.95-4.30	28	

TABLE 2. Continued

GLOC 5		*		3.94	3.70-4.35	23	
GLOC 7		*		4.01	3.64-4.27	25	
				Breadth of rostrum			
GLOC 1	*			4.34	3.58-4.81	32	<0.001
GLOC 8	*	*		4.40	3.76-4.90	29	
GLOC 6	*	*		4.46	4.10-4.85	27	
GLOC 2		*		4.49	4.18-5.01	30	
GLOC 5		*		4.54	4.12-5.12	22	
GLOC 4		*		4.58	4.29-4.96	13	
GLOC 3		*		4.58	4.12-4.80	17	
GLOC 7		*		4.59	3.87-5.11	25	
				Zygomatic breadth			
GLOC 1	*			12.34	10.95-13.19	27	<0.001
GLOC 8	*			12.43	11.05-13.22	20	
GLOC 2		*		12.84	12.13-13.91	30	
GLOC 4		*		12.99	12.50-13.33	11	
GLOC 6		*		13.00	12.15-13.84	28	
GLOC 3		*		13.01	12.57-13.51	16	
GLOC 5		*		13.03	12.28-13.75	22	
GLOC 7		*		13.40	12.47-14.12	24	
				Total length			
GLOC 8	*			132.80	112-147	25	<0.001
GLOC 1	*			137.69	125-160	29	
GLOC 5		*		147.26	133-171	23	
GLOC 3		*		147.29	135-158	14	
GLOC 2		*		150.41	137-179	27	
GLOC 4		*		150.50	141-164	12	
GLOC 6		*	*	154.71	127-189	28	
GLOC 7			*	160.17	144-180	23	
				Length of tail vertebrae			
GLOC 1	*			53.83	41-68	29	<0.001
GLOC 8	*	*		57.04	43-67	25	
GLOC 2	*	*		57.41	50-64	27	
GLOC 4		*		60.55	57-64	11	
GLOC 3		*		60.93	54-68	14	
GLOC 5		*		61.70	34-71	23	
GLOC 6			*	67.39	52-85	28	
GLOC 7			*	68.08	58-82	24	
				Length of hind foot			
GLOC 1	*			17.96	15-20	28	<0.020
GLOC 8	*			18.68	14-21	20	
GLOC 2	*	*		19.04	18-20	27	
GLOC 4	*	*		19.42	19-22	12	
GLOC 3	*	*		19.50	18-21	14	
GLOC 7	*	*		20.08	18-24	24	

TABLE 2. Continued

GLOC 5	*	*		20.22	18-22	23	
GLOC 6		*		21.89	18-70	28	
				Length of ear			
GLOC 8	*			14.39	11-18	20	<0.001
GLOC 1	*			14.50	12-17	28	
GLOC 3	*	*		15.14	13-17	14	
GLOC 2	*	*		15.22	11-18	27	
GLOC 5		*		15.70	14-19	23	
GLOC 7		*		15.71	13-18	24	
GLOC 4		*		15.75	13-17	12	
GLOC 6			*	17.57	14-21	28	

found in those from Nebraska. Based on the results of the multiple range tests and qualitative pelage characteristics, we conclude that mice in the Lubbock area are intergrades, which we tentatively assign to *luteus* at the present time.

Results of DFA indicate that the influence *P. m. pallescens* diminishes in Hale County, from which four individuals fell out with Gloc 3 and only two with Gloc 8. However, the area of intergradation also may include areas along the eastern edge of the Llano, possibly immediately to the north of Lubbock and certainly to the south, once adequate material is at hand for study. Additional specimens also are needed from the extreme southern and southwestern parts of the Llano to confirm certainly that mice from there should be assigned to *luteus*. [It should be noted here that even though more than 30 specimens were examined from Andrews and Ector counties, most had not yet been associated with cleaned skulls at the time of our study.]

Using discriminant function analysis, ungrouped specimens were aligned with those groups that they most closely resembled in terms of measurements. Of eight specimens from Garza County, Texas, for

TABLE 3. Results of discriminant function classification.

Actual groups	Predicted group membership							
	1	2	3	4	5	6	7	8
1	14	5	1	2	0	1	0	1
2	1	15	2	2	4	2	1	2
3	1	5	7	0	1	0	1	1
4	1	4	0	5	0	0	1	0
5	1	1	1	2	11	1	2	0
6	0	1	1	0	0	21	1	0
7	1	1	0	1	1	3	15	0
8	4	1	0	0	2	0	1	11

example, four were distributed through DFA with the Lubbock sample, but two were placed with Gloc 2, and one each with Gloc 3 and 4, all representing areas occupied by *luteus*. Therefore, Garza County, like Lubbock County immediately to the northwest, appears to represent an area of intergradation between *luteus* and *pallescens*, but specimens are here assigned to the former. Of seven unknowns from Hale County, four were placed with Gloc 3, two with Gloc 8, and one with Gloc 7. The individual placed with Gloc 7 is an unusually large specimen, but the others indicate a reduced influence of *pallescens* in Hale County. Of two specimens examined from Collingsworth County, Texas, one aligned with Gloc 5 and the other with Gloc 8. Due to the small sample size no taxonomic judgement concerning relationships should be made, and more material clearly needs to be obtained from this area of the eastern Panhandle.

Peromyscus maniculatus blandus and *P. m. rufinus* formed subsets for 14 of the 16 characters tested under the Student-Neuman-Keuls procedure. Although size may be similar in *P. m. blandus* and *P. m. rufinus*, pelage, habitat, and other distinctions continue to support their status as distinct races. A list of the total number of specimens examined of the several subspecies follows.

Peromyscus maniculatus blandus Osgood, 1904

Specimens examined (41).—TEXAS. *Pecos Co.*: 4 mi. S, 14.5 E Imperial, 16. *Winkler Co.*: Winkler County Airport, 6 mi. S Kermit, 17; 1 mi. S Kermit, 2; 2.5 mi. NE Winkler County Airport, 1; 19 mi. E Kermit, base Concho Bluff, 1; 19 mi. E Kermit, 1; vicinity Wink, 3.

Peromyscus maniculatus luteus Osgood, 1905

Specimens examined (334).—NEBRASKA. *Cherry Co.*: 2.9 mi. N, 1.1 mi. E Valentine, 4; Valentine National Wildlife Refuge, Hackberry Lake, 11; Rice Lake, 10. *Thomas Co.*: Nebraska National Forest, Bessey Division, 13.

TEXAS. *Andrews Co.*: 4 mi. N, 9 mi. W Andrews, 1; 3 mi. N, 11 mi. W Andrews, 6; 18 mi. E Andrews, 1; 7 mi. S, 3 mi. E Andrews, 1. *Bailey Co.*: 2 mi. S, 10 mi. W Muleshoe, 1; 2.2 mi. S Muleshoe, 3; 5.1 mi. S, 2 mi. W Needmore, 7; 1.7 mi. W Needmore, 1; 5.3 mi. S, 0.8 mi. W Needmore, 3. *Briscoe Co.*: Los Lingos Canyon, 1. *Carson Co.*: Pantex Research Farm, 12 mi. E Amarillo, 23. *Castro Co.*: 8 mi. N, 1.5 mi. W Hart, 8; 4 mi. NW Hart, 9; Dimmit, 6. *Collingsworth Co.*: 9 mi. E Lutie, 7; 2 mi. N, 9 mi. E Lutie, 4. *Ector Co.*: 4 mi. W Goldsmith, 1; 9 mi. N Odessa, 5; 4 mi. N Notrees, 3; 1 mi. N Notrees, 1; 3.5 mi. S, 1 mi. E Notrees, 1; 2 mi. N Odessa, 3; 10 mi. E Loop 338, Odessa, 10. *Garza Co.*: 12 mi. S Post, 2; 6 mi. SE Southland, 1; 1 mi. W Post, 3; 8.5 km NE Southland, 9. *Hale Co.*: 4 mi. N, 5.5 mi. W Cotton Center 2; 5 mi. N, 12.5 mi. W Hale Center, 3. *Hemphill Co.*: Howe Wildlife Refuge, 5; Lake Marvin, 12 mi. E Canadian, 3. *Hockley Co.*: 14 mi. NW Levelland, 3; 8.5 mi. NW Levelland, 4. *Lamb Co.*: 7.2 mi. S Olton, FM 168, 4; 4 mi. N Fieldton, 3; 6 mi. S Spring Lake, 6; 8 mi. S Spring Lake, 1; 3.5 mi. S Earth, 1; 5.5 mi. N FM 168, 1.7 mi. W FM 1842, 2 mi. N dirt road near Running Water Draw, 3. *Lipscomb Co.*: 2 mi. N, 8 mi. E Lipscomb, 2. *Lubbock Co.*: 3.5 mi. N Slaton, 5; 8 mi. W Lubbock on 4th St., 1; 3.4 mi NW Lubbock, 4; Lubbock, 10; 10 mi. SW Lubbock, 1; 7.5 mi. N Lubbock, 15; 5 mi. N Lubbock, 4; 11 mi. S Lubbock on U.S. Hwy. 62, 3 mi. S FM 179, 1 mi. E dirt road, 0.5 mi. S, 1; 8 mi. N, 6 mi. NE Lubbock, 2; 5 mi. N Lubbock Lake, 1; 0.5 mi. N Lubbock Lake, 5; 2.8 mi. E Idalou, 4; 1 mi. N, 5 mi. W Lubbock, 4; 1 mi. N, 1.5 mi. W Lubbock, 4; 7 mi. W

FM 1264 and Loop 289, 10; 4 mi. S, 5.7 mi. E Lubbock, 16. *Moore Co.*: 4 mi. N, 1 mi. E Dumas, 8. *Randall Co.*: Palo Duro State Park, 7 mi. S entrance, 1; 9.2 mi. S, 13.7 mi. E Canyon, 1; 1 mi. S Umbarguer, 1; Buffalo Lake Wildlife Refuge, 3. *Roberts Co.*: 6 mi. N Miami, 2. *Sherman Co.*: 8 mi. S, 2 mi. E Stratford, 17; 10 mi. N Stratford, 15.

Peromyscus maniculatus nebrascensis (Coues, 1877)

Specimens examined (18).—WYOMING. *Unita Co.*: 3.6 mi. W, 0.8 mi. N Fort Bridger, 12 (NMSU); 7.1 mi. W, 1.9 mi. S Robertson 6 (NMSU).

Peromyscus maniculatus pallescens J. A. Allen, 1896

Specimens examined (41).—TEXAS. *Hill Co.*: 3 mi. S, 0.5 mi. W Hillsboro, 12 (TCWC); 3.1 mi. S, 6.6 mi. W Hillsboro, 5 (TCWC); 3.1 mi. S, 0.9 mi. W Hillsboro, 6 (TCWC); 3.4 mi. S, 1.6 mi. W Hillsboro, 2 (TCWC); 5.8 mi. S, 3.4 mi. W Hillsboro, 1 (TCWC); 5.8 mi. S, 3.1 mi. W Hillsboro, 7 (TCWC); 6 mi. S, 4.2 mi. W Hillsboro, 3 (TCWC); 6 mi. S, 3.9 mi. W Hillsboro, 1 (TCWC); 3.4 mi. S, 1.6 mi. W Hillsboro, 4 (TCWC).

Peromyscus maniculatus rufinus (Merriam, 1890)

Specimens examined (65).—NEW MEXICO. *Lincoln Co.*: 2.5 mi. W Bonito Lake, 15; 2.5 mi. N Bonito Lake, 5; 4 mi. N, 5 mi. W Bonito Lake, 1; 4.9 mi. E, 1.3 mi. N Sierra Blanca, 4 (NMSU); Oak Grove Camp, Sierra Blanca, 6 (NMSU); 1.7 mi. N, 1.2 mi. E Sierra Blanca, 1 (NMSU). *Otero Co.*: 20 mi. S Cloudcroft, 12; Lightning Lake, 7; Cloudcroft, 14.

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A SENSITIVE SPECTROPHOTOMETRIC TECHNIQUE FOR MEASURING PHOTOTAXIS IN CHLAMYDOMONAS REINHARDTII

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Abstract.—A sensitive and convenient method was developed for measuring phototaxis of algal cells using a Gilford Response UV-VIS Spectrophotometer with attached printer. Wild type cells of *Chlamydomonas reinhardtii* were exposed to light continuously for eight minutes at selected wavelengths between 400 and 850 nm. The change in optical density resulting from cells swimming into or out of the light path was continuously recorded and printed. Positive phototaxis, manifest as an increase in OD, was observed for wavelengths between 440 nm and 538 nm with a maximum phototactic response at 503 nm. Other wavelengths induced negtive phototaxis, vacillation between positive and negative phototaxis, or no phototaxis, depending upon conditions of growth and phototaxis assay. The maximum positive phototactic response was +0.72 at 500 nm. A study of various factors that may influence the results of the phototaxis assay was conducted. Several parameters of phototaxis of *C. reinhardtii* measured in the Gilford compared favorably with literature values. *Key words*: *Chlamydomonas reinhardtii*; algae; motility; phototaxis; spectrophotometry.

Phototaxis in algae has been studied since 1817 (reviewed by Foster and Smyth, 1980). The techniques that have been developed for measuring phototaxis in microorganisms may be divided into two basic procedures: 1) direct microscopy of individual cells, and 2) spectrophotometric or phototube measurement of populations of microorganisms moving toward or away from a photostimulating light.

Both procedures have advantages and disadvantages. Single-cell observations allow rapid study of behavioral responses and measurement of both speed and directness of movement, but are time consuming and a large number of individuals must be studied to yield statistically valid data. Population methods quantify the movement of the population that is an admixture of directness and speed, but give no direct information on individual cell behavior.

Several effective methods have been developed for measuring population movements. Lindes et al. (1965) developed a phototaxigraph in which an actinic beam is used to photostimulate the algae and an observing beam that presents no stimulus to the algae, but passes through the algal suspension at right angles to the actinic beam to the detection system. Feinleib and Curry (1967) improved on the assay of population movements by adapting two photocells connected in a comparison circuit. Nultsch et al. (1971) and Nultsch and Throm (1975) constructed a monitoring device also based on photocell measurements but possessing the capability of being connected to a continuous culture device from which samples could be withdrawn. Stavis and Hirschberg (1973), in a thorough study of *Chlamydomonas* phototaxis, adapted a spectrophotometer to use two light sources, an actinic beam and an 800 nm light to measure population movement.

All of these population measuring procedures require construction or modification of pre-existing equipment. In this paper, we describe a simple, rapid, yet sensitive method of measuring phototaxis using an unmodified commercially available instrument, the Gilford computerized "Response" spectrophotometer. The characterization of the phototaxis of *Chlamydomonas reinhardtii* using the Gilford compares quite well with characterizations found in the literature. In the process of refining this phototaxis assay technique, a simple, rapid, and inexpensive procedure for culturing vegetative cells of *C. reinhardtii* on a liquid medium overlay of an agar medium base also was developed. The procedure yields cells that are immediately motile and reproducibly phototactic.

Materials and Methods

Algal Strain and Conditions of Growth

Chlamydomonas reinhardtii strain 137c (CC-125 mt+) was obtained from the *Chlamydomonas* Genetics Center, Department of Botany, Duke University, Durham, North Carolina, and was used for these studies. Minimal (HS) and acetate (HSA) media were prepared by the Harris et al. (1977) formulation modification of the original Sueoka (1960) medium. The algae were generally grown in a liquid medium overlay over an agar base, for example, five milliliters of HS broth over a 25-milliliters HS agar base in standard (100 × 15 mm) Petri plate or three milliliters HSA broth over 8 milliliters HSA agar base slant in a standard (125 × 20 mm) glass screw-capped culture tube. Cultures were inoculated with 10^6 algal cells per milliliter or more final concentration of cells in their log phase of growth, and yielded 150 to 600 million cells per plate after two to three days of incubation at 23°C in continuous light at 81 ft. Lamberts. Cultures under continuous light yielded significantly better growth than did identical cultures grown under a 12-hour light-dark cycle.

Cell Harvest and Cell Counts

Cells are harvested from the broth overlay by adding fresh HS or HSA broth and triturating to suspend the cells in a final volume of 7.0 milliliters. The cells were diluted (equivalent to 5 to 7 × 10^6 cells per milliliter) in HS broth to a target OD (600) of 0.8 to 1.0 in a 10-mm cuvette (but an OD (600) range of 0.4-1.2 was satisfactory). This range of dilutions of cells was used to perform time scans (TS) (phototaxis assays) and wavelength (WL) scans. An aliquot of this TS dilution (usually 25, 50, or 100 μl) was removed and diluted into 20.0 milliliters Isoton II (Coulter Diagnostics, Hialeah, Florida). The number of cells and the size distribution of the cells were determined in a Coulter Electronic Cell Counter (Model ZBI) and Channelizer. The size standard was provided by Rhesus monkey red blood cells with a volume of 72 μm^3. Cell counts and cell size distributions of the algae were performed according to instruction provided by the manufacturer. If the raw count was above 10,000, the count was corrected for coincidence using a chart provided by the manufacturer. Motility of the cells was routinely estimated by visual examination of a hanging drop.

Spectrophotometry of the Cell Suspensions

Although any spectrophotometer with suitable absorbance versus time and absorbance versus wavelength capability and a beam distribution of about 20 mm^2 would function satisfactorily for these experiments, a Gilford Response UV-VIS Spectrophotometer was used for this work. The spectrophotometer was set to a "continuous Time Scan Mode" and the band width of light was set to a maximum of 4 nm to give adequate light to attract the organisms. A time scan could not be less than four minutes, but for our studies eight minutes was optimum. The first author can provide a protocol to interested individuals wanting to use the Gilford instrument.

Evergreen 201-3125-010 standard (10 mm), four sides clear, disposable cuvettes were used for these studies. The time scans were performed on an algal suspension in a cuvette using the suspending medium, HS or HSA, as a blank. The cell suspensions in the cuvette were mixed using air bubbling from a pipet prior to spectrophotometry time scans. After a time scan was performed on a cell suspension, the cuvette of cells was returned to room light for a 15-minute adaption period before subsequent time scans were performed.

RESULTS

The performance of many phototaxis assays brought out several factors that may influence the results. These factors were: cell motility; handling of the cells from time of harvest to phototaxis assay; wavelength of photostimulating light; length of time scan; concentration of cells; repeating of time scans.

Cell Motility

The majority of cultures harvested from liquid medium overlays were 90 percent or more actively motile. We have found (unpublished data) that cultures of *C. reinhardtii* grown on plates as described in this paper show a periodic fluctuation in the percentage of motile cells in the population as it progresses through the growth curve.

Handling of the Cells from Time of Harvest to Phototaxis Assay

The phototactic response at 500 nm of a *C. reinhardtii* culture grown on an HS plate in continuous light for three days and then preadapted to light or dark is compared in Figure 1. The culture was harvested as described, then separated into two groups—one handled in the light and the other in the dark—prior to subjecting the cells to spectrophotometer time scan. All other conditions of the two groups were identical. The cells preconditioned in light responded by a roughly linear swimming into the light path with a $+0.40$ $\Delta OD(500)$. The cells preconditioned in dark responded to the light similarly for about four minutes but then gradually began to plateau in their attraction to 500 nm light. The dark preadapted cells had a $\Delta OD(500)$ of $+0.27$. Thus, subsequent studies were performed with cells handled in the light.

Several other factors also encouraged the handling of cells in room light. It was easier to manipulate them in room light, and dark-adapted

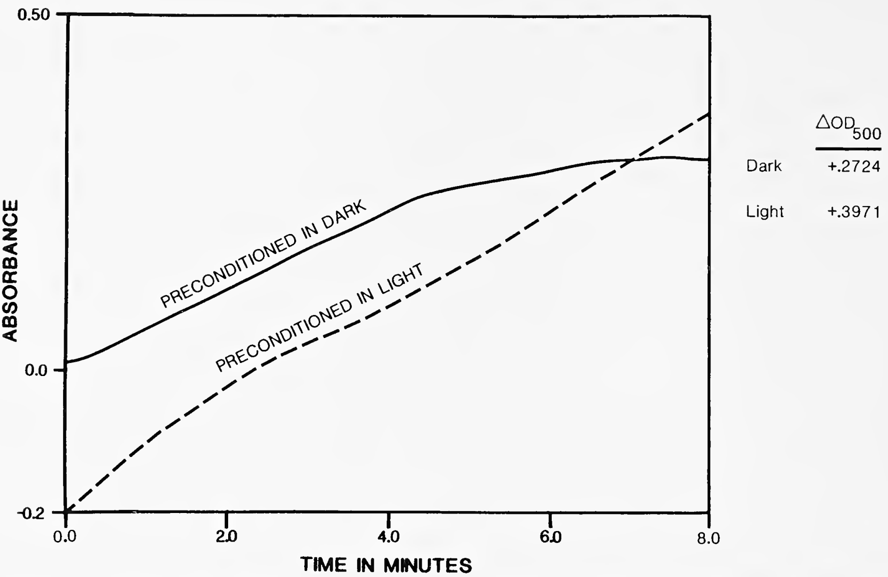

FIGURE 1. Effect of preconditioning of algal cells in dark or light on phototactic response of *C. reinhardtii* to 500 nm light. A three-day-old HS plate culture grown under continuous light was harvested and diluted with HS broth as described. The harvest was separated into two groups, one preadapted and handled in the light and another in the dark, and both groups of cells were tested for phototaxis to 500 nm light. In the test shown here, light preadapted cells responded to the 500 nm light with a roughly linear profile, whereas dark preadapted cells responded by a linear accumulation in the light followed by a plateau after about four minutes. The ΔOD(500) for light preadapted cells was +0.3971 and for dark preadapted cells it was + 0.2724.

cells had a tendency to stick to the sides of the cuvette at the entrance and exit of the light beam. By comparison, if the cuvette with the algal suspension was preadapted to the light, then returned to room light after the phototaxis assay, the cells would then release from the cuvette surface spontaneously. It also is shown in Table 1 that cells preconditioned to light show less fluctuation in repeated phototaxis assays than cells stored in the dark. The magnitude of the ΔOD(500) varied in different cell harvests between being higher for dark-preadapted or light-preadapted cells. The greater precision of repeated phototaxis assays and the greater ease of handling in room light outweighed any benefit of greater ΔOD(500) of dark-preadapted cells.

Wavelength of Photostimulating Light

Positive phototaxis for strain CC-125 was observed between 440 and 563 nm. Negative or undulating phototaxis was observed below 400 nm and above 600 nm (Fig. 2). The algae responded to wavelengths of 400 and 800 nm with an undulating positive-negative phototaxis initially, then

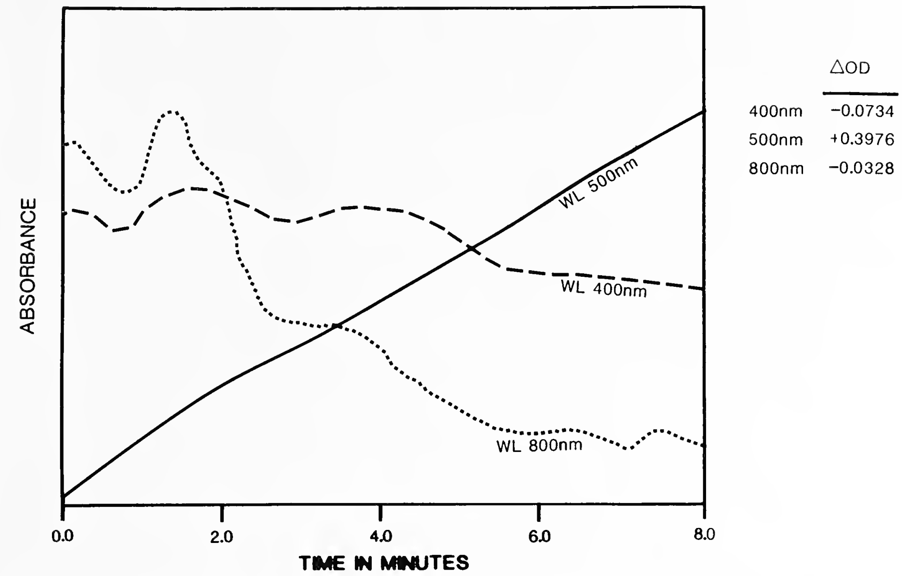

FIGURE 2. Time scan profiles of *C. reinhardtii* to 400 nm, 500 nm, and 800 nm light. A 3-day-old HS plate culture was harvested and after one hour in room light, time scans were performed on the same cell suspension at 400, 500, and 800 nm light. The ΔOD values were ΔOD(400) = -0.07, ΔOD(500) = + 0.40 and ΔOD(800) = -0.03 for the same cells.

followed by a smoother avoidance of those wavelengths of light. The greatest negative phototaxis we have observed was ΔOD(683) = -.010. The greatest positive phototaxis we have observed was ΔOD(500) = +0.72.

Length of Time Scan

The length of the spectrophotometer time scan is determined by how long it takes algae to reach their maximum ΔOD. In our earlier studies, it required an eight minute exposure to the photostimulating light for cell suspension to reach a maximum ΔOD(500). In these earlier studies, some of our cultures were contaminated with bacteria. With contaminated algae, the OD(500) was reached in about three minutes with a gradual drop in OD(500) thereafter. We continued to use eight-minute time scans to insure that phototaxis assays were not terminated before maximum OD(500) was reached.

Concentration of Cells

Results of two experiments that addressed the question of the effect of the number of cells per unit volume in the cuvette on the ΔOD(500) of the cell suspension are shown in Figure 3. A fresh culture was serially

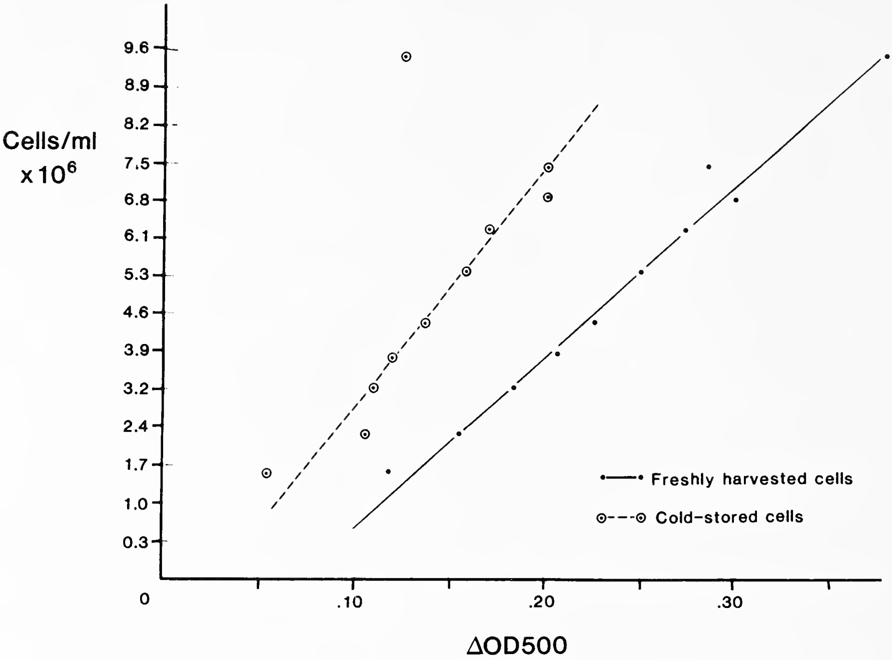

FIGURE 3. Effect of cell concentration on the magnitude of the ΔOD(500). A four-day-old HS plate culture was harvested and diluted in HS broth to produce an initial cell suspension of OD(600) = 1.3737 ($9.6 X 10^6$ cells per milliliter). This was diluted through a series of 10 dilutions with HS to a minimum OD(600) = 0.2803. A phototaxis assay at 500 nm was performed on each of the dilutions and the ΔOD(500) plotted (____.____.____) against the cell concentration. The culture dilutions were stored overnight at 5° C and the phototaxis assay performed again with the same dilutions of cells. These data were plotted as ΔOD(500) versus cell density (0----0----0). The number of particles per milliliter was counted in triplicate in the Coulter Counter as described in Materials and Methods and the correlation between the average of the cell count and the cell suspension OD(600) plotted.

diluted over a range of 1.7 to 10.8×10^6 cells per milliliter in HS medium and time scans were performed on each dilution. The dilutions were cold stored in dark overnight and the time scans were repeated. In both instances, the ΔOD(500) varied linearly with the cell concentration. The magnitude of the ΔOD(500) of the cold-stored cells was less than the same cells that had been freshly harvested. It is clear from these two experiments that the number of cells entering the photostimulating light path varied directly with cell concentration.

Repetition of Time Scan Responses

It was of interest to determine if a single algal suspension could be used for multiple phototaxis analyses or if fresh cells had to be prepared for each analysis. Cells preadapted to light and dark and held under

TABLE 1. Comparison of the precision of the phototactic response of *C. reinhardtii* using cells preadapted to the light or dark.[1]

Cells preconditioned to light		
Trial no.	Fresh cell suspension ΔOD(500)	Cell suspension cold stored in light ΔOD(500)
1	.34	.17
2	.31	.19
3	.32	.18
Mean	.32	.18
S. D.	.0171	.0074
S. D. (%)	5.3	4.1
Cells preconditioned to darkness		
Trial no.	Fresh cell suspension ΔOD(500)	Cell suspension cold stored in dark ΔOD(500)
1	.37	.20
2	.49	.19
3	.45	.19
Mean	.44	.19
S. D.	.0617	.0067
S. D. (%)	14.1	3.4

[1] Cells were harvested from a three-day-old HS agar plate and diluted in HS broth to produce a WLTS sample with OD(600) = 1.04. The algal cells were aliquoted into two cuvettes; one to be exposed continually to light and one to be kept in the dark. Each set of identical suspensions was assayed for phototaxis using HS broth as reference. The data are presented as ΔOD(500) and rounded to two places. After the phototaxis assays were completed, the cuvettes with the algal suspensions were placed at 5°C in light or dark for 24 hours. The algal suspensions were warmed to room temperature and the phototaxis assays repeated. The percent S. D. is the percent variation that the standard deviation varies from the mean.

those respective conditions were used. A phototaxis assay was performed on a cuvette of cells; then the cells were returned to room light (17.5 ft. Lamberts) or darkness. A minimum of 15 minutes to re-equilibrate was required before another trial could be conducted (cells re-equilibrated less than 15 minutes were not consistent in their phototactic response). The cells always were mixed with a disposable Pasteur pipet prior to each time scan. Three separate trials were performed. Results along with the mean, the standard deviation from the mean, and the percent from the mean that the standard deviation represents all are given in Table 1. These data support the contention that the same suspension of cells may be used for at least three trials without significant decay of the algal cells ability to phototax. Time scans may be repeated over a period of six hours. The data presented in Table 1 also show that light-adapted, one-hour post harvest cells showed a smaller data scatter for replicate runs than did cells preadapted and stored in darkness. Cells can be stored overnight in the cold at 5°C in the light or dark and the cells remain phototactic, but the sample suspension showed a ΔOD(500) about 50 percent less than that for the preceding day. It also was observed that freshly harvested cells gave high ΔOD(500) values, but that the cells were quite erratic in repeated phototaxis assays, thus yielding poor precision. Repetition of assays with the same initial dilution cell suspension sample showed that cells must be held for one hour in room light after harvest prior to phototaxis assay in order to yield the data precision shown in Table 1.

Discussion

This paper describes a procedure for assaying phototaxis using an unmodified commercially available computerized spectrophotometer. In contrast to previously published methods, this procedure does not use a separate actinic light to photostimulate the cells and a nonstimulating light to measure cell population movements. Instead, it measures the number of cells that swim into or out of a beam of light with reference to a randomly moving background population. The single beam of light serves as both the photostimulating light and the measuring light, which is recorded as change in absorbance or ΔOD with respect to the absorbance of the randomly moving cell population. Because the phototaxis assay does not employ separate actinic and measuring light beams, it was important to show that this technique could duplicate some landmark experiments on phototaxis available in the literature. It was also important to show what effect certain experimental variations may have on the results of a phototaxis assay.

Our experiments are in accord with those of Stavis and Hirschberg (1973) in that phototaxis is dependent upon motility, but that the control of phototaxis is independent of the control of motility. Because Stavis and Hirschberg (1973) observed that dark-grown *Chlamydomonas* showed poor motility and phototaxis coefficients, a brief experiment was conducted to determine if the history of light exposure of the cells would affect the results of the phototaxis assays. Our experiments, recorded in Figure 1, show that there are minor differences in shape of the time-scan profile. The magnitude of the ΔOD(500) varied between being greater in dark or light-preadapted cells from different cell harvests, but experiments reported in Table 1 show that the precision of the data from replicate runs is better for cells maintained in room light. The reason (s) for this variation in ΔOD(500) in response to light or dark preadaptation is not clear, but is most likely related to effects of culture age. The relationship between ΔOD(500) and cell concentration shown in Figure 3 also compares well with the similar experiment of Starvis and Hirschberg (1973). Our procedure does not have the advantage of the procedure of

Pfau et al. (1983) in that it cannot simultaneously measure the effect drugs have on both motility and phototaxis. Our procedure requires motile cells for phototaxis, although it may be possible eventually to evaluate the motility component by the rate of change of optical density with respect to time. We have observed roughly two classes of motility—rapid and sluggish—but usually the motility is rapid. We have occasionally observed motile cells that were nonphototactic; the reason(s) for this were not apparent. The shape of many of our time-scan profiles was quite similar to those of Pfau et al. (1983) in that the cells reach a maximum ΔOD in two to four minutes, after which they leave the light and the absorbance gradually decreases. The shape of the time scan profile may vary from experiment to experiment, but is generally uniform for repeated phototaxis assays on the same cell suspension without changes in conditions. We observed that in preadaptation to light or dark, storage overnight in the cold, or exposure to different wavelengths of light induced changes in the ΔOD as well as in the shape of the time-scan profile (Figs. 2 and 3). Cells cultured under the conditions described here are quite durable in their phototactic ability and repeated spectrophotometry time scans on the same cell suspension may be conducted over a six-hour period or longer without significant decay of phototactic response. The cells must be allowed to recover in room light between scans.

ACKNOWLEDGMENTS

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RESPONSE OF SMALL MAMMALS TO CONVERSION OF A SAND SHINNERY OAK WOODLAND INTO A MIXED MID-GRASS PRAIRIE

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Abstract.—Shrubs were removed in two areas of a sand shinnery oak woodland via the aerial application of tebuthiuron, an herbicide that eliminates at least 90 percent of the shrub component (*Quercus havardii*). A circular grid containing 260 traps was established at each of four sites: two tebuthiuron treated areas and two untreated or control areas. Estimates of density (total rodents and *Dipodomys ordii* alone) based upon the minimum number known to be alive were obtained for each area during each of four phenological seasons. Habitat variables (percentages of bare ground, ground litter, canopy cover, shrubs, forbs, and grasses, as well as vertical height) were determined for tebuthiuron treated and control sites. Statistical analyses revealed that both total rodent density and *D. ordii* density changed in response to tebuthiuron-related effects. Species composition (proportional species densities) also differed significantly between treated and untreated areas. Seasonal effets on density and species composition occurred and probably were related to behavioral responses of rodents to temperature and precipitation regimes. *Key words*: small mammal community; rodents; mixed grass prairie; sand shinnery oak woodland; *Dipodomys*; tebuthiuron.

Habitat characteristics clearly affect rodent populations. It is well documented that a variety of vegetational characteristics affect species composition of local rodent communities as well as the density of component species (Hansen and Ward, 1966; Tietjen et al., 1967; Johnson and Hansen, 1969; Rosenzweig and Winakur, 1969; Parmenter and MacMahon, 1983; Schroder, 1987; Wywialowski, 1987; Abramsky, 1988; Brown, 1989; Brown and Zeng, 1989). The community and population responses of small mammals to vegetational changes have been studied by inducing modifications through the use of chemical treatment (Johnson, 1964; Johnson and Hansen, 1969; Christian, 1977; McGee, 1982; Sullivan and Sullivan, 1982; Zou et al., 1989), fire clearcutting (Gashwiler, 1970; Sullivan, 1979; Van Horne, 1981), and mechanical removal of select plant species (Parmenter and MacMahon, 1983). Percent cover (Allred and Beck, 1963; Brown et al., 1972; M'Closkey, 1975; M'Closkey and Lajoie, 1975; Rosenzweig et al., 1975; Feldhamer, 1979), vegetation-precipitation relationships (Reynolds, 1958; Brown, 1973; Hafner, 1977), foliage height diversity (Allred and Beck, 1963; Rosenzweig and Winakur, 1969; M'Closkey, 1975; Morris, 1979), foliage density (Rosenzweig and Winakur, 1969; Brown et al., 1972; M'Closkey and Lajoie, 1975; Hafner, 1977), and ground litter (Morris, 1979) are among the many variables that have been correlated or associated with changes in small mammal densities and community composition.

Munger et al. (1983) suggested that bushes are favorable resource patches that act as proximate cues for rodent activity, whereas results from several other studies pointed toward cover as the main factor affecting rodent populations in arid and semiarid environments (Rosenzweig and Winakur, 1969; Price, 1978; Thompson, 1982; Parmenter and MacMahon, 1983). Nontheless, Hafner (1977) contended that desert rodent species diversity does not respond to a particular parameter because even animals of the same species are influenced by different environmental factors in different geographical situations. This leads to the question of the importance of shrubs in determining small mammal species composition and abundance in a sand shinnery oak woodland.

Sand shinnery oak (*Quercus havardii*) predominates on sandy soils in semiarid environments in western Texas, southeastern New Mexico, and western Oklahoma, where it grows on about 2.7 million hectares (Pettit and Jones, 1986). The sand shinnery oak ecosystem is essentially a monoculture, with at least 80 percent of the herbage being oak (Pettit and Jones, 1986). The effect of the shrub component on rodent population parameters has not been studied even though removal of the sand shinnery oak via tebuthiuron treatment drastically alters the habitat by changing cover, food resources, foliage height diversity, and water availability to other plants (McIlvain, 1954; Elwell, 1964; Rechenthin and Smith, 1967; Robison and Fisher, 1968; Jones and Pettit, 1984; Pettit and Jones, 1986). Herein, we assess the response of small mammals to the tebuthiuron-induced conversion of a sand shinnery oak woodland into a mid-grass prairie. We also attempted to identify the potential ecological variables associated with changes in small mammal population density or community composition. The hypotheses for evaluation were that the removal of the sand shinnery oak would affect a change in the overall abundance of small mammals, and that there would be an alteration in species composition, possibly because of herbicide-induced changes in habitat variables. Moreover, *Dipodomys ordii* density should change in tebuthiuron-treated areas because kangaroo rats, in general, avoid areas of thick cover and are associated more frequently with sparsely vegetated areas (Rosenzweig and Winakur, 1969; Rosenzweig, 1973).

MATERIALS AND METHODS

Study Site

The study site is located on the Southern High Plains of Texas (33°22′-33°26′ N, 102°37′-102°50′ W), about 19 miles N and 4 miles E Plains, Yoakum County. The terrain is relatively flat at an elevation of about 1260 meters. The climate is warm-temperate and semiarid, with fluctuating temperatures during the winter. Annual precipitation averages 41 centimeters, with the majority of the rainfall occurring from May through October (Jones and Pettit, 1984).

The vegetation on the untreated control sites is at least 80 percent (biomass) sand shinnery oak (Pettit and Jones, 1986). Other plants found on the control sites include soapweed (*Yucca angustifolia*), sand sagebrush (*Artemesia filifolia*), and prickly pear cactus (*Opuntia polyacantha*). The vegetation on the treated site is predominantly grasses and forbs; the more common plants include little bluestem (*Schizachyrium scoparium*), purple threeawn (*Aristida purpurea*), annual buckwheat (*Erigonum annuum*), and fleabane (*Erigeron modestus*). A complete plant species list for the area is presented in Colbert (1986). Mammals known from the study area include *Dipodomys ordii* (Ord's kangaroo rat), *Onychomys leucogaster* (northern grasshopper mouse), *Perognathus flavescens* (plains pocket mouse), *Peromyscus maniculatus* (deer mouse), *Reithrodontomys montanus* (plains harvest mouse), *Sigmodon hispidus* (hispid cotton rat), *Neotoma micropus* (wood rat), *Spermophilus spilosoma* (spotted ground squirrel), *Canis latrans* (coyote), *Taxidea taxus* (badger), *Lepus californicus* (black-tailed jackrabbit), *Sylvilagus audubonii* (desert cottontail), *Antilocapra americana* (pronghorn), and *Bos bos* (cattle).

Shrub Removal

The study area was chosen because shrubs had been removed via the application of tebuthiuron (Graslan^R; N-(5-(1, 1- dimethylethyl) -1,3,4-thiadizol-2yl)-N,N'- dimethylurea) pellets (20 percent active ingredients) that were aerially broadcast at an application rate of one-half pound per acre. Grid I was treated in May 1982, whereas grid II was treated in May 1980 and retreated in May 1983. The use of tebuthiuron is the only method that essentially eliminates sand shinnery oak for an extended period and does not directly affect other components of the plant community, except for initial damage to forbs (Jones and Pettit, 1984). Tebuthiuron has been documented to kill more than 90 percent of the sand shinnery oak in the community (Pettit, 1975; Jones et al., 1978; Jones and Pettit, 1984). The two treated areas, although different in treatment times, were chosen because of their current similarity in vegetation, previous and present grazing pattern, and topography. Within each treated area, grid sites were selected randomly. Trapping sites were established on two control areas where sand shinnery oak had never been treated with tebuthiuron. All four sites were within a 1500-hectare area.

Rodent Trapping

We used a circular grid to trap rodents. Thirteen lines, each comprising 20 medium-sized Sherman live-traps, radiated from a center stake, with the first trap in each line 2.5 meters from the center stake. The remaining traps were placed at five-meter intervals. This spacing was used in order to 1) insure at least eight to 12 traps per home range in the center of the grid, and 2) facilitate the capture of approximately 60 individuals during a trapping session (Anderson et al., 1983). Preliminary results from trapping a circular grid from 25 May to 15 July 1984 suggested that the previously described trap spacing and grid size were appropriate given the small mammal fauna at the sites. Four permanent grids were established, one in each of the treated areas, and one in each control area. Trapping continued until all animals from the center of each grid were captured in accordance with the recommendations of Anderson et al. (1983). This usually required three or four nights of trapping. Trapping sessions were scheduled during the dark phase of the moon to restrict any variation in activity that might be affected by moon light (Price et al., 1984). Because of limitations in the number of available traps, one control site and one treated site were trapped at the same time. The traps were then moved to the replicate sites for additional trapping. The complete trapping regime required eight or nine days each season.

Trapping was aimed at nocturnal and crepuscular rodents only. Larger mammals such as desert cottontails (*Sylvilagus audubonii*) and black-tailed jackrabbits (*Lepus californicus*) were excluded because of trap size. Diurnal rodents such as the spotted ground squirrel (*Spermophilus spilosoma*) were not marked when captured, and thus do not appear in the overall evaluation of rodent density and species composition. A granola mixture was used as bait; cotton Nestlets^{P} were placed in each trap to prevent rodent hypothermia. Upon initial capture, rodents were uniquely toe-clipped, weighed, and identified to sex and species. Trap location was recorded for initial as well as subsequent captures of previously caught individuals.

Trapping was conducted in four sessions defined by seasonal foliage changes that occur in the area. The first session was in the winter after all leaves had fallen from the oaks (19 to 27 January 1985). Trapping was restricted to only three nights on each grid. The second period occurred during oak refoliation in the spring (13 to 20 May 1985). The third trapping session occurred in the summer during maximum plant development (10 to 17 August 1985). The last period was during the autumn dormancy, after the first frost but before leaf fall (9 to 19 November 1985).

Vegetation Sampling

A summary of vegetation sampling methods is offered by Daubenmire (1968), the original source for most of the following procedures. A permanent line transect was established across each grid to measure the same points every trapping season. A frame of 0.25 square meter was placed at 30 points spaced equidistantly along the transect. At each point, the highest vegetation within the frame was measured for vertical height. Then, using either a Canon AE-1 35-mm or a Minolta XG-7 35-mm camera, and focusing from directly above the center of the frame, a photograph was taken of the quadrat. The resultant slides were projected onto a screen of 0.5 by 0.5 meters that was divided into 100 sections. This enabled an accurate estimation of the percentages of bare ground, ground litter, and canopy cover. Also, a step-point analysis was performed to determine vegetation composition. A transect was walked for 100 steps across each grid. Bare ground, litter, or plant species identity was recorded at the end of each step. If bare ground or litter was recorded, the identity of the closest plant species was also noted. Percentage of shrubs, forbs, and grasses was determined from these data.

Population Estimation

We designed the study to take advantage of features of plotless or distance sampling (Anderson et al., 1983), but because of methodological limitations associated with low capture sucess, limited our analyses to a more simple index of density. The minimum number of individuals known to be alive (N_{min}) on each grid per trapping session was used as the index of density. This enumeration method has been used serveral times in studies concerning dispersal (Krebs et al., 1976; Stafford and Stout, 1983; Williams and Cameron, 1984) and demography (Krebs, 1966; Yahner, 1983). Moreover, recent studies indicate density estimates based upon N_{min} and more complex procedures (JOLLY method for open populations, CAPTURE method for closed populations) are highly correlated; in fact, the magnitude of these estimates differed by no more than 30 percent (S. Blair, personal communication). Regardless, the bias of underestimating density should be consistent in all treatments, thereby not affecting statistical comparisons.

Statistical Methods

Model I two-way (tebuthiuron treatment versus season) Analysis of Variance (ANOVA) was used to compare the relative abundance after arcsine (angular) transformation (Sokal and Rohlf, 1981) of shrubs, forbs, and grasses, as estimated from the step-point analysis, using SAS program Proc GLM (SAS Institute, 1985). Four ecological variables (vertical height, percent bare ground, percent ground litter, and percent canopy cover) were analyzed via mixed-model nested two-way ANOVA, with two grouping factors and one trial factor (BMDP2V—Dixon and Brown, 1979). The two grouping factors were tebuthiuron

Table 1. Pure model 1 two-way (tebuthiuron treatment versus season) ANOVA calculated for percent occurrence of forbs, grasses, and shrubs, respectively.

Source of variation	DF	Sum of squares	Mean squares	F	Significance
		Forbs			
Treatment (T)	1	0.151	0.151	6.02	0.049
Season (S)	2	0.280	0.140	5.59	0.043
T x S	2	0.217	0.109	4.33	0.068
Error	6	0.150	0.025		
		Grasses			
Treatment (T)	1	0.405	0.405	27.30	0.002
Season (S)	2	0.419	0.210	14.14	0.005
T x S	2	0.265	0.133	8.95	0.016
Error	6	0.089	0.015		
		Shrubs			
Treatment (T)	1	0.083	0.083	111.11	0.001
Season (S)	2	0.010	0.005	0.67	0.548
T x S	2	0.046	0.023	3..09	0.120
Error	6	0.045	0.007		

treatment and season; the trial factor comprised two grids within each treatment. The vertical height analysis had 30 replications within each grid, whereas each of the other three variables had 19 replications within each grid. Percent bare ground, percent canopy cover, and percent ground litter were subjected to arcsine transformation, in order to meet the assumption of normality and homoscedasticity for ANOVA (Sokal and Rohlf, 1981); tebuthiuron treatment and season were the main effects tested. Population size, as estimated by minimum numbers known to be alive, was analyzed by model I two-way ANOVAs (tebuthiuron treatment versus season), followed by the Welsch Step-Up Procedure, a multiple comparison test (Sokal and Rohlf, 1981). Regardless of the significance of the ANOVA, a series of more powerful *a priori* comparisons of tebuthiuron treated versus control grid densities were conducted within each season (Sokal and Rohlf, 1981).

A Chi-Square Contingency Test (Zar, 1984) was conducted on the number of initial captures of each species for each season to determine if tebuthiuron treatment affected small mammal species composition. If a significant Chi-square value resulted, the proportional contribution of each species to the overall Chi-square value was calculated as a means of identifying taxa affecting significance.

Results and Discussion

Floral Analysis

Composition.—The two-way ANOVA for shrub abundance (Table 1, Fig. 1) indicated a highly significant difference ($P = 0.001$) between tebuthiuron treated and untreated areas. Season did not have an effect ($P = 0.548$), and season affected all tebuthiuron treated and untreated areas equally, as no evidence suggested an interaction ($P = 0.120$). Grass abundance also showed effects of tebuthiuron treatment (Table 1); however, the treatment effects were dependent on season (the interaction was significant, $P = 0.016$). In particular, the greater abundance of

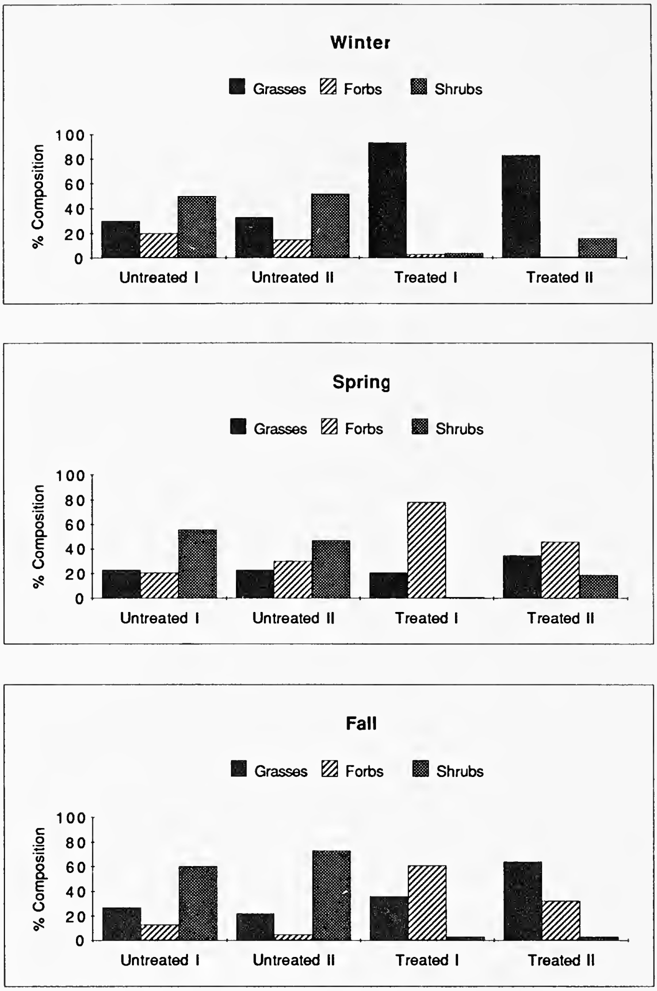

FIGURE 1. Seasonal comparison (winter, spring, and autumn) of floral composition (percent grasses, forbs, and shrubs) in the tebuthiuron treated and untreated grids within the sand shinnery oak woodland.

grasses in tebuthiuron treated grids is magnified in the winter compared to spring or autumn (Fig. 1). The percentage of forbs was significantly different between tebuthiuron treated and untreated areas ($P = 0.049$); a consistent difference existed among seasons ($P = 0.043$) as well (Table 1, Fig. 1). In general, tebuthiuron treatment caused a singificant change in shrub, grass, and forb abundance, whereas seasonal variation existed in forb and grass abundance, but not in shrub abundance.

Habitat variables.—Four habitat variables (percent bare ground, percent canopy coverage, percent ground litter, and vertical height) were chosen to evaluate differences between untreated sand shinnery oak and tebuthiuron treated areas of shrub removal. The data for each variable were compared in a mixed model two-way nested ANOVA, evaluating differences related to tebuthiuron treatment, season, and grids within treatment (Table 2). Percent ground litter was not significant for main treatment effects or for interaction terms. Percent bare ground also was not significantly different between tebuthiuron treatments ($P = 0.092$); however, a significant difference among seasons was detected ($P = 0.003$). No interaction between tebuthiuron treatment and season occurred ($P = 0.253$). Vertical height was significantly different only between tebuthiuron treated and control areas ($P = 0.012$). Percent canopy cover was significantly different between tebuthiuron treated and control areas ($P = 0.005$), as well as among seasons ($P = 0.006$). These differences were consistent in that the interaction between tebuthiuron treatment and season was not significant ($P = 0.588$). Canopy cover and vertical height were the only variables significantly affected by tebuthiuron application, whereas canopy cover and bare ground were the only variables that differed seasonally. No evidence of interaction between tebuthiuron treatment and season existed for any of the four habitat variables.

Faunal Analysis

Species composition.—Rodent species captured in the treated area included *D. ordii, O. leucogaster, Perognathus flavescens, R. montanus, N. micropus, S. hispidus,* and *Peromyscus maniculatus. D. ordii* was the most often captured every season, except in the autumn, when *O. leucogaster* was trapped most often. Both *D. ordii* and *O. leucogaster* were captured in every season. *S. hispidus* was caught only in summer. *Perognathus flavescens* was trapped in every season except winter. *N. micropus* and *Peromyscus maniculatus* were caught only in the spring (one individual of each species). *R. montanus* was captured in the spring and autumn.

The rodent species trapped in the untreated areas were *D. ordii, O. leucogaster, P. maniculatus, N. micropus, P. flavescens,* and *Mus musculus. D. ordii* and *O. leucogaster* were caught in every season, with *D. ordii* being captured most often every season except autumn, when trap success for every species was low. *N. micropus* was caught in winter, whereas *M. musculus* was caught only in the autumn. Overall, seven species were captured in treated areas and six species were trapped in control areas. In both areas, *D. ordii* was captured most often except in autumn. It is possible that *O. leucogaster* was more abundant in both the treated and control areas in the autumn because of an unusually high population of grasshoppers, one of their chief sources of food (Davis, 1978) in summer and early autumn. All species caught in the untreated areas were caught in the treated areas, with the exception of *M.*

TABLE 2. Mixed model two-way (tebuthiuron treatment versus season) nested (replicate grids within cells) ANOVA for ground litter, bare ground, vertical height, and canopy cover. Abbreviations are: DF, degrees of freedom; MS, mean square; *P*, significance level.

Source	Ground litter				Bare ground				Vertical height				Canopy cover			
	DF	MS	F	*P*	DF	MS	F	*P*	DF	MS	F	*P*	DF	MS	F	*P*
Tebuthiuron (T)	1	1.767	3.43	0.113	1	0.457	4.02	0.092	1	12651.064	12.56	0.012	1	3.405	19.42	0.005
Season (S)	2	2.330	4.52	0.063	2	1.953	17.16	0.003	2	2131.029	2.12	0.202	2	2.380	13.58	0.006
T x S	2	0.322	0.62	0.567	2	0.198	1.74	0.253	2	993.542	0.99	0.426	2	0.102	0.58	0.588
Error I	6	0.515			6	0.114			6	1007.541			6	0.175		
Grids (G)	18	0.092	1.02	0.440	18	0.058	0.73	0.774	29	210.236	0.84	0.699	18	0.051	1.10	0.361
T x G	18	0.072	0.80	0.695	18	0.140	1.78	0.037	29	316.741	1.27	0.176	18	0.074	1.60	0.072
S x G	36	0.071	0.79	0.783	36	0.050	0.63	0.943	58	226.850	0.91	0.657	36	0.034	0.73	0.633
T x S x G	36	0.065	0.72	0.872	36	0.053	0.67	0.918	58	191.692	0.77	0.878	36	0.062	1.34	0.124
Error 2	108	0.090			108	0.079			174	249.550			108	0.046		

Table 3. Pure model I two-way ANOVA of variance (tebuthiuron treatment versus season) comparing density indexes for all species and only *D. ordii* based upon minimum number known to be alive (N_{min}).

Source	DF	Sums of squares	Mean squares	F	Significance
		Total Species			
Treatment (T)	1	506.25	506.25	27.37	0.001
Season (S)	3	2696.75	898.92	48.59	0.000
T x S	3	244.75	81.58	4.41	0.041
Error	8	148.00	18.50		
		Dipodomys ordii			
Treatment (T)	1	441.00	441.00	22.05	0.002
Season (S)	3	2225.25	741.75	37.09	0.000
T x S	3	367.50	122.50	6.12	0.018
Error	8	160.00	20.00		

musculus, whereas *S. hispidus* and *R. montanus* were the only species from the treated area that were not caught in the untreated area.

In Chi-Square Contingency Tests for spring, autumn, and winter, species composition (the number of individuals captured in summer was too low to perform a meaningful test), data from untreated grids were combined and data from control grids were combined. These combined data sets were tested as untreated and treated areas for each season. Species composition for the autumn season was independent of tebuthiuron treatment ($X^2 = 5.52$, $df = 2$, $P > 0.05$). No significant difference in species composition existed between treated and untreated areas. In contrast, a highly significant difference in species composition ($X^2 = 165.23$, $df = 2$; $P < 0.001$) occurred in winter because of tebuthiuron treatment. More than half the Chi-square value (approximately 56 percent) was attributable to the higher than expected number of *O. leucogaster* captured in the untreated areas, and about 30 percent was due to *Peromyscus maniculatus* and *N. micropus*, which were combined to meet Chi-square grouping rules (Sokal and Rohlf, 1981). The remainder was due to the larger than expected numbers of *D. ordii* in the treated areas. Species composition in spring was significantly different in treated and untreated areas ($X^2 = 7.04$, $df = 2$, $0.05 > P > 0.025$), also mainly because of the high numbers of *O. leucogaster* (approximately 71 percent). The remaining 29 percent of the deviation was due to the slightly higher numbers of *D. ordii, P. maniculatus, R. montanus, P. flavescens*, and *N. micropus* in the treated areas.

Species densities.—The way in which tebuthiuron affected rodent density (N_{min}) depended upon season (a significant interaction, $P = 0.041$; Table 3); for the most part, the interaction related to the magnitude of the effect of the conversion, rather than to its direction. Mean densities

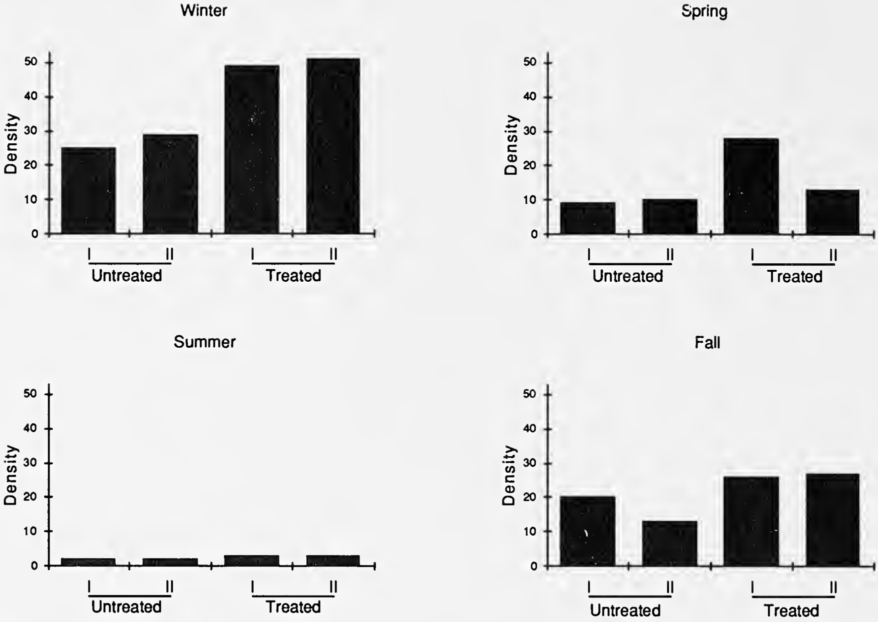

FIGURE 2. Seasonal comparison (winter, spring, summer, and autumn) of densities (N_{min}) of all rodents in the tebuthiuron treated and untreated grids within the sand shinnery oak woodland.

of all rodents were never higher in the untreated areas compared to the treated areas (Fig. 2). The two-way ANOVA for abundances (N_{min}) of *D. ordii* (Table 3) produced similar results, with a significant season by tebuthiuron treatment interaction ($P = 0.018$). Again, the interaction was affected mostly by variation in the degree to which tebuthiuron areas exhibited elevated densities compared to untreated areas. The average density of *D. ordii* on the untreated areas never exceeded that of the treated areas (Fig. 3). Orthogonal *a priori* comparisons (Sokal and Rohlf, 1981) of total rodent numbers within each season indicated significant differences between treated and untreated areas in all seasons except summer; whereas, only winter showed a significant difference in *D. ordii* densities between treated and control areas. The Welsch Step-Up Procedure (Sokal and Rohlf, 1981), although less powerful than either ANOVA or *a priori* comparisons, revealed seasonal differences in rodent density within treated and within control areas in tebuthiuron treated areas. Winter and summer total density indices were each significantly different ($P < 0.05$) from all other seasons; whereas autumn and spring total density indices were statistically indistinguishable ($P > 0.05$). In the control areas, winter total density was significantly different than both spring and summer total density indices, whereas spring, summer, and autumn densities were statistically indistinguishable. In tebuthiuron

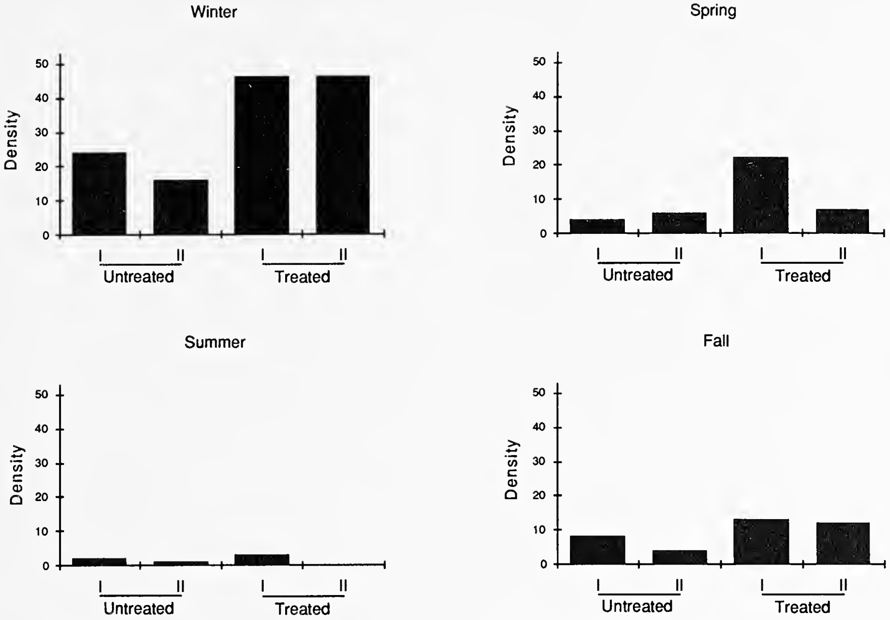

FIGURE 3. Seasonal comparison (winter, spring, summer, and autumn) of densities (N_{min}) of *Dipodomys ordii* in the tebuthiuron treated and untreated grids within the sand shinnery oak woodland.

treated areas, the winter density index for *D. ordii* was statistically different than that for all other seasons; spring, summer, and fall density indices for *D. ordii* were statistically indistinguishable. In untreated areas, density indices of *D. ordii* were statistically indistinguishable.

OVERVIEW

Canopy cover and vertical height are important determinants of rodent species composition and abundance in arid or semiarid environments (Rosenzweig and Winakur, 1969; Price, 1978). In our study also, rodent densities were higher in treated areas, which exhibited greater canopy cover and vertical height, than in control areas in each season. *D. ordii* abundance paralleled seasonal changes in percent bare ground; abundance was highest in the winter, followed by autumn, spring, and summer. This parallels observations that Merriam's kangaroo rat (*D. merriami*), a congener of *D. ordii*, had an affinity for feeding in areas of bare ground (Rosenzweig and Winakur, 1969; Rosenzweig, 1975).

Like other studies involving habitat manipulation (Rosenzweig and Winakur, 1969; Brown et al., 1972; Rosenzweig et al., 1975; Feldhamer, 1979), rodent species composition and density were affected by tebuthiuron-induced changes in sand shinnery oak habitats. Rodent numbers increased in tebuthiuron treated areas. Moreover, seasonal fluctuations in N_{min}, whether indicative of behavioral responses or actual changes in density, were different in treated and untreated areas, as indicated by significant interaction terms in the ANOVA and detailed in *A priori* and *A posteriori* analyses. In part, these results contrast with those of Parmenter and MacMahon (1983), who found that shrub removal had no effect on *Peromyscus maniculatus*, *Perognathus parvus, Onychomys leucogaster,* and *Spermosphilus armatus* in a sagebrush dominated shrub-steppe ecosystem in southwestern Wyoming. In that study, shrubs were removed manually without subsequent replacement by other plants. In our study, the absolute increase in rodent density may be a response to shrub removal, the subsequent dominance of the grass component, or both. As in the work of Parmenter and MacMahon (1983), species composition did not change in our study. Rosenzweig and Winakur (1969) considered the biotic variability of arid environments to provide many opportunities for specialization. The sand shinnery oak ecosystem, as well as the mid-grass prairie that resulted from tebuthiuron application, was dominated by generalist rodents. *D. ordii* has been described as a good generalized competitor (Garner, 1974, Parmenter and MacMahon, 1983); the other species caught in this study are plastic with regard to food and habitat requirements (Davis, 1978).

We hypothesize that the rodent community that presently characterizes sand shinnery oak habitats is a relictual subset of the original mid-grass prairie rodent fauna that was sufficiently generalized to survive the transition. More specialized rodents may not have persisted in the shrub-dominated flora and insufficient time has elapsed to obtain a shrub-adapted suite of species. It is not surprising then, to observe no change in species composition as a result of tebuthiuron-induced reconversion to mid-grass prairie. The effect of the drastic alteration in plant species composition and structure was to differentially modify constituent species abundances, rather than alter species composition.

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FOOD HABITS OF MALE BIRD-VOICED TREEFROGS, *HYLA AVIVOCA* (ANURA: HYLIDAE), IN ARKANSAS

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Abstract.—We analyzed stomach contents of 56 male bird-voiced treefrogs, *Hyla avivoca* Viosca, 1928, collected in late spring and early summer 1991 from sites in central Arkansas. Ants and beetles were the predominant prey items; the next most abundant group was caterpillars. Ants of the genus *Cremastogaster* were the most common food source. Several ground-dwelling arthropods found in the diet of other species of *Hyla* were noticeably absent from the diet of *H. avivoca*. Our data suggest that calling male *H. avivoca* forage largely on tree-dwelling insects when compared to sympatric *Hyla*, and this mode may be a reflection of habitat preference and prey availability rather than prey selection. *Key words*: ants; arthropods; insects; bird-voiced treefrog; *Hyla avivoca*; food habits; diet.

The bird-voiced treefrog, *Hyla avivoca* Viosca, 1928, has a sporadic and poorly-documented distribution in three states (Arkansas, Louisiana, and Oklahoma) from which the species is known west of the Mississippi River (Smith, 1966; Dundee and Rossman, 1989; Conant and Collins, 1991). Recent investigations by Trauth and Robinette (1990a, 1990b) into the distribution and life history of Arkansas populations have revealed this frog to be more common in the state than previously understood. The species generally inhabits large rivers, headwater swamps, and swampy floodplains and lakes in Arkansas. Although much has been documented about the natural history and ecology of other *Hyla* species, little ecological data are available for bird-voiced treefrogs, and nothing, to our knowledge, is known about the diet of *H. avivoca*.

The diet of gray treefrogs, *Hyla versicolor* LeConte, 1825, and *H. chrysocelis* Cope, 1880 (considered by some to be the closest living relatives of *H. avivoca*), was investigated in Texas by Ralin (1968). He reported that both species fed extensively on click beetles (Coleoptera: Elateridae) and harvester ants (*Pogonomyrmex*). He also concluded that both species fed not only while perched on the bark and foliage of trees, but also, to some extent, on the ground. Interestingly, harvester ants are not known to occur in trees; rather, they are especially common in cultivated fields and bare sandy areas near roads. In addition, other insect orders found in stomachs included grasshoppers (Orthoptera—only in *H. versicolor*), flies (Diptera), and caterpillar larvae (Lepidoptera). Brown (1974) studied the food habits of several anurans from southeastern Arkansas. He found that green treefrogs, *H. cinerea* (Schneider, 1792), primarily fed on insects found on the leaves of plants and included leafhoppers (Homoptera:

Cicadellidae), acridid grasshoppers, caterpillars, leaf beetles (Chrysomelidae), and spiders (Arachnida). *Hyla cinerea* consumed mosquitoes (Diptera: Culicidae) and houseflies (Muscidae) in laboratory experiments (Freed, 1980). Freed also reported that prey selection was dependent upon prey species activity rather than size of prey. In a field study, Freed (1982) reported that *H. cinerea* consumed mostly noctuid caterpillars, cantharid beetle larva, and, to a lesser extent, field crickets (Orthoptera: Gryllidae) and stink bugs (Hemiptera: Pentatomidae).

The purposes of our study are to describe feeding patterns for calling male *H. avivoca* from central Arkansas and compare our results with what is known of diet in other arboreal treefrogs.

MATERIALS AND METHODS

Fifty-six adult and juvenile male *H. avivoca* were collected from six localities in four counties (Conway, Faulkner, Grant, and Monroe) of central Arkansas from late May through mid-July, 1991. All frogs were taken from breeding colonies at dusk or after dark as they called several meters above water from trees (primarily cypress-tupelo gums) and buttonbush shrubs (*Cephalanthus*). Specimens were placed in plastic bags on ice following capture and processed within 24 hours in the laboratory at Arkansas State University (ASU). Frogs were killed in a dilute chloretone solution and fixed in 10 percent formalin for 48 hours prior to examination. Stomachs were removed and stored in individual vials containing 70 percent ethanol. Food items were removed, counted, and identified using a binocular dissecting microscope and dichotomous keys provided in Creighton (1950), Cook (1953), and Borrer et al. (1989). A food item consisted of a whole specimen or parts representing a whole specimen. Whenever possible, insect taxa were identified to family. Prey availability was not assessed quantitatively; however, some qualitative assessment was made by collecting and observing arthropods in each study area. Voucher specimens of *H. avivoca* are deposited in the ASU Herpetological Museum (nos. 17766; 17770-77; 17787-88; 17799-17834; 17860-67).

RESULTS AND DISCUSSION

Of the 56 stomachs examined, 51 (91 percent) contained food items. There was an average of 3.9 food items per stomach (range one to 14). The total number and percent occurrence of food items are given in Table 1. Ants (Hymenoptera: Formicidae) and beetles (Coleoptera) were the predominant prey items; the next most abundant group was lepidopteran larvae. Of the 75 identifiable ants, 72 (96 percent) were *Cremastogaster* workers ranging from 2.5 to 4.0 mm in length. According to Cook (1953), these ants often nest under the bark of trees and can be recognized by the unique way they climb trees in straggling files. Ant collections made at one locality revealed that *Cremastogaster* workers were common on the bark and foliage of trees in a cypress-tupelo swamp. As many as 14 *Cremastogaster* were found in a single stomach and several stomachs contained only *Cremastogaster*. Although ant trails were observed on the surfaces of several overhanging tree limbs, it was not determined whether these ants were being consumed as they crawled near the frogs or whether the frogs actively pursued them. Duellman and Trueb (1986) suggested

TABLE 1. Percent occurrence and total number of food items from stomachs of male *Hyla avivoca* from Arkansas.

Taxa	Percent occurrence in stomachs ($N = 51$)	Total number of food items
Arachnida		
Acarina	5.4	8
Araneae	1.8	1
Insecta		
Unidentifiable	7.1	4
Coleoptera		
Cantharidae	1.8	1
Carabidae	1.8	1
Coccinellidae	9.0	5
Cucujidae	5.4	3
Elateridae	5.4	3
Unidentifiable	9.0	5
Hemiptera		
Reduviidae	1.8	1
Homoptera		
Cicadellidae	1.8	1
Hymenoptera		
Formicidae		
Cremastogaster	39.3	72
Camponotus	5.4	3
Unidentifiable	28.6	36
Lepidoptera		
Geometridae (larvae)	3.6	2
Unidentifiable (larvae)	9.0	5
Unidentifiable (adult)	1.8	1
Odonata		
Zygoptera		
Unidentifiable	1.8	1
Psocoptera	3.6	4

that some ant specialists, particularly several microhylid species, locate ant trails by olfaction. The frogs may then "sit and wait" to capture ants as they pass by. Although the method of ant capture by *H. avivoca* remains unclear, the large number of ants in several stomachs suggest that *H. avivoca* may sit motionless near ant trails and consume individuals of *Cremastogaster* as they parade by in their characteristic straggling files. However, frogs might locate and raid ant nests under the bark of trees. Our data do not distinguish between these alternatives.

Coccinellids were the most frequently encountered beetles followed by cucujids and elaterids. Coccinellids (ladybird beetles) are predaceous and are abundant on aphid-infested vegetation whereas cucujids (flat bark beetles) occur on and under the bark of trees where they feed on mites and other small insects (Borrer et al., 1989). Ralin (1963) stated that elaterids (click beetles) are generally arboreal and concluded that *H. chrysoscelis* was a more arboreal feeder than *H. versicolor* based on a higher percent occurrence of elaterids in the diet of *H. chrysoscelis*.

Unfortunately, because lepidopteran larvae are soft-bodied and digested quickly, few in our sample were identifiable to family. Lepidopteran larvae were encountered in 11 percent of the stomachs of *H. avivoca* compared to 15 percent reported by Freed (1982) for *H. cinerea* and 21 percent and 14 percent for *H. chrysoscelis* and *H. versicolor*, respectively (Ralin, 1968).

The presence of barklice (Psocoptera) and flat bark beetles indicate that *H. avivoca* spends some time feeding on insects that occur in the tree-bark crevice microhabitat. Unlike *H. avivoca*, these insects were not consumed by *H. cinerea, H. chrysoscelis,* or *H. versicolor* (Brown, 1974; Freed, 1982).

There was a conspicuous absence of ground-dwelling arthropods in the diet of *H. avivoca* when compared to other *Hyla* species. Moreover, data from Table 1 suggest that during the study period, *H. avivoca* rarely, if ever, fed on the ground. This feeding mode may be a reflection of habitat preference rather then prey selection. Unlike *H. chrysoscelis, H. cinerea*, and *H. versicolor* (all of which are found in a myriad of habitats), *H. avivoca* seems to be restricted to old-growth, cypress-tupelo swamps or similar aquatic habitats in Arkansas. Because of the permanent-water situation associated with these environments, *H. avivoca* would have to leave the site (or, at least, the inundated areas) in order to encounter ground-dwelling insects. Thus, calling males appear to have a foraging tactic that precludes movement away from breeding perches or sites. During the breeding season, calling males appear to specialize on arboreal insects in central Arkansas. However, the diet of calling male frogs may not be typical of the population in general that does not approach a maintenance diet. Thus, additional study utilizing female *H. avivoca* and males collected outside the breeding season is certainly warranted.

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AMERICAN ALLIGATOR (*ALLIGATOR MISSISSIPPIENSIS*) NESTING AT AN INLAND TEXAS SITE

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Abstract.—Fifteen alligator nests were examined at Brazos Bend State Park, Fort Bend Co., Texas, in 1990. One nest fell victim to a predator, apparently a raccoon. Of 13 nests monitored during incubation, adult alligators were observed in close proximity of 12, and two nests were actively defended by adults. Islands were more commonly used nesting sites (11) than banks (four); only those water bodies without islands contained bank nests. One nest was opened prior to hatching by an adult after approximately 75 days of incubation, and intact eggs removed from the nest hatched four to 12 days later. *Key words*: *Alligator mississippiensis;* American alligator; nests; nesting ecology; Texas.

One of the earliest accounts of alligator nests and eggs was by Reese (1907). He discussed time of nesting, nest materials, location, size of nest, numbers and dimensions of eggs, and vocalization of the young before hatching. McIlhenny (1935) collected similar information in greater depth, had observations on nest defense by the adult, and took nest temperatures. The first quantitative study was by Joanen (1969), who examined 315 nests from 1964 to 1968 in a Louisiana coastal marsh, and is the most comprehensive to date. Other studies were conducted in Georgia (Metzen, 1977; Ruckel and Steele, 1984), South Carolina (Bara, 1972), and Florida (Hines et al., 1968; Fogarty, 1974; Goodwin and Marion, 1978; Deitz and Heinz, 1980). Additionally, there are a substantial number of publications dealing with certain aspects of nesting biology.

In Texas, there have been aerial nests counts conducted by the Texas Parks and Wildlife Department (TPWD) since the 1970s for use as a census tool (Potter, 1975, 1981; Thompson et al., 1984; Johnson et al., 1989). There are limited data for coastal habitat on nesting materials, clutch size, and fertility rates (Johnson et al., 1989; TPWD unpublished data). However, inland sites with heavy tree cover cannot be adequately censused by air, and there is a paucity of information on alligator nesting in this type of habitat in Texas.

In this study, nests were examined in 1990 at Brazos Bend State Park. Prior to the opening of the park in 1984, Onadeko (1983) collected limited data on four nests at Brazos Bend. From 1986 to 1989, dates of nest completion and hatching were noted due to concern for park visitors coming in contact with an adult guarding a nest or hatchlings. Known nest locations were mapped, but no diligent effort was made to find nests located on islands not easily visible from shore. The focus of this research was to study aspects of nesting ecology at the park (such as location and composition of nests, time of nesting and incubation period, and adults associated with nests) and correlate it with previous studies from other states. Possible changes and adaptations in nesting due to human contact are discussed.

MATERIALS AND METHODS

Brazos Bend State Park is located in Fort Bend County, Texas, less than 32 kilometers southwest of the Houston city limits, and consists of 1982 hectares of Brazos River floodplain and upland coastal prairie. The park is on the Texas Gulf Coastal Plain and is included in the Coastal Prairie Vegetational Region (Singleton et al., 1978). Major water bodies in the park are a freshwater marsh (Pilant Lake), three lakes (Elm, Forty Acre, Creekfield), four oxbows (Old Horseshoe, New Horseshoe, Hale, Creekwood), and a slough (Pilant Slough). Tall grass prairie uplands form seasonal wetlands as a result of water-filled depressions and swales. The Brazos River forms the eastern park boundary, and Big Creek and various bayous transect the park. A series of foot trails intersperse the marsh, lakes, and two oxbows, and border at least a portion of their perimeters, sometimes in the form of levees between adjacent impoundments.

Mixed hardwoods, including water oak (*Quercus nigra*), pecan (*Carya illinoiensis*), elm *(Ulmus* sp.) Shumard oak *(Q. shumardii)*, burr oak *(Q. macrocarpa)*, and various shrubs and vines are associated with the Brazos River bottomland and parts of Big Creek. Gallery forests along the waterways consist of sycamore *(Platanus occidentalis)*, eastern cottonwood *(Populus deltoides)*, and black willow *(Salix nigra)*. Live oak *(Q. virginiana)*, along with vines and Spanish moss *(Tillandsia usneoides)*, characterizes the meander escarpment of the Brazos River.

We estimated the park's alligator population to be between 1000 and 1500 animals as calculated through censuses, and the nest multiplying factors of Taylor and Neal (1984).

Nests were located by walking the perimeters of the major bodies of water that contained the majority of the alligator popultion, and consecutive numbers were assigned in the order of discovery. Binoculars were used to find and observe nests on islands, and a visit was made at least once to each island by boat (nonmotorized) when possible for closer examination of known nests and to find additional nests not visble from the shore. Nesting materials, condition, and appearance of the nests, as well as the presence, size, and behavior of adults associated with the nests were noted. Nests accessible on foot were visited one or more times per week; a 35-mm camera and two VCR camcorders were used to document visual data.

RESULTS

Location of Nests

Fifteen nests were discovered at Brazos Bend State Park in 1990. A summary of pertinent information for each nest is listed in Table 1. Nest location is shown in Figure 1. All nests were shaded by at least partial tree cover. Eleven nests (73 percent) were on islands and four nests (27 percent) were bank nests. Bank nests were accessible by foot and were found only on the lakes without islands—Creekfield, which has a long, narrow shape, and New Horseshoe and Creekwood, both oxbows. Islands were rectangular-shaped spoilbanks of varying length and width, except for some islands at Pilant Lake, which were circular mounds built for alligator basking. Some of the islands in the center of Elm Lake (location

TABLE 1. Summary of nest information for 1990 at Brazos Bend State Park.

Nest	Location	Island/bank	Nest composition	Size class of adult at nest	Fecal meterial on nest
1	Forty Acre	island	dirt with vines and blackberry	1.8 - 2.1 m	yes
2	Forty Acre	island	dirt with vines and blackberry	2.4 - 2.7 m	yes
3	Forty Acre	island	dirt with vines and willow	1.8 - 2.1 m	no
4	Creekfield	bank	dirt with sticks and blackberry	1.8 - 2.1 m	no
5	Elm	island	dirt with some vegetation	1.8 - 2.1 m	yes
6	N. Horseshoe	bank	Johnson and paspalum grass	1.8 - 2.1 m	no
7	N. Horseshoe	bank	Johnson and paspalum grass	2.1 - 2.4 m	no
8	Pilant	island	dirt with some vegetation	2.4 - 2.7 m	unknown
9	Pilant	island	dirt with sticks	2.7 - 3.0 m	unknown
10	Pilant	island	dirt with sticks	2.4 - 2.7 m	unknown
11	Forty Acre	island	dirt with some vegetation	not applicable	unknown
12	Elm	island	egret guano/dirt	unknown	no
13	Elm	island	dirt with some vegetation	unknown	yes
14	Elm	island	unknown grass	no adult	no
15	Creekwood	bank	dirt with sticks	not applicable	unknown

of nests 12, 13, 14) were utilized as an egret rookery, and areas heavily used by the egrets had a spongy substrate due to decomposed guano. There were no signs of alligators (trails, footprints, or nests) on islands or parts thereof where dense vegetation existed; extremely overgrown areas also lacked egrets. One island had steep banks, and was not selected for use by alligators. Islands with more favorable conditions consistently had evidence of utilization by alligators in some form.

Nest Composition and Appearance

The nests were composed either of dirt with little or no vegetation, or grass with a paucity of dirt. All nests were directly associated with the amount and type of vegetation in the immediate area. The vegetation encountered in dirt nests was Louisiana blackberry (*Rubus louisianus*), black willow (*S. nigra*), assorted vines, and sticks. The grass nests were composed of paspalum (*Paspalum floridanum*) and Johnsongrass (*Sorghum halepense*). One unusual dirt nest (no. 12) consisted largely of decomposed egret guano. It was compact, 137 centimeters in diameter by 45 centimeters

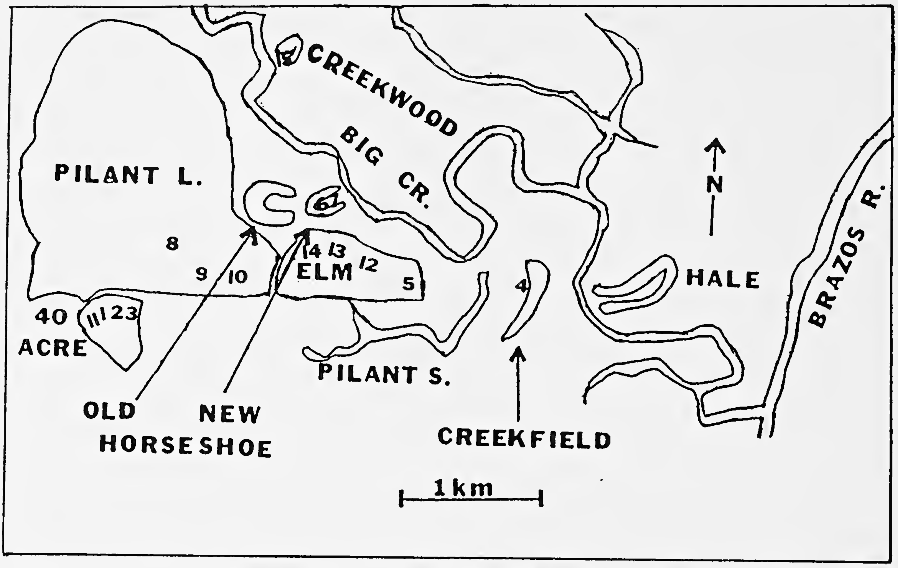

Figure 1. Location of alligator nests built in 1990 at Brazos State Park, Fort Bend Co., Texas. Nests were numbered in order of discovery.

high, and it was opened to confirm that it did contain eggs. Of the 15 nests, 12 were dirt (80 percent) and three were grass (20 percent). Four of the 12 nests intact at the time of discovery (33 percent) had white fecal material on top of the nest. Nests, 4, 6, and 12 were opened to check for eggs and stage of development, and nest 4 was found to contain fire ants. Nests on islands were not excluded from the possiblility of invasion by fire ants, because these ants were encountered even on islands located in the center of lakes.

Nest Predation

Predation, probably by a raccoon, destroyed one nest. It was located on the end of an island, approximately six meters from the shoreline. Low water levels coupled with its proximity to shore presumably enhanced its susceptibility to predation.

Time of Nesting and Incubation

One of the authors (DJ) has monitored time of nesting and incubation periods since 1987. He noted that nesting usually occurs from late June to early July at Brazos Bend, with the earliest nest from the period 1987 to 1989 being discovered on 17 June 1987, shortly after egg deposition. In 1990, a nest was discovered on 26 May and two additional nests were found about 1 June. Joanen and McNease (1979, 1989) found a direct correlation between the March - April - May ambient temperatures and time of nesting. When nesting took place early, they noted that temperatures

TABLE 2. Mean monthly temperatures for 1990 compared to 1987-1989 and the 30- year average for Brazos Bend State Park.

	Temperatures (°C)				
Month	1990	1989	1988	1987	30- year average
March	17.2	16.3	16.3	14.9	16.1
April	20.8	20.8	19.8	19.6	20.4
May	25.6	25.4	23.1	25.1	23.8
June	29.3	26.6	26.9	27.4	27.0
July	27.8	28.0	29.1	28.8	28.4
August	29.5	27.6	29.6	30.1	28.1

for those months were correspondingly higher. In a comparison of 1990 mean monthly temperatures for those months with the 30-year average (Houston Area National Weather Service data), it was found that temperatures were higher for each of the three months in 1990 (Table 2). It should also be noted tht the previous winter temperatures were colder than usual, 23 December 1989 was the coldest day with a low of -13.9°C. The usual low based on the 30 year average was 5.6°C (Houston Area National Weather Service data). When comparing temperatures for March to May for the years 1987, 1988, and 1989 to the 30-year average, the year 1989 exhibits temperatures above the 30-year average for all three months. A possible explanation for the lack of early nesting for that year was that drought conditions existed from 1988 until spring 1989, and nesting activity was depressed. Joanen and McNease (1989) also reported an association between water levels and the degree of nesting, with drought resulting in greatly decreased nesting.

Observed incubation periods for 1990 were longer (more than 70 days) than for those known from 1987 to 1989 at the site for at least the three nests for which approximate incubation starting dates were recorded. The incubation period normally extends from late June through early September. Nest 4 was completed and contained eggs by at least 26 May. When the nest was opened on 2 July (~37 days) the opaque banding had only covered one half of the total egg length. According to the staging table for alligator embryos via banding by Ferguson (1985), this corresponded to 20 days. On 9 August, after at least 75 days of incubation, the female opened the nest before most, perhaps all, of the young were ready to hatch. The young appeared fully developed in regards to external morphology, but were unable to hold themselves up and possessed a substantial amount of yolk within the yolk sac. Of the 31 intact eggs removed from the nest, one egg was rotten, one egg was infertile or early dead, one hatched on 13 August (~79 days), another hatched on 14 August (~80 days) and the hatchlings died soon afterwards, and the rest of the eggs hatched from 17 to 21 August (~83 to 87 days) with viable young. The hatchlings were released at Creekfield

Lake within a few meters of their mother, and as of late May 1991 at least 15 were still with her.

Nests 6 and 7 were discovered about 1 June with eggs. On 2 July (~30 days) an egg was removed from nest 6 and opaque banding covered one third of the total egg length. This degree of banding was comparable to 12 days for the staging table by Ferguson (1985). On 16 August (~75 days) young were heard vocalizing at both nests. Eggs in nest 6 hatched successfully on 17 August (~76 days) and those in nest 7 on 19 August (~78 days).

Nests 1, 2, 3, and 5 hatched out sometime between 19 and 31 August as numerous hatchlings were observed at the water's edge near each nest site. The Creekwood nest (no. 15) was discovered at the end of August because of the presence of hatchlings. Nests at Pilant Lake and the central islands of Elm Lake were too remote for hatching time or hatching success to be determined easily.

Adults Associated With Nests

Of the 13 intact nests, an adult was sighted at 12 (92 percent) or immediately adjacent to the nest at least once. This exception was nest 14, which was visited only once. Adults sighted near two nests splashed and quickly submerged in the water so their size could not be determined. The total length of adults associated with the other 10 nests were 1.8 - 2.1 meters (50 percent), 2.1 - 2.4 meters (10 percent), 2.4 - 2.7 meters (30 pecent), and 2.7 - 3.0 meters (10 percent).

The nests that could be monitored closely were nos. 4, 6, and 7 as they were accessible on foot. Nest 4 at Creekfield Lake, which was prematurely opened, was located adjacent to the adult's small circular pond. As the water in this shallow 3.2-hectare lake receded, the pond dried up and the adult moved to the less than 1.0 hectare of remaining water located in the central part of the lake in late July. The only other alligators seen in the lake were four subadults. The adult was seen at the lake, but not at the nest, on each visit. Throughout the incubation there was evidence that an adult visited the nest consistently during the night or early morning hours. The nest appeared to be "tidied" regularly. On 2 July (~37 days incubation), there was the imprint of a tail dragged over the nest, and large sticks had been placed on top of the nest on 6 July (~41 days incubation). Beginning on 5 August (~71 days incubation), a small indentation (approximately 20 centimeters in diameter) was noted on the east side of the nest, facing the water and alligator trail. It looked as though an alligator had rubbed the area smooth with its snout. On 6 August, the indentation increased to about 50 centimeters in diameter. On 7 August, it had been enlarged in length to 60 centimeters and was shaped like the snout of an alligator.

This nest was checked periodically on 7 and 8 August for changes or for vocalizations by young; as of the last visit to the nest, just after dusk on 8 August, neither had occurred. On 9 August at 0830, the nest was found open on the east side. There were intact eggs visible in the nest cavity and a few outside along the nest mouth. Three cracked eggs, four dead embryos, and five eggshells were strewn outside the nest. Fire ants were swarming in the vicinity of the nest, especially on the dead alligators and partially opened eggs. Inasmuch as there were four dead alligators but five eggshells (all with evidence of containing well-developed embryos), at least one alligator was unaccounted for. On the same morning as the nest opening, the adult that had been observed throughout the study was located in Creekfield Lake and was joined by a second adult perhaps as long as 3.0 meters. Both alligators had just their heads above the water, were swimming back and forth quickly, and appeared alert and wary.

Nest 6 and 7 were adjacent to each other but separated both visually and physically by thick bushes. They were located at the 3.5-hectare New Horseshoe Lake, which was characterized by steep sides and deep water except in the vicinity of the nests. An adult was present at nest 6 on three of nine visits, and at nest 7 on one of nine visits. The adult at nest 6 came up from the water side of the nest by way of a well worn path, stood beside the nest with its body inflated and mouth gaping, then lunged toward the human intruders, performing a high walk for a short interval. This basic sequence was repeated for each visit to the nest when the alligator was present. For the first two encounters, those present backed away from the nest a substantial distance (at least 15 meters). After the lunge portion of the third encounter, one investigator backed up approximately 1.5 meters, then remained stationary. The alligator stopped moving but maintained an inflated posture and was still in this stance at the time all present left the nest site five minutes later.

The single encounter with the adult at nest 7 resulted in a similar behavioral sequence as displayed by the adult at nest 6, even to stopping forward movement when confronted with a human that did not retreat from the nest site. The only difference in behavior noted between the adults at the two nests was that the alligator at nest 7 did not gape and lunge immediately upon reaching the nest. The animal maintained a defensive posture at the nest until one of us moved to the side to view the animal, which immediately resulted in a lunge. The adults also responded if humans were standing at the outside of the oxbow arm directly across the water from both nests. Two adult alligators were sighted in the water near the center and went to the nests immediately after becoming aware of the presence of humans.

On 7 August (~67 days incubation), nest 7 had an indentation similar to that described for nest 4. On 16 August, chirping of the young was clearly heard from both nests 6 and 7. No adult was sighted in the vicinity of either nest. On 17 August, nest 6 had hatched out, but nest 7 still was intact with the young vocalizing and no adult was visible. The same was true on 18 August. The young were liberated from the nest by an adult on 19 August. Because adults had aggressively defended the nests previously, this suggests that they were not in the vicinty when the young were vocalizing until the time that they opened the nests. Both adults had previously been sighted sufficient distances from the nests that they would have been unaware of human intrusion to their nests from visual or auditory cues.

Discussion

The choice of islands over banks as nesting sites may possibly function in increasing nest security from predation and human disturbance. An island may serve as a deterrent to, but not total protection from, predation as evidenced by the island nest that was destroyed during this study. The remoteness (distance) of an island from shore and water levels probably determine how safe it is from predators. Because public use of boats is prohibited within the park, islands do effectively deter human contact with nests.

In this study the majority of nests (92 percent) had adults associated with them, but only two of 13 (15.4 percent) nests were actively defended by an alligator. Kushlan and Kushlan (1980) found that about 43 percent of the nests they surveyed had an adult nearby, Goodwin and Marion (1978) observed an alligator at 21.4 percent of nests they studied and Metzen (1977) noted that females were usually in the vicinity of their nests. Joanen (1969), Metzen (1977), Goodwin and Marion (1978), Deitz and Hines (1980), Kushlan and Kushlan (1980), and Ruckel and Steele (1984) found none to 15 percent that defended or closely attended their nests. The literature is not always clear or consistent in terminology used in recording association of alligators with nests. Moreover, data bias (even within a study) due to such factors as unequal number of visits to nests, the use of airboats or marsh buggies (Deitz and Hines, 1980), and different habitat types, make it difficult to quantify and compare information.

Our data suggest that water levels, habitat, and size of the territory of the attending adult may influence movements of the adult and its proximity to the nest. The nest at Creekfield Lake had the total water-filled area greatly reduced in diameter and depth during the nesting season, restricting the adult to a small central pond where it could easily be seen and in turn it could easily monitor the nest. In contrast, adults at New Horseshoe Lake inhabited a deeper body of water that was not subject to decreased area on a seasonal basis, and they were seen at distances more than five times as great from the nest as in comparison to the adult at Creekfield (their home ranges could have been considerably larger).

The adults that displayed aggressive behavior at nests 6 and 7 were located at a lake that is popular for bank fishing, and thus they were habituated to people. Some alligators at this lake are known to take fish off baited hooks and stringers. Deitz and Hines (1980) found evidence suggesting that alligators that become habituated to humans, but are not harassed, tend to remain with the nest and even defend it. They had five of 11 nests (45.4 percent) attended; our rate was even greater with 12 of 13 nests (92.3 percent) attended. Elsey et al. (1990) reported that approximately 80 percent of their captive penned alligators defended nests. In an examination of four nests at Brazos Bend prior to opening of the park, Onadeko (1983) did not observe adults in the vicintiy of them. This supports the contention that active nest defense at New Horseshoe Lake was due to frequent human contact and may even indicate that the number of adults seen in the vicinity of nests at the park is higher than it would be otherwise. The adult at nest 6 displayed the same aggressive behavioral sequence each time it was present during our visits, which is in agreement with Kushlan and Kushlan (1980) that an adult behaves consistently in its response to the nest being approached.

When comparing the usual peak nesting periods recorded by Joanen (1969), Bara (1972), Metzen (1977), and Goodwin and Marion (1978), they fall collectively into the time span of mid-June through the first week of July. Although the bulk of nesting at Brazos Bend has a slightly later time frame in comparison (late June through the second week of July for the discovery of completed nests), the early nesting dates recorded in 1990 would be considered early also for the sites those researchers studied.

That an incubation of more than 70 days is not normal for most nests is supported by McIlhenny (1935), Joanen (1969), and Goodwin and Marion (1978), who found incubation periods varying between 59 and 65 days. Two possible explanations of the observed extended incubation relate to monthly air temperatures during the incubation period (Table 2). The July 1990 mean temperature was lower than that of the 30- year average and 1987 to 1989 mean temperatures for July. Also, because nesting was one month early, air temperatures during the first month of incubation were lower than if eggs had been laid in June or July.

When opening nest 4 on 2 July, this dirt nest did not seem moist relative to other nests that had been opened previously. McIlhenny (1935) monitored a "fairly dry" dirt nest in which it took more than 100 days for the embryos to reach full term, and attributed the lengthy development to the lack of green nest material. Chabreck (1973) noted a lower temperature in nests made of soil or partially decomposed vegetation. Nests 6 and 7 were both grass nests so the latter explanation would not be relevant to them. Joanen (1969) did find that eggs in some nests that were frequently opened during research activities took 75 to 80 days to hatch. Nests 4 and 6 each were opened a single time for approximately one minute and only a small portion of the nest cavity was exposed, so this would be expected to have had little effect on the incubation period.

Regarding the extra eggshell found at the Creekfield nest, we believe it to have contained a young alligator. The youngster may have been taken to the water by the adult, or if dead, eaten. A possible explanation for the early nest opening is that because the incubation period was at least 75 days, the adult opened the nest even though vocalizations of the young were not heard. Based on his experience, Joanen (personal communication) felt that the adult heard at least one youngster vocalizing and took whatever young were ready to hatch to the water, abandoning the rest. The large alligator first sighted at the nest immediately after the nest opening may have been the male parent. It is possible that he came to the lake to open or assist in opening the nest and that both adults were protecting at least one hatchling.

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INDIVIDUAL AND SECONDARY SEXUAL VARIATION IN THE MEXICAN GROUND SQUIRREL, *SPERMOPHILUS MEXICANUS*

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ABSTRACT.—One hundred fifty-three adult specimens (73 males and 80 females) of the Mexican ground squirrel, *Spermophilus mexicanus*, from the eastern part of the Edwards Plateau in Texas were analyzed to ascertain differences in size related to age and sex. Variation in cranial dimensions was found to be dependent on age, and was highly affected by sex. *Key words*: morphometrics; secondary sexual and age variation; ground squirrel; *Spermophilus mexicanus*; Texas.

Where it occurs, the Mexican ground squirrel, *Spermophilus mexicanus* (subgenus *Ictidomys*), frequently is a common and widespread species. It ranges from central Texas and southeastern New Mexico southward to central México (Hall, 1981). In a part of its distribution in Texas and adjacent New Mexico, it barely overlaps the range of the closely related *Spermophilus tridecemlineatus*, and hybrids between the two have been reported (Cothran, 1983). Nonetheless, hybrid sites are rare and genetic exchange between the two taxa is limited and locally restricted, no doubt the result of secondary contact of populations once geographically isolated.

This ground-dwelling sciurid is abundant in many places, especially in parks and cemeteries, on golf courses, along highway rights-of-way, and the like. Nonetheless, few assessments of morphologic variation in the species have been reported since Howell's (1938) review of the ground squirrels. Cothran's (1983) important study involved primarily variation between two different species of *Spermophilus*, and no other large series of *S. mexicanus* have been studied (Young and Jones, 1982). Our work was focused on nongeographic variation and secondary sexual dimorphism at the population level.

Using the Texas Tech University Center at Junction as a focal point, students in various courses and others have collected, over the years, a number of Mexican ground squirrels in Kimble and surrounding counties on the eastern edge of the Edwards Plateau, near the eastern terminus of the range of the species. Of the two recognized subspecies, the northern race, *S. m. parvidens*, occurs in that region.

MATERIALS AND METHODS

From the collections of The Museum at Texas Tech University, we were able to accumulate 158 specimens, 76 males and 82 females, mostly conventional museum skins accompanied by skulls, but including a few complete skeletons, all collected in the months of April and May in the years 1973 to 1991. Almost half were obtained by students in classes in mammalogy supervised by Jones and Manning in the last three years of that period. April and May were chosen because females are not often visibly pregnant by the end of that time frame, and because all animals in the population are adults (born at least in the previous year). The sample contained material from the following counties: Gillespie (four specimens); Kerr (three); Kimble (117); Mason (27); McCulloch (two); Menard (one); Sutton (four).

For external measurements, we did not apply standard statistical tests simply because it was evident that many of the measurements had been taken in different ways by inexperienced collectors. For example, measurements of length of ear ranged from four to 16 mm. We selected 19 specimens of each sex for which we felt measurements were reasonably accurate, and those data are presented to help establish parameters for external size of *S. m. parvidens.*

Cranial measurements were taken by the same person (Yancey) using a pair of Fowler digital calipers calibrated to 0.01 millimeter. Most cranial measurements were recorded for most specimens (143 of 158 for mastoid breadth being the fewest). All morphometric characters were conventional and thus no description of them is needed in most cases. They were greatest length of skull (GLS), condylobasal length (CBL), zygomatic breadth (ZB), least postorbital constriction (POC), least interorbital constriction (IOC), mastoid breadth (MB), greatest alveolar breadth across upper molars (ABTR); alveolar length of maxillary toothrow (MAXTR), depth of skull (DS)—taken with skull on microscope slide to topmost point of cranium, then subtracting depth of the slide, and alveolar length of mandibular toothrow (MANTR). Univariate and multivariate statistical tests were performed using SPSSX statistical packages on a VAX 860, and were made available through Academic Computing Services at Texas Tech University.

RESULTS AND DISCUSSION

We initially attempted to assign our spring-taken specimens to discrete age groups based primarily on wear on the upper cheekteeth. It seemed reasonable that, because *S. mexicanus* hibernates, animals taken shortly after termination of hibernation might evidence wear patterns that would allow assignment of them to a specific age group (yearling, two years old, and so on) at least through the first few years of life.

Our expectations were only partly fulfilled. Based on wear patterns involving the protocone and metacone on the M1 and M2, but taking into account also wear on P3, P4, and M3, we finally established three categories: 1) young adults (yearlings)—slight to moderate wear on labial cones of M1 and M2 but cones well formed and discrete, and P3 and M3 showing little wear; 2) adults—labial cones still evident but with heavy wear, P4 and M3 worn and P3 showing some wear; 3) old adults—labial cones almost completely worn away in terms of recognition, all cheekteeth flattened or nearly so with wear. We likened these three groups to first year animals, those two years old, and squirrels older than two years, but this is only an educated guess on our part. The young adult category totaled 123 of 158 specimens, adults 30, and old adults five. Old adults were excluded from statistical analysis because of the small sample size.

Cranial measurements were analyzed using multivariate analysis of variance (MANOVA). There was a significant difference between specimens in age groups 1 and 2 ($P = 0.012$) and between the sexes ($P < 0.001$), but there was no interaction between age and sex ($P = 0.481$).

Univariate analysis of variance (ONEWAY) was used to test each dependent variable by age group and sex. Males of age group 2 were significantly larger than those of age group 1 in three cranial dimensions, ZB, IOC, and MB. Females of age group 2 were significantly larger than females of age group 1 in only two cranial dimensions (ZB and DS).

Males of age group 1 were significantly larger than females of the same group in all cranial dimensions except POC and MAXTR. Males of age group 2 were significantly larger than females of that age group in all cranial dimensions except POC, MAXTR, and MANTR (Table 1).

Discriminant function analysis (DISCRIMINANT) was employed to ascertain whether cases entered as "unknowns" could be correctly classified as to age group. Significant differences were detected between age groups of males ($P = 0.0011$) and females ($P = 0.0061$). This test correctly classified 76.47 percent of the males and 67.50 percent of the females as to age. Therefore, age should be taken into account in any analysis of geographic variation in *S. mexicanus.*

Principle component analysis (FACTOR) was used to determine which variables explain the greatest amount of total variation in the sample. CBL, ZB, and POC explain 66.0 percent (males) and 73.1 percent (females) of the variation in age group 1 (Table 2), and 80.2 and 70.6 percent, respectively, in age group 2.

Using discriminant function analysis with sex as the main criterion, individuals of age group 1 were correctly classified 82.02 percent of the time, and those of age group 2 correctly classified 82.76 percent of the time. Thus, size is not independent of sex, and the sexes should be treated separately in any future taxonomic considerations of *S. mexicanus.*

As previously noted, we did not include external measurements with any statistical package because of the broad variation in those taken by different collectors. However, in order to provide descriptive data on these dimensions, we selected 19 specimens of each sex, all of which had complete external measurements, from among those collected in 1989, 1990, and 1991. For all measurements, the sample mean of males was noticeably larger than that of females, except for weight (in which the sexes were essentially the same). Excepting weight in females, our measurements accord fairly well with those given for fewer animals of each sex by Edwards (1946). Average external dimensions (mm) and weights (grams) of males, followed by those of nonpregnant females (minima and maxima in parentheses) are as follows: total length, 327.4 (311-362), 313.9 (292-333); length of tail, 125.3 (110-147), 120.9 (103-134);

TABLE 1. Variation in cranial dimensions (mm) of males and females of age groups one and two in *Spermophilus mexicanus*.

Sex	Age	N	Mean ± 1 SD	Minimum-maximum	Coefficient of variation
Greatest length of skull					
M	1	58	46.69 ± 0.95	44.60 — 48.53	2.02
	2	11	47.20 ± 1.45	43.66 — 49.08	3.07
F	1	58	44.90 ± 1.07	42.38 — 47.47	2.24
	2	18	45.20 ± 0.98	43.45 — 46.95	2.17
Condylobasal length					
M	1	60	42.94 ± 0.97	40.84 — 44.77	2.25
	2	12	43.52 ± 1.62	39.47 — 45.87	3.73
F	1	62	41.22 ± 1.22	37.38 — 43.83	2.96
	2	18	41.59 ± 1.01	39.62 — 43.38	2.43
Zygomatic breadth					
M	1	59	27.94 ± 0.68	26.56 — 29.50	2.43
	2	12	28.77 ± 0.88	26.35 — 29.68	3.07
F	1	62	26.91 ± 0.85	24.78 — 28.89	3.15
	2	18	27.63 ± 0.83	26.43 — 30.00	2.99
Postorbital constriction					
M	1	61	13.15 ± 0.55	11.90 — 14.86	4.17
	2	12	12.85 ± 0.61	12.05 — 13.70	4.71
F	1	62	13.03 ± 0.53	11.72 — 14.32	4.08
	2	18	12.90 ± 0.61	11.82 — 14.15	4.69
Interorbital constriction					
M	1	59	9.97 ± 0.42	9.15 — 10.95	4.21
	2	12	10.43 ± 0.59	9.71 — 11.89	5.58
F	1	62	9.60 ± 0.52	8.45 — 10.72	5.45
	2	18	9.79 ± 0.49	8.53 — 10.26	4.98
Mastoid breadth					
M	1	58	21.26 ± 0.46	19.92 — 22.18	2.14
	2	11	21.78 ± 0.77	19.94 — 22.70	3.52
F	1	55	20.80 ± 0.58	19.37 — 22.36	2.81
	2	15	20.99 ± 0.67	19.81 — 21.98	3.20
Alveolar breadth across upper molars					
M	1	61	11.84 ± 0.31	10.97 — 12.72	2.61
	2	12	12.01 ± 0.33	11.34 — 12.61	2.76
F	1	62	11.70 ± 0.30	10.63 — 12.41	2.60
	2	18	11.74 ± 0.34	11.17 — 12.11	2.85
Length of maxillary toothrow					
M	1	61	8.67 ± 0.28	8.06 — 9.52	3.18
	2	12	8.64 ± 0.25	8.29 — 9.02	2.95
F	1	62	8.58 ± 0.29	7.93 — 9.21	3.43
	2	18	8.50 ± 0.40	7.77 — 9.26	4.69

TABLE 1. Continued

			Length of mandibular toothrow		
M	1	61	8.12 ± 0.38	7.11 – 9.59	4.67
	2	12	8.16 ± 0.23	7.82 – 8.53	2.79
F	1	62	7.95 ± 0.34	7.22 – 8.70	4.25
	2	18	7.95 ± 0.37	7.28 – 8.52	4.70
			Depth of skull		
M	1	60	19.51 ± 0.50	18.35 – 20.62	2.56
	2	12	19.72 ± 0.53	18.61 – 20.37	2.70
F	1	62	18.95 ± 0.53	17.58 – 20.50	2.81
	2	18	19.31 ± 0.49	18.61 – 20.46	2.52

TABLE 2. Results of principle component analysis (FACTOR) for 10 cranial characters for males and females of *Spermophilus mexicanus* from age groups 1 and 2. Unique variation attributed to each variable and the cumulative percentage of variance attributed to that factor (and those that precede it in the table) are given. See text for abbreviations.

Variable	Age group 1				Age group 2			
	Males		Females		Males		Females	
	Unique variance	Cumulative variance	Unique variance	Cumulative variance	Unique variance	Cumulative variance	Unique variance	Cumulative variance
CBL	38.9	38.9	44.3	44.3	41.3	41.3	41.1	41.1
ZB	15.7	54.7	16.9	61.2	22.4	63.7	18.9	60.0
POC	11.3	66.0	11.9	73.1	16.5	80.2	10.6	70.6
IOC	8.8	74.8	7.7	80.8	9.1	89.3	9.6	80.2
MB	7.2	82.0	6.3	87.1	6.3	95.6	7.0	87.2
ABTR	5.2	87.2	5.6	92.7	3.6	99.2	5.2	92.9
MAXTR	5.0	92.1	2.8	95.5	1.0	100.0	3.4	96.3
DS	3.6	95.8	2.1	97.6	0.4	100.0	2.1	98.4
MANTR	3.6	100.0	0.9	100.0	0.8	100.0	0.7	100.0

length of hind foot, 43.1 (41-45), 42.8 (41-45); length of ear, 12.3 (10-16), 11.5 (9-15); weight, 249.5 (200-290), 249.8 (190-274).

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EFFECT OF FEED QUALITY ON GROWTH OF THE GULF OF MEXICO WHITE SHRIMP, *PENAEUS SETIFERUS*, IN POND PENS

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Abstract.—To evaluate the effect of feed quality on growth and survival of *Penaeus setiferus* in an intensive culture system, a trial was conducted using commercially manufactured feeds varying in total protein and squid meal content. Juveniles (3.6 grams initial weight) were stocked at 40 per square meter in bottomless pens of one cubic meter in an earthen pond and were fed different quality feeds for 56 days. The effect of feed quality on instantaneous growth rate of *P. setiferus* was significant ($P = 0.0001$). Shrimp fed high quality feed (50 percent protein-15 percent squid meal) grew faster than those fed medium (40 percent protein- five percent squid meal) and low (30 percent protein only) quality feed, and shrimp fed medium quality feed grew faster than those fed low quality feed. Survival was not affected by feed quality ($P = 0.8715$) and averaged 90.3 percent. Weekly growth, final weight, and harvest biomass of fed shrimp ranged from 0.93 to 1.04 grams per week, 11.0 to 11.9 grams, and 398 to 421 grams per square meter, respectively. Unfed shrimp at the same density grew 0.47 grams per week, had 95 percent survival and were harvested at a final weight of 7.3 grams and biomass of 279 grams per square meter. It was estimated that natural forage contributed ≤ 52 percent to shrimp growth. Unfed shrimp stocked outside the pens in the open pond at a density of 0.5 per square meter grew 1.56 grams per week, had 92.3 percent survival, and were harvested at a weight of 16.1 grams and biomass of eight grams per square meter.

Results showed that *P. setiferus* has the potential to grow at commercially acceptable rates and indicated that quality of presented feed was important for growth of the species under intensive culture conditions even when natural foods were available. *Key words*: feed quality; pond culture; *Penaeus* sp.

Historically, results achieved with the Pacific white shrimp, *Penaeus vannamei* in pond culture have surpassed those obtained with the Gulf of Mexico white shrimp, *P. setiferus* (Parker et al., 1974; Chamberlain et al., 1981; McKee, 1986). Consequently, *P. vannamei* is the most widely cultured marine shrimp in the United States. Yet, continued progress of the shrimp culture industry in this country is limited at times by an inadequate supply of postlarval *P. vannamei*, and is threatened by the possibility of import restrictions. For these reasons, it is prudent to reevaluate the native white shrimp as an alternative culture candidate.

Although past experience with *P. setiferus* has not been encouraging, current pond production technology may improve results. Recently, production of *P. setiferus* in experimental growout trials in South Carolina was comparable to that achieved with *P. vannamei* (Sandifer et al., 1990; Browdy et al., 1991). Experience with *P. setiferus* in the 1950s, 1960s, and 1970s generally relied on low quality feeds, many of which were not formulated specifically for marine shrimp; poor water stability also was a problem. Although the nutritional requirements specific to *P. setiferus* still have not been adequately defined, vast improvements have been made in formulating feeds. Pond management strategy also has evolved in the United States from semi-intensive to intensive and super-intensive systems. It is generally believed that the greater the culture intensity the greater the role of presented feeds in supplying the required nutrients for growth and survival. Thus, although the nutritional requirements of shrimp may not change with increased intensity, the nutritional quality of feeds is more critical.

The present trial was undertaken to determine the effect of different quality feeds, varying in protein level and squid meal content, on growth and survival of *P. setiferus*. In this study, use of a higher quality feed under more intensive growout conditions than previously investigated with this species is examined.

MATERIALS AND METHODS

A feeding trial was conducted with *P. setiferus* (3.6 grams initial mean weight) stocked at a density of 40 shrimp per square meter in bottomless pens of one cubic meter in an 0.1-hectare earthen pond. The pen system used has been described previously (Robertson et al., 1992).

Shrimp were fed 50, 40, and 30 percent protein commercially manufactured feeds (Rangen, Inc., Buhl, Idaho), which will be hereafter referred to as high, medium, and low quality feeds, respectively. The high quality feed contained 50 percent protein with 15 percent squid meal as fed, the medium quality feed had 40 percent protein and five percent squid meal, and the low quality feed had 30 percent protein and no squid meal. Each of the three experimental treatments consisted of 12 replicate pens situated diagonally in a block design. Additionally, an "unfed" pen of shrimp adjacent to the experimental block design was included to estimate the potential contribution of natural foods to shrimp growth. Another group of unfed shrimp was stocked outside the pens in the open pond at 0.5 shrimp per square meter to estimate potential low density growth. Rations were fed four times daily at 0100, 0700, 1300, and 1900 hours at an estimated feed rate of four percent body weight per day.

One month before filling the pond, approximately 400 grams per square meter of lime was tilled into the pond bottom inside each pen. The 0.1-hectare pond was fertilized at the time it was filled eight days before stocking with 2.5 kilograms of urea, one liter of phosphoric acid, and 0.6 kilogram of sodium silicate. After five weeks, it was fertilized again with three kilograms of urea and one liter of phosphoric acid. Seawater for the pond was pumped daily from the Laguna Madre. The seawater was filtered to 400 μ as it entered the pond and was diluted with municipal freshwater as needed. Dissolved oxygen level and percent saturation were measured daily at 0700 and 1900 hours. Salinity, minimum and maximum temperatures, and Secchi disk readings were measured once daily. Total ammonia, nitrite, and pH determinations were made six times throughout the trial. The pond was harvested after 56 days and shrimp in each pen were counted and group weighed. Survival, instantaneous growth rate (IGR), final weight, weekly weight gain, and final biomass were determined for each pen. Comparisons among fed treatments were made on the basis of survival and IGR:

$$IGR = \ln (W_1/W_0) \ / \ (t_1 - t_0),$$

TABLE 1. Water quality during a feed quality growth trial with *P. setiferus.*

Parameter	*N*	Mean ± S.D.	Range
Salinity (ppt)	55	32.4 ± 2.2	28-42
Dissolved oxygen (mg/l)			
A.M.	55	4.6 ± 0.6	3.1-5.9
P.M.	52	6.9 ± 0.6	5.9-8.8
Oxygen saturation (%)			
A.M.	55	68.0 ± 7.4	50-84
P.M.	51	111.9 ± 8.9	94-144
Temperature (°C)			
Minimum	55	26.8 ± 1.2	24-29
Maximum	52	31.4 ± 1.1	28-33
Secchi (cm)	48	77.2 ± 15.6	45-90
pH	6	8.12 ± 0.19	7.8-8.4
Ammonia (mg/l)	6	0.055 ± 0.052	0.007-0.125
Nitrite (mg/l)	6	0.022 ± 0.010	0.006-0.032

where W_1 is weight at t_1 and W_0 is weight at t_0. Multiplying the IGR by 100 gives the percent body weight change per day. Growth and survival differences due to feed quality were tested for statistical significance by analysis of variance (ANOVA) followed by a Student-Neuman-Keul multiple range test where appropriate. Survival data were transformed (arcsine) prior to statistical analysis but are presented as percentages for clarity.

RESULTS

Water quality parameters monitored throughout the trial are summarized in Table 1. Salinity averaged 32.4 parts per thousand, mean daily low temperature was 26.8°C, and daily high temperature was 31.4°C. Morning dissolved oxygen level and percent saturation averaged 4.6 milligrams per liter and 68 percent, respectively. Afternoon dissolved oxygen level and saturation were 6.9 milligrams per liter and 112 percent, respectively. Water was exchanged at a rate of 11 percent daily.

The effect of feed quality on instantaneous growth rate of *P. setiferus* was significant ($P = 0.0001$). Shrimp fed high quality feed (50 percent protein- 15 percent squid meal) grew faster than those fed medium (40 percent protein- five percent squid meal) and low (30 percent protein only) quality feed, and shrimp fed medium quality feed grew faster than those fed low quality feed. Growth increased significantly from 2.01 percent to 2.11 percent to 2.15 percent per day for shrimp fed low, medium and high quality feeds, respectively (Fig. 1).

Survival was not affected by feed quality ($P = 0.8715$) and averaged 90.3 percent. Weekly growth, final weight, and harvest biomass of fed shrimp ranged from 0.93 to 1.04 grams per week, 11.0 to 11.9 grams, and 398 to 421 grams per square meter, respectively (Table 2). Unfed shrimp stocked at the same density (40 per square meter) in a pen grew 0.47 grams per week, had 95 percent survival, and were harvested at a final weight of 7.3 grams and biomass of 279 grams per square meter.

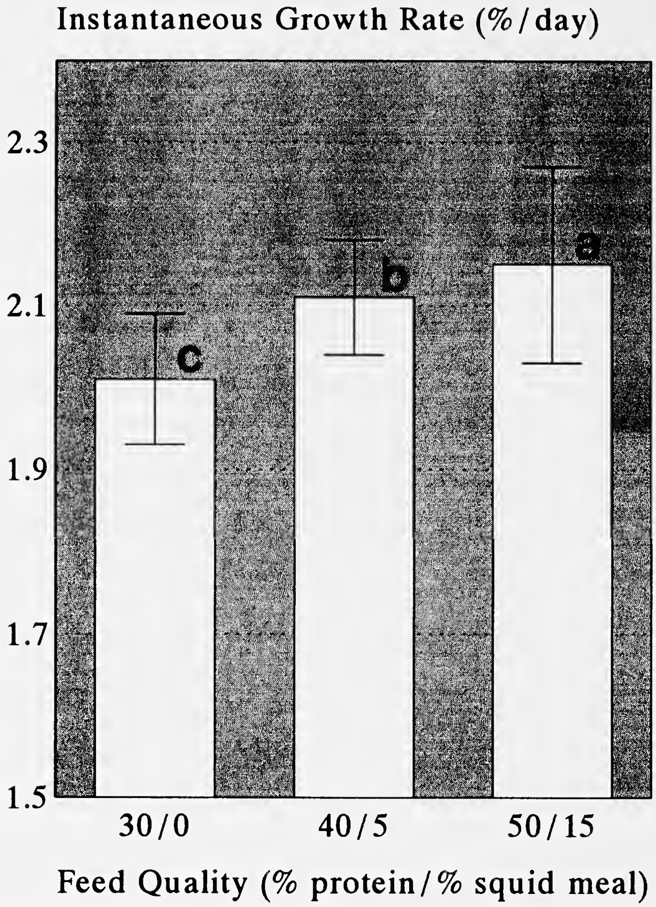

FIGURE 1. Effect of feed quality on instantaneous growth rate (IGR) of *P. setiferus*. Bars represent means plus or minus one standard deviation. Lowercase letters denote statistical differences (SNK, $P = 0.05$).

Comparing the biomass gain of unfed shrimp (137 grams per square meter) with the average biomass gain of the fed groups (266 grams per square meter) gives 52 percent as an estimate of the contribution of natural forage to shrimp growth in this experiment. Unfed shrimp stocked outside the pens in the open pond at a density of 0.5 per square meter grew 1.56 grams per week, had 92.3 percent survival, and were harvested at a weight of 16.1 grams and biomass of eight grams per square meter.

DISCUSSION

Ammonia and nitrite levels were within safe limits as determined for other penaeids (Wickens, 1976; Chen and Lei, 1990) and the other water quality conditions during the trial with the exception of salinity were

TABLE 2. Weekly growth, final weight, final biomass, and survival of *P. setiferus* fed different quality feeds. Values are means plus or minus one standard deviation.

Feed quality (% protein/ % squid meal)	*N*	Weekly growth (g)	Final weight[1] (g)	Final biomass[2] (g/m^2)	Survival (%)
30/0	12	0.93 ± 0.07	11.0 ± 0.5	398 ± 25	90.4 ± 4.6
40/5	12	1.00 ± 0.06	11.6 ± 0.5	421 ± 26	90.8 ± 4.8
50/15	12	1.04 ± 0.1	11.9 ± 0.8	406 ± 74	90.0 ± 7.8

[1] Initial weight was 3.6 ± 0.2 grams for all treatments.

[2] Initial biomass was 142 grams per square meter for all treatments.

within the ranges considered favorable for growth of some commercially important penaeids (Hanson and Goodwin, 1977; Clifford, 1985). Although *P. setiferus* inhabits a wide range of salinities in nature, reduced salinity appears to be better for pond growout, despite conflicting reports of the best salinity. Zein-Eldin (1963) reported the lack of an effect of salinity on growth of postlarval *P. setiferus*. Hysmith and Colura (1976) reported improved growth of *P. setiferus* during growout in reduced salinity, whereas Johnson and Fielding (1956) reported that white shrimp grew better in 34 parts per thousand than in 18.5. Even though salinity during the present trial (32.4 parts per thousand) may not have been ideal, the growth rate achieved with *P. setiferus* at a low density of 0.5 per square meter (1.56 grams per week) is among the highest reported for the species.

Dietary intake of amino acids is essential to shrimp growth. Generally, the quality of formulated feed increases as the amount of protein and squid meal increases because the amino acid profile (quality and quantity) of the feed is improved. Commercially manufactured feeds are typically formulated so that overall feed quality increases with percent protein.

It has been shown in the present study that growth of *P. setiferus* increased as feed quality increased. The highest quality feed tested (a combination of 50 percent protein and 15 percent squid meal) resulted in the best growth. These are higher values than previously reported in studies in which percent protein and percent squid meal were examined independently. Andrews and coworkers (1972) reported the optimal dietary protein level for *P. setiferus* to be in the range of 28 to 32 percent. In indoor tanks, *P. setiferus* grew faster when fed 30, 38, and 50 percent protein rations as opposed to a 22 percent protein feed (Lee and Lawrence, 1985). Johns and coworkers (1981) found no differences in *P. setiferus* growth when fed 25, 35, and 45 percent protein feeds during semi-intensive growout. The incorporation of squid meal in feeds, even in small quantities, is recognized to enhance growth (Fenucci and Zein-Eldin, 1976; Cruz-Ricque et al., 1987). In feeds containing 30 to 36 percent total protein, Fenucci et al. (1980) suggested using five to six percent squid meal for *P. setiferus*. The differences between results from these previous studies and results of the present trial may be due to widely different feed formulations and culture conditions.

Growth rates of fed *P. setiferus* in the present study (0.93 to 1.04 grams per week) are higher than those reported in the literature. Historical survival, growth, and production data for *P. setiferus* was summarized in McKee (1986). In a recent study of *P. setiferus*, Browdy et al. (1991) reported lower growth rates (0.73 grams per week for a density of 40 postlarvae per square meter) than those realized in the present trial initially stocked with 40 3.6-gram shrimp per square meter.

Growth of unfed shrimp in the pens indicated that natural forage was available and contributed to the nutritional needs of the shrimp. Maguire and Leedow (1983) made this same observation for *Metapenaeus macleayi* cultured in pond pens. Stomach content analysis of the same species suggested that presented feed used in semi-intensive conditions comprised approximately 58 percent of the shrimp diet, making the contribution of natural productivity 42 percent (Maguire and Bell, 1981). Stable carbon isotope tracer studies demonstrated that presented feeds contributed between 14 and 66 percent of the organic carbon assimilated by *P. vannamei* cultured indoors and outdoors at a density of 20 per square meter (Anderson et al., 1987; Parker et al., 1989). The ratio of biomass gain of unfed shrimp harvested in the present study to that of shrimp presented feed (initial stocking density identical for both groups) indicated that natural productivity had the potential to contribute 52 percent toward shrimp growth. Even so, the effect of feed quality on shrimp growth was significant, which emphasizes the importance of presented feed during intensive culture of this species.

In the open pond at low density (0.5 per square meter), *P. setiferus* grew faster (1.56 grams per week) than those in the pens (0.93 to 1.04 grams per week). This difference is probably an effect of density (0.5 as opposed to 40 per square meter), but also may indicate that the quality of the presented feeds was less than that provided by natural foods.

Results with *P. setiferus* were encouraging. Growth better than one gram per week was reached in pens harvested with biomass equivalent to 4000 kilograms per hectare. The growth rate achieved outside the pens (1.56 grams per week) indicates that the species has the potential to approach growth rates achieved with *P. vannamei*. Aside from the obvious advantage to United States shrimp producers of having access to *P. setiferus* in native waters, this species survives temperatures as low as 9°C (Harris and Kilgen, 1974) and can be overwintered in the United States (Harris and Kilgen, 1974; Sandifer et al., 1990). However, *P. setiferus* requires more animal protein when fed a 28 percent total protein ration than does *P. vannamei* (Chen et al., 1985), which means that feeds formulated for *P. setiferus* may be more expensive than *P. vannamei* feeds.

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EFFECTS OF MICROHABITAT ON NEST BOX SELECTION AND ANNUAL PRODUCTIVITY OF EASTERN BLUEBIRDS (*SIALIA SIALIS*) IN SOUTHEASTERN GEORGIA

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Abstract.—We assessed the effects of 15 microhabitat variables (that is, habitat variables measured within a 10-meter radius of the nest box) on artificial nest site selection and on annual productivity (total number of eggs per nest per year = TOTEGGS) of eastern bluebirds (*Sialia sialis*) in southern Georgia. Sixty-nine (1990) and 74 (1991) artificial nesting boxes were monitored near Statesboro, Georgia, from March through July during both years of the project.

A Multivariate Analysis of Variance (MANOVA) was used to compare the raw microhabitat variables surrounding selected boxes as opposed to unselected boxes. In both years of the study, microhabitat surrounding selected and unselected boxes did not differ significantly. The raw variables surrounding boxes that were occupied were further recombined using Principal Components Analysis (PCA). Annual productivity (TOTEGGS) was regressed against the resulting first six principal component scores. During the 1990 breeding season, TOTEGGS was significantly correlated with PRIN1 (openness) and PRIN4 (orientation of nest box). In 1991 however, none of the first six principal components were significantly correlated with TOTEGGS.

Our results suggest that nest box selection and annual productivity in eastern bluebirds do not appear to be based on microhabitat variables. *Key words*: eastern bluebird; nesting; microhabitat; Georgia.

Many aspects of the breeding biology of eastern bluebirds (*Sialia sialis*) have been studied extensively (Peakall, 1970; Pitts, 1976; White and Woolfenden, 1973; Thomas, 1946; Hartshorne, 1962; Pinkowski, 1975a, 1975b, 1979; Gowaty, 1981, 1983; Gowaty and Karlin, 1984; and Gowaty et al., 1989). However, little quantitative information exists regarding the effects of microhabitat characteristics on annual productivity (total eggs per nest per breeding season). For other species, studies have demonstrated that microhabitat variables could influence nesting success in several ways, including the likelihood of predation (Martin and Roper, 1988) or availability of adequate food supplies (Martin, 1987). Rendell and Robertson (1989) reported that cavity height and floor area influenced the reproductive success of tree swallows (*Tachycineta bicolor*) nesting in natural cavities.

The relationship between habitat characteristics and nesting success in secondary cavity-nesting species using artificial nesting sites has been studied in few species (Nilsson, 1984). Finch (1989) reported that characteristics of habitat surrounding artifical nest boxes influenced reproductive outcome in house wrens, *Troglodytes aedon* (a secondary cavity nester) in Wyoming, as did Belles-Isles and Picman (1986) in Ontario. Muldal et al. (1985) found that tree swallows (also secondary cavity nesters) preferred nest sites as far from conspecifics as possible presumably because of their territorial nature.

With this in mind, the goals of our study were to assess, quantitatively, the influence of microhabitat characteristics on artificial nest site selection and annual productivity in eastern bluebirds in southern Georgia.

Specifically, we tested the following two hypotheses: 1) no differences exist in microhabitat variables surrounding selected versus unselected nest boxes; 2) microhabitat did not influence annual productivity.

METHODS

Our study was conducted in Bulloch County, near Statesboro in southeastern Georgia during the 1990 and 1991 breeding seasons. For a thorough description of the study site see Scott (1992).

In 1990, 59 artificial nest boxes were set out at Meadow Lakes Golf Course, approximately 4.8 kilometers by road southeast of Statesboro. In 1991, five additional nest boxes were placed at this site. In both years, 10 additional boxes were monitored along an established bluebird trail west of Statesboro. This bluebird trail is located approximately 8.1 kilometers from the Meadow Lakes Golf Course.

In 1990, 69 artificial nest boxes (59 at Meadow Lake Golf Course plus an additional 10 along the established bluebird trail west of Statesboro) were monitored throughout the nesting season. In 1991, we monitored a total of 74 nest boxes (64 at Meadow Lakes Golf Course and the 10 along the bluebird trail).

In 1990, all nest boxes were in place by 10 February and monitoring began on 1 March. Prior to the 1991 breeding season, five boxes were moved (these boxes were judged to be too close to other boxes) and five new boxes were placed at Meadow Lakes. All boxes were in place by 15 January, and monitoring began on 20 February. Prior to the actual nesting season, each nest box was checked at least once a week for signs of bluebird activity. Once nesting began (late March or early April) the boxes were inspected at least every other day, to determine when the nesting cycle began, as well as the duration of all phases of the cycle (that is, nest building, egg laying, incubation, and brooding).

In principle, a number of microhabitat characteristics could influence the outcome at a particular box. In selecting the suite of microhabitat characteristics, the goal was to include as much information as possible regarding the habitat in the immediate vicinity (arbitrarily defined as 10 meters) of the nest box. With this in mind we selected 15 variables (see Table 1).

To obtain measurements of the microhabitat variables the area around each nest box was divided into four quadrants following north-south and east-west compass points. Each quadrant was further subdivided into segments within five meters and 10 meters of the box. All vegetative measurements were taken within the 10-meter radius in each quadrant. Analysis of ground cover was determined by placing one 0.25-square-meter quadrat at the five-meter and 10-meter marks within each quadrant. Percent basal cover by bare ground, grasses, and forbs (herbaceous dicotyledonous plants) was estimated in each .025-square-meter quadrat. To obtain percent cover by the substrate variables at five meters and 10 meters, the two values were averaged for the four quadrats at each distance (five meters and 10 meters). A PVC pole marked at 25-centimeter intervals was used to determine the height of the surrounding shrub cover. Percent canopy cover within five meters of the nest box was measured using an ocular tube (Finch, 1989).

Distances to the nearest occupied nest box and nearest human dwelling were measured with a (6-1000 meter) rangefinder, and orientation of the nest box opening was determined with a compass.

TABLE 1. Means and ranges for the 15 microhabitat variables for all boxes by year. BG5, FOR5, GR5 are average percent cover by bare ground, forbs and grasses based on four, 0.25-square-meter quadrats; BG10, FOR10, and GR10 same as BG5, FOR5 and GR5 except this is the average between five meters and 10 meters of the nest box; MXSHR = maximum percent shrub cover in four quadrats around the nest box; CON5 and DEC5 are the numbers of coniferous and deciduous trees within five meters of the box diameter of breast height (dbh) < less than five centimeters; CONM5 and DECM5 are the same as CON5 and DEC5 except here these are numbers of trees with dbh more than five centimeters; CAN = percent canopy cover; DTNHS = distance to nearest human structure; DTNOB = distance to nearest occupied box; NOR = degrees from North.

Variable	1990 Mean (range)	1991 Mean (range)
BG5	47.2% (0.3-100%)	42.4% (11.3-77.5%)
BG10	47.6% (0.0-100%)	42.4% (1.3-97.5%)
FOR5	21.8% (0.0-79.8%)	21.2% (0.0-81.3%)
FOR10	23.3% (0.0-82.5%)	22.7% (0.0-91.3%)
GR5	30.8% (0.0-87.5%)	36.7% (0.0-82.5%)
GR10	31.8% (0.0-99.0%)	33.7% (0.0-88.8%)
MXSHR	3.8% (1.0-9.0%)	2.8% (0.0-6.0%)
CON5	.28 (0.0-10.0)	0.1 (0.0-1.5)
CONM5	0.20 (0.0-1.8)	0.1 (0.0-1.8)
DEC5	1.3 (0.0-18.8)	0.6 (0.0-3.3)
DECM5	1.2 (0.0-8.0)	0.6 (0.0-4.5)
CAN	23.7% (0.0-94.3%)	17.7% (0.0-88.8%)
DTNHS	468.8m (20.0-1500m)	192.7m (25-800m)
DTNOB	255.8m (20.0-1500m)	269.6m (50-1500m)
NOR	156.6* (0.0-350.0)	88.2* (0.0-225.0)

We organized boxes into two categories for statistical analysis: 1) unselected boxes showed no sign of bluebird activity; 2) selected boxes showed some evidence of bluebird activity (that is, from the mere placement of straw in a box to a completed nest); 3) occupied boxes were those which produced at least one egg; and 4) successful boxes were those from which at least one young fledged.

To test our hypotheses we used a Multivariate Analysis of Variance (MANOVA) (Tatsuoka 1971) on the 15 microhabitat variables to compare: 1) selected versus unselected boxes; and 2) successful boxes versus the combination of unsuccessful and unoccupied boxes.

We further tested the effects of microhabitat on annual productivity, using multiple regression. We recombined the raw microhabitat variables surrounding occupied boxes with a Principal Component Analysis (Harman, 1976).

We factored the correlation matrix of raw microhabitat variables to obtain our principal components, and retained only those components with eigenvalues greater than 1.0 (Wiens and Rotenberry, 1980).

We then tested the relationship between annual productivity and microhabitat variables by regressing total eggs produced per box per season (TOTEGGS) against the principal component scores.

RESULTS

Because the microhabitat measurements in the two years were taken by different individuals, we did not pool the data. Our results are presented below.

In the 1990 breeding season, 31 boxes were selected; of these 24 were occupied, and young were fledged successfully in 18. Of the 24 occupied boxes, 10 produced one clutch, 13 produced two clutches and one produced three clutches. One hundred sixty-eight eggs and 85 young were produced resulting in a nesting success (number fledged per number of eggs) of 50.6%.

The mean clutch size was 4.3 eggs ($N = 39$ clutches), with clutch size ranging from two to five eggs. Four clutches contained two eggs, 15 contained four eggs, and 20 contained five eggs. Of the 168 eggs produced, 99 (58.9 percent) hatched and of these, 85 (85.9 percent) fledged young. The first clutch of the season was completed on 30 March 1990, and the last clutch of the season was initiated on 13 July 1990. Mean values and ranges for each of the 15 microhabitat variables for all 69 boxes in 1990 are listed in Table 1.

In our MANOVA, comparing the 15 microhabitat characteristics between the 31 selected and 38 unselected boxes, we found no significant differences between groups (Pillai's Trace = 0.164, $P = 0.78$). Moreover, significant differences did not exist when the 13 unsuccessful and unoccupied boxes were combined and compared with the 18 successful boxes (Pillai's Trace = 0.551, $P = 0.348$).

In our analysis of annual productivity we included only the occupied boxes. In our principal component analysis, only the first six principal components had eigenvalues greater than 1.0, so we excluded the remaining principal components (Wiens and Rotenberry, 1980). Correlations between the first six principal components and the raw variables are listed in Table 2. Eigenvalues and percent of total variance accounted for by each of the first six principal components are listed in Table 3. All six of the principal components were significantly correlated with at least one raw variable and all the raw variables were significantly correlated with at least two of the principal components (see Table 2).

TABLE 2. Pearson product moment correlation coefficients between raw variables and the first six principal components for 1990 and 1991 (in parentheses) nesting seasons. Only the largest correlation coefficients per row are listed.

Variable	PRIN1	PRIN2	PRIN3	PRIN4	PRIN5	PRIN6
BG5	.89067	*	*	*	*	*
	(*)	(.48032)	(-.71194)	(*)	(*)	(*)
BG10	.87772	*	*	*	*	*
	(*)	(.54672)	(*)	(*)	(.47004)	(*)
GR5	−.76660	*	*	*	*	*
	(.80183)	(*)	(*)	(*)	(*)	(*)
GR10	−.80430	*	*	*	*	*
	(.78581)	(*)	(*)	(*)	(*)	(*)
FOR5	*	−.53490	.74054	*	*	*
	(−.71237)	(*)	(.50404)	(*)	(*)	(*)
FOR10	*	−.50906	.76274	*	*	*
	(−.66879)	(*)	(.63901)	(*)	(*)	(*)
MXSHR	*	*	.76172	*	*	*
	(*)	(.71242)	(*)	(*)	(*)	(*)
CON5	*	.76220	.47085	*	*	*
	(*)	(.55413)	(*)	(*)	(−.48882)	(*)
CONM5	*	.77115	*	*	*	*
	(*)	(.36879)	(*)	(−.66114)	(*)	(*)
DEC5	*	.68299	.49592	*	*	*
	(.60648)	(.58723)	(*)	(*)	(*)	(*)
DECM5	.45644	*	*	*	.62019	*
	(.56973)	(*)	(*)	(*)	(.42499)	(*)
CAN	.64298	*	*	*	*	*
	(.36076)	(*)	(*)	(−.55013)	(.40497)	(*)
DTNHS	.61313	*	*	*	.49178	*
	(*)	(*)	(.44006)	(.45005)	(*)	(.48213)
DTNOB	*	.49672	*	*	*	−.60996
	(*)	(.35813)	(*)	(.41142)	(*)	(−.53445)
NOR	*	*	*	.69816	*	.58987
	(.53730)	(*)	(.50044)	(*)	(*)	(*)

PC1 was positively correlated with DTNHS, BG5, and CAN, and negatively correlated with GR5 and GR10. PC2 was positively correlated with CON5, CONM5, and DEC5. PC3 was positively correlated with FOR5, FOR10, and MXSHR. PC4 was positively correlated with DECM5 and can be interpeted as a measure of the density of large deciduous trees; and PC6 was negatively correlated with DTNOB and is a measure of the distance to the nearest occupied box.

We regressed the total number of eggs (TOTEGGS) against the first six principal components to test the hypothesis that a relationship existed between annual productivity (TOTEGGS) and microhabitat (the principal components). However, only PC1 and PC4 explained significant amounts of variation in TOTEGGS.

In 1991, more boxes were available than in 1990 and more were used. Thus, of the 74 boxes monitored, 35 were selected, 32 were occupied, and

TABLE 3. Eigenvalues and proportions of total variance accounted for by each of the first six principal component for 1990 and 1991 (in parentheses).

Principal Component	Eigenvalue	Percent of total variance
PRIN1	4.27711	28.5%
	(3.48670)	(23.2%)
PRIN2	3.00222	20.0%
	(2.35072)	(15.7%)
PRIN3	2.82706	18.8%
	(1.96963)	(13.1%)
PRIN4	1.28196	8.5%
	(1.36525)	(9.1%)
PRIN5	1.12005	7.5%
	(1.25767)	(8.4%)
PRIN6	1.03136	6.9%
	(0.94580)	(6.3%)

young were successfully fledged in 27. Of the 32 occupied boxes, 11 produced one clutch, 16 produced two clutches and five produced three clutches. Two hundred forty-two eggs and 123 young were produced during the season. Nesting success (number of young fledged per total number of eggs) was 50.8 percent. Fifty-eight clutches were completed, ranging in size from one to five eggs. Of those, one clutch contained one egg, two contained two eggs, five contained three eggs, 28 contained four eggs, and 22 contained five eggs. The mean clutch size was 4.17 eggs.

The first clutch was completed on 5 April and the last clutch was initiated on 28 July 1991. The incubation period for 27 clutches during this season ranged from 11 to 16 days with an average incubation period of 13.92 days.

In our MANOVAS no significant differences in microhabitat characteristics were found for 35 selected versus the 39 unselected boxes (Pillai's Trace =0.249, P=0.243) or for 27 successful boxes as opposed to the combined total of unoccupied and unsuccessful boxes (Pillai's Trace = 0.177, P=0.993).

In our PCA, we included the microhabitat variables for the 32 occupied boxes. We again retained just the first six principal components. Correlations and eigenvalues are listed in Table 3. A glance at Tables 2 and 3 reveals that the PCA results differed from those derived from the 1990 breeding season.

In 1991, PC1 was positively correlated with GR5, GR10, DECM5, and NOR and negatively correlated with FOR5 and FOR10; PC2 was positively correlated with BG10, MXSHR, CON5, and DEC5; PC3 was negatively correlated with BG5; PC4 was negatively correlated with CONM5 and CAN; PC6 was positively correlated with DTNHS and negatively correlated with DTNOB.

In the regression of TOTEGGS against the six principal components, we found no significant amounts of variation in annual productivity explained by any of the first six principal components (F = 1.31, $P > F = 0.29$).

Three patterns emerge when the two breeding seasons were compared. First, the selection rate of boxes did not differ significantly between years, but there was an increase in the rates of occupancy and success in 1991. Although there were more successful boxes in 1991, nesting success for the two seasons was approximately equal 50.6 percent (1990) and 50. 8 percent (1991).

Second, the MANOVA's for selected boxes as opposed to unselected boxes showed no significant differences in either year. Likewise, the MANOVA's comparing successful boxes to the combined unsuccessful and unoccupied boxes showed no significant differences for either season.

Third, in 1990, we found that annual productivity varied with PC1 (openness) and PC4 (orientation of nest box), but no such significant relationships were found in 1991.

Discussion

There are at least four possible explanations for the lack of a significant difference in microhabitat variables between selected and unselected boxes in the two years of our study.

First, it is possible that eastern bluebirds do not select nest sites on the basis of microhabitat variables. They might select nest boxes on the basis of some larger scale habitat characteristic shared by all the boxes such as Martin and Roper (1988) reported for hermit thrushes.

Second, it is possible that too few boxes at the golf course were selected for any patterns in microhabitat preference to emerge. The selection rate of nesting boxes 44.9 percent (1990) and 47.3 percent (1991) was low. The selection rate for just those boxes at the golf course was 39.0 percent for both years, compared to 80 percent (1990) and 100.0 percent (1991) on the long established bluebird trail. If one views the bluebird trail as a control of sorts, it would seem possible that over time the selection rate on the Meadow Lakes site could increase. Because eastern bluebirds remain in Georgia during the winter, they are able to defend nest sites throughout the year. It is possible that newer nest boxes may attract younger, less experienced birds and this may account for the low selection rate. This would also explain the difference in selection rate of the new (Meadow Lakes Golf Course) as opposed to old (established bluebird trail) nest boxes. If this is the case we would anticipate a difference in microhabitat between selected and unselected boxes in the future.

Third, it is possible that another factor may be influencing nest site selection. One possibility is nest site fidelity: eastern bluebirds might simply select nest sites based on nesting success in the previous year. Some studies indicate that males and females tend to return to the same nest site year after year (Laskey, 1939, 1940). Nest site fidelity has been reported in cup nesting species (Lanyon and Thompson, 1986; Benard and LaPointe, 1984).

Fourth, we may have failed to include some unknown, yet important, microhabitat variable in our analyses. We know of no way to evaluate this possibility, and it seems unlikely to us given the diversity of the 15 variables that we included.

Results of our analyses of annual productivity and microhabitat were inconclusive. In 1990, TOTEGGS was negatively related to PRIN1 (openness) and positively related to PRIN4 (orientation of nest box), whereas in 1991, however, no significant relationships were found. We believe that this difference may exist partly because the microhabitat data were collected by different individuals. In any case, it is presently unclear if microhabitat variables influence annual productivity.

ACKNOWLEDGMENTS

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MAMMALS FROM THE BEACH MOUNTAINS OF CULBERSON COUNTY, TRANS-PECOS TEXAS

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Abstract.—The Beach Mountains are a small extension of the Trans-Pecos Central Range in Culberson County, and like so many of the desert ranges of western Texas, almost nothing is known of the resident mammalian fauna. At least 35 species are herein documented to occur in the Beach Mountains, including a successfully transplanted stock of desert bighorn (*Ovis canadensis*), which occupies this last known stronghold of the extirpated native herd. Desert scrub species predominate locally, but grasslands species also are well represented. Noteworthy records include an unusually high population of *Ammospermophilus interpres*, and an apparently isolated group of *Chaetodipus nelsoni*, which provides the northernmost record for the species in the Trans-Pecos, and evidence of the continuing northern expansion in western Texas of the javelina (*Tayassu tajacu*). *Key words*: Beach Mountains; mammals, Trans-Pecos Texas.

The Central Range, the middle of three major ranges that bisects Trans-Pecos Texas from northwest to southeast, straddles the Hudspeth-Culberson county line, and is bordered to the east by the Salt Basin and to the west by the elevated Diablo Plateau (Fig. 1). The Beach Mountains are one of a series of smaller constituent ranges that lie entirely in southwestern Culberson County.

Virtually nothing is known of the small mammals from the Central Range and its components, save for the well-documented history of the last of the native herds of Texas bighorn, *Ovis canadensis* (Davis and Taylor, 1939; Carson, 1941). The report on the mammals of Culberson County by Davis and Robertson (1944) concentrated on the Guadalupe Mountains; limited material was recorded from the Wylie Mountains south of Van Horn and from along the margin of the Sierra Diablo. A compilation of Trans-Pecos mammals by Schmidly (1977) further illustrated the lack of specimens from the Beach range, as well as the general paucity of records from the southwest corner of Culberson County.

In February of 1991, we responded to the report of caves in the Beach Mountains, in hopes of discovering the remains of Pleistocene mammals. While the caves were not suitable for deposition of such sediments, we did make collections of small mammals. The results of these collections comprise the basis for this report, which includes a new species record for Culberson County, and delineates the northern periphery of the regional ranges for *Chaetodipus hispidus, C. nelsoni, Reithrodontomys fulvescens,* and *Tayassu tajacu.*

Methods

Collections were made by the first two authors and students from Midwestern State University

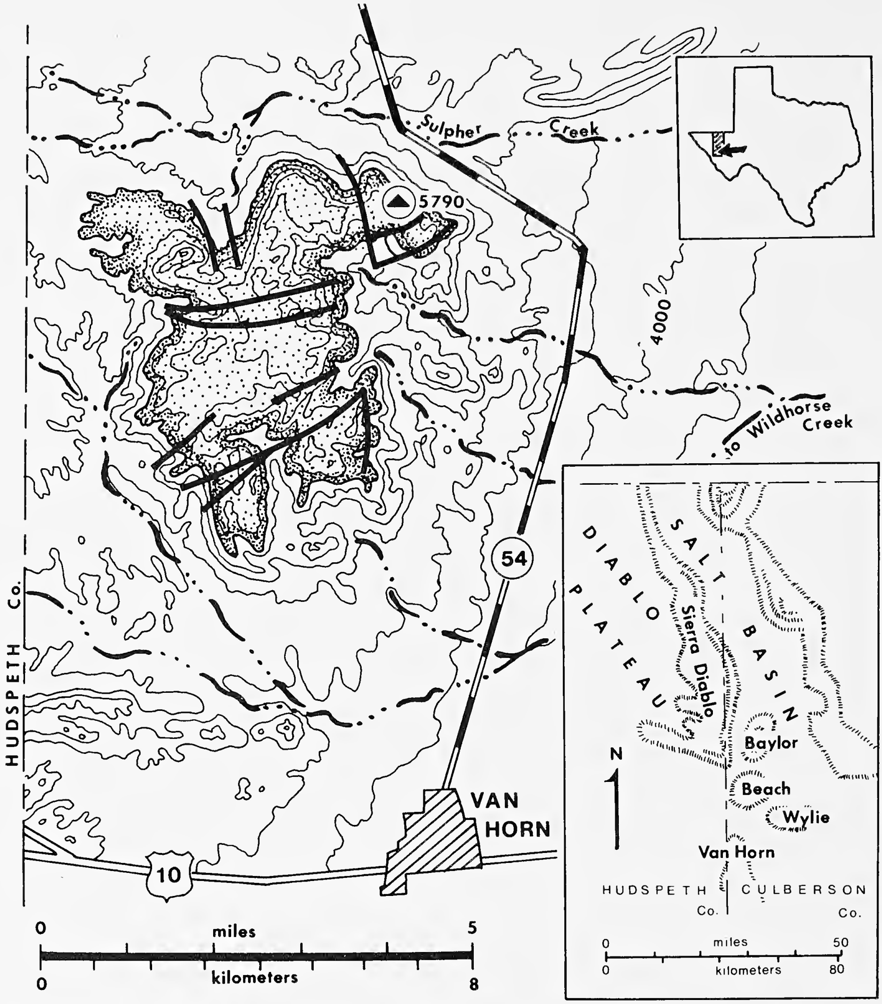

Figure 1. Map of the Beach Mountains in Culberson County, Texas. Stippled regions are 5000 feet or more above sea level, and bold lines indicate fault lines. Inset at upper right indicates relative placement of lower inset in Trans-Pecos Texas. Inset at lower right includes labeled component ranges of northern Central Range, situated along the Hudspeth-Culberson county line.

in the spring (16-18 March) of 1992. Field observations were recorded, and the 117 specimens collected during this period comprise the basis for this report. Most small species were taken with snap traps (Museum Special and rat-sized) or Sherman live traps. Sciurids and lagomorphs were shot, and most bats were taken in mist nets set over water. Most specimens were prepared as standard museum skins accompanied by skulls, although some were saved as whole skeletons or preserved in alcohol. Skulls and skeletons were saved from the few salvaged bats and carnivores. All specimens have been cataloged and deposited in the Collection of Recent Mammals, Midwestern State University (MWSU).

Literature providing the historical perspective, and information on larger species was provided by the third author, who is the resident foreman and manager for the Beach Mountains Ranch.

DESCRIPTION OF STUDY AREA

The Beach Mountains (Fig. 1) are a series of closely associated peaks rising abruptly more than 1500 feet above the floor of the southern margin of the Salt Basin. The higher reaches are comprised mostly of a hard, erosion-resistant Ordovician dolomite of the El Paso Formation. Several fault lines, converging in the immediate vicinity, contribute to a terrain that is noticeably more rugged and of sharper relief than the adjacent Baylor Mountains. Most of the central highlands lie above 5000 feet in elevation, the highest point being 5790 feet. A few shallow caves occur there. Rather extensive red sandstones of the Bliss Formation are exposed in lower parts of the southwestern corner of the range.

A series of strategically placed circular stock tanks presently provide most of the permanent water for range cattle. A permanent spring in the southwestern corner was dammed in the 1920s, and since has been periodically maintained. Seasonally dry creek beds originate in narrow, steep-walled header canyons and drain to the southeast, ultimately into Wildhorse Creek.

Scattered stands of juniper (*Juniperus*) occur along the higher ridges and peaks, but the rocky slopes predominantly support desert scrub. Dominant plants include ocotillo (*Fouquieria splendens*), sotol (*Dasylirion leiophyllum*), various yuccas (*Yucca* sp.), and lechuguilla (*Agave lechuguilla*). Stands of creosote (*Larrea tridentata*) occupy the surrounding plain and alluvial slopes. Floors of canyons support a variety of annual vegetation, cacti (*Opuntia* sp.) and such woody plants as mormon tea or ephydra (*Ephydra* sp.), mesquite (*Prosopis glandulosa*), and allthorn (*Koeberlinia spinosa*). A profusion of a variety of grasses merges with creosote at lower elevations, and extends up into canyon floors and onto the rocky slopes.

Our collecting efforts were confined to the Beach Mountains Ranch, which encompasses nearly all of the range. The history of this ranch extends back to J. H. Beach, who settled in Van Horn in 1887, and established the ranch in 1895. The abundance of bighorn, mountain lions, and bobcats on this isolated range during the early part of the century was particularly worthy of note. Hunters and trappers took a heavy toll (Carson, 1941). An intervening sucession of owners have grazed cattle and sheep, culminating with the present owner, who acquired the property in October of 1984. Presently, the ranch encompasses about five square miles, and is only lightly grazed by cattle.

SPECIES ACCOUNTS

Common names are used in accordance with Jones and Jones (1992).

Comments directed to our experiences with mammals from elsewhere in Trans-Pecos Texas, as well as the basis for subspecific treatments, are found in Stangl et al. (1993). The following accounts are abbreviated, but more information on the regional occurrence of these and other mammals is presented by Stangl et al. (1993).

Myotis californicus californicus (Audubon and Bachman, 1842), California myotis.—An adult of this small bat, a nonpregnant female, was taken in a mist net set over a nearly empty circular stock tank 3.3 mi. NNW Van Horn. The locality was along the lower flank of the mountains, and dominated by creosote. Rocky cliffs affording suitable roosts were within 100 yards. Other bats taken were all *Pipistrellus hesperus*.

Pipistrellus hesperus maximus Hatfield, 1936, western pipistrelle.—Shortly before sunset, this species was seen in abundance around the stock tank described in the above account. Four specimens taken there were adult non-pregnant females. Many more of these agile fliers avoided our mist net, or escaped after brief entanglement.

Antrozous pallidus pallidus (Le Conte, 1856), pallid bat.—In the sediments of the nearly empty tank described above, the decomposed carcasses of a pallid bat and four pipistrelles were recovered. Shortly after sundown, a large bat, presumably an *Antrozous*, briefly became ensnared in our mist net before escaping.

Sylvilagus audubonii minor (Mearns, 1896), desert cottontail.—Most sightings of this cottontail were in the dense vegetation along dry washes and canyon floors. We were unsuccessful in our attempts to collect voucher specimens.

Lepus californicus texianus Waterhouse, 1848, black-tailed jackrabbit.—An occasional jackrabbit was routed from its form during our field activities, but we obtained no specimens.

Ammospermophilus interpres (Merriam, 1890), Texas antelope squirrel.—Nowhere else in Culberson County have we found the antelope squirrel as abundant as in the Beach Mountains. This sciurid is notoriously difficult to take in traps, but we shot two, and retrieved another from a low-walled watering trough into which it had fallen and drowned. The three animals, all from 3.3 mi. NNW Van Horn, were adult males with scrotal testes.

Spermophilus variegatus grammurus (Say, 1823), rock squirrel.—This squirrel is a common but elusive resident of the Beach Mountains. Most sightings were little more than glimpses of animals among rock faces and along boulder-strewn canyon floors.

Thomomys bottae scotophilus Davis, 1940, Botta's pocket gopher.—This subspecies was described on the basis of a specimen from 15 miles north of the Beach Mountains, in the Sierra Diablo range. The Beach Mountains are one of the few remaining strongholds in the county for this species, which is elsewhere being displaced by the larger *Cratogeomys castanops*. We noted sign of Botta's pocket gopher only where a locally concentrated population was found to exist along a level canyon floor, 5.3 mi. N Van Horn. We took six specimens there; one of five females carried two fetuses measuring 9 mm. Less than a dozen specimens are otherwise known to exist in collections.

Cratogeomys castanops clarkii (Baird, 1855), yellow-faced pocket gopher.—This large gopher is locally uncommon in the Beach Mountains. We found no sign attributed to this species, and our one specimen, from 3.3 mi. NNW Van Horn, is the skull of a decomposed animal retrieved from a stock tank.

Perognathus flavus flavus Baird, 1855, silky pocket mouse.—This tiny heteromyid rodent probably occurs over most of the Beach Mountains. Our single specimen was taken on a creosote-dominated alluvial slope, where *Dipodomys merriami* and *Peromyscus maniculatus* were common, 3.3 mi. NNW Van Horn.

Chaetodipus hispidus paradoxus (Merriam, 1889), hispid pocket mouse.—Largest of pocket mice in the region, this typically prairie species is also the scarcest member of the genus *Chaetopidus* in the Trans-Pecos, where it usually is restricted to relict grasslands. We took one specimen from a heavily vegetated draw 5.3 mi. N Van Horn, where *Thomomys bottae* and *Sigmodon hispidus* were common.

Chaetodipus nelsoni canescens (Merriam, 1904), Nelson's pocket mouse.—This is one of two species of rock-dwelling *Chaetodipus* in the Trans-Pecos. Both seem to prefer arid, rocky, sparsely vegetated slopes. Where suitable conditions exist, only one species or the other occurs. Only in western Jeff Davis County are the two species known to occur in sympatry (Wilkins and Schmidly, 1979). Generally, the rock pocket mouse (*C. intermedius*) occupies the lower desert ranges to the north, whereas *C. nelsoni* occurs no farther north than central Jeff Davis County. Our four specimens from 3.3 mi. NNW Van Horn constitute the first record for Culberson County, and are of further interest because they appear to be isolated by populations of *C. intermedius*. Perhaps the exceptionally rugged nature of the Beach range confers some competitive advantage to *C. nelsoni* over the rock pocket mouse.

Dipodomys merriami ambiguus Merriam, 1890, Merriam's kangaroo rat.—This little kangaroo rat is one of the most common of Trans-Pecos mammals. It occurs in the Beach Mountains along the peripheral lower elevations where the land is level or gently sloping, and penetrates the mountains along canyon corridors. It was particularly common in the vicinity of creosote. We saved only representative series of three animals from 5.3 mi. N Van Horn and nine from 3.3 mi. NNW Van Horn.

Reithrodontomys fulvescens canus Benson, 1930, fulvous harvest mouse.—The Beach Mountains record is at the northern periphery of the range of animal in the Trans-Pecos. The fulvous harvest mouse typically is an inhabitant of developed grasslands, and consequently it is an uncommon species of local occurrence in the region. Like the hispid pocket mouse, its presence is indicative of healthy range conditions. One specimen each was trapped from 5.3 mi. N Van Horn and 3.3 mi. NNW Van Horn.

Reithrodontomys megalotis megalotis (Baird, 1858), western harvest mouse.—We have found no other species of small mammal as regionally widespread as this little harvest mouse. It can be expected from practically any of the diverse elevations and habitats. Locally, this mouse was most common along rugged, grass-covered hillsides shared with *Peromyscus eremicus* and *P. pectoralis*. Six specimens were taken from 5.3 mi. N Van Horn, and another from 3.3 mi. NNW Van Horn.

Peromyscus eremicus eremicus (Baird, 1858), cactus mouse.—This rodent was the most commonly collected species along the lower and more barren slopes of the Beach range. Particularly favored areas are dominated by lechuguilla, where it was often taken in association with *Chaetodipus nelsoni*. One female carried three fetuses measuring 4 mm. We took two specimens from 5.3 mi. N Van Horn and 12 from 3.3 mi. NNW Van Horn.

Peromyscus pectoralis eremicoides Osgood, 1904, white-ankled mouse.—This mouse is the most abundant mammal in the Beach Mountains. Ten animals were collected 5.3 mi. N Van Horn, and nine from 3.3 mi. NNW Van Horn. Most specimens were taken at intermediate and higher elevations where woody vegetation was present. It is most commonly associated with juniper.

Peromyscus leucopus tornillo Mearns, 1896, white-footed mouse.—This species was common along the fringes of washes and canyon floors where woody vegetation exists. Under such circumstances, it was most commonly associated with *Sigmodon hispidus*. We saved three specimens from 5.3 mi. N Van Horn and seven from 3.3 mi. NNW Van Horn.

Peromyscus maniculatus blandus (Wagner, 1845), deer mouse.—The deer mouse seems quite localized in distribution; our four specimens were taken only on alluvial slopes covered by creosote, 3.3 mi. NNW Van Horn. Common associates were *Dipodomys merriami* and *Onychomys arenicola*.

Onychomys arenicola arenicola Mearns, 1896, Mearns' grasshopper mouse.—All of our eight specimens of this grasshopper mouse were taken in the creosote association where *Peromyscus maniculatus* and *Dipodomys merriami* also were trapped. Of four adult females, one carried a single tiny embryo.

Sigmodon hispidus berlandieri Baird, 1855, hispid cotton rat.—The hispid cotton rat was abundant in the dense vegetation along washes and canyon floors. We found them active throughout the day and night. Ground cover was seldom sufficient to permit the well-defined runways so typical of this animal, but individuals often were seen scurrying under cover of cacti, mesquite, and other woody vegetation. Five specimens were saved from 5.3 mi. N Van Horn and one from 3.3 mi. NNW Van Horn.

Neotoma albigula albigula Hartley, 1894, white-throated woodrat.—Characteristic woodrat sign of stick nests and piles of fecal pellets can be noted almost anywhere along the rock faces, slopes, and canyon walls. Caves and crevices all are occupied by *Neotoma albigula.* Six animals were taken from 5.3 mi. N Van Horn and five from 3.3 mi. NNW Van Horn. Of the six adult females we collected, two were lactating, and two were pregnant, carrying one and two fetuses measuring 15 mm and 25 mm, respectively.

Erethizon dorsatum epixanthum Brandt, 1835, porcupine.—The porcupine is usually associated with woodlands, but it is presently widespread in the Trans-Pecos, and is commonly seen in the Beach Mountains.

Canis latrans texensis Bailey, 1905, coyote.—Our only specimen was the skull from a mummified young adult from 3.3 mi. NNW Van Horn. The coyote is common in the Beach Mountains, and its evening seranades are heard almost nightly. The species is not considered an important threat to ranch livestock.

Vulpes velox neomexicana Merriam, 1902, kit fox.—No specimens of the kit fox were obtained, and we saw no evidence of its presence. Nevertheless, our experience in the Trans-Pecos is that ranchers are always aware of this species. The little carnivore, locally referred to as the "red fox," seems always to be tolerated and usually is protected by landowners. This is true on the Beach Mountains Ranch, where the species is fairly common.

Urocyon cinereoargenteus scotti Mearns, 1891, gray fox.—The gray fox is one of the more commonly taken furbearers in these rugged hills. It is a secretive species, but frequently seen at dusk or under the glare of headlights at night.

Bassariscus astutus flavus Rhoads, 1894, ringtail.—Like the gray fox, the ringtail is common, but seldom observed. We had no opportunity to collect an example of this species.

Procyon lotor fuscipes Mearns, 1914, raccoon.—Regionally, the raccoon is largely restricted to the montane woodlands of the Davis and Guadalupe mountains. However, we found tracks around the muddy margins of a permanent spring, near where the third author once trapped an individual.

Taxidea taxus berlandieri Baird, 1858, badger.—The badger is common locally, and we occcasionally observed their characteristic diggings at the lower elevation where pocket gophers and kangaroo rats occur. This species is often sighted moving about in daylight hours during the spring months. The third author recently released into the mountains a young adult animal that his son had raised and kept for a pet the previous year.

Mephitis mephitis varians Gray, 1837, striped skunk.—Skunks are less often seen than detected by their characteristic odor. The striped skunk is usually seen only when taken in traps set for furbearers.

Conepatus mesoleucus mearnsi Merriam, 1902, hog-nosed skunk.—This is the more common of the two skunk species in the mountains, based on the take by fur trappers.

Felis concolor stanleyana Goldman, 1936, mountain lion.—No resident animals occur in the Beach Mountains, but individuals regularly venture there from adjacent ranges. Most recently (February 1992), a large male weighing about 180 pounds was caught 3.3 mi. NNW Van Horn with the aid of hounds. From the post-cranial material we were able to salvage a month later, we found that the animal must have been an aged individual, for the vertebrae showed sign of extensive osteoarthritis. Locally, the mountain lion is persecuted more for its predation on the mule deer and bighorn than for any threat posed to livestock.

Lynx rufus texensis J. A. Allen, 1895, bobcat.—We did not obtain a specimen of a bobcat from the Beach Mountains, but the species seems to be particularly abundant there and elsewhere in the Central Range. It is considered the most desirable of the furbearing species.

Tayassu tajacu angulatus (Cope, 1889), javelina or collared peccary.—We have observed that the javelina is presently expanding its range northward in Jeff Davis and Culberson counties. Only during the past few years was its presence first noted in the southern canyons of the Beach Mountains, and it is now found throughout the range.

Odocoileus hemionus crooki (Mearns, 1897), mule deer.—The mule deer was most often observed when our trapping activity on hillsides routed deer from their daytime bedding areas. We obtained no specimens of the species. However, we did examine several cast-off antlers, and some atypical examples of these superficially resemble those of a white-tailed deer (*Odocoileus virginianus*). The latter species is not known from nearer than the Davis Mountains, and is considered by local ranchers to be a less desirable species than the mule deer.

Ovis canadensis mexicana Merriam, 1901, bighorn or mountain sheep.—The rugged Beach Mountains provide ideal habitat for *Ovis canadensis*. It was here that the last of the native herds ranged as recently as the late 1950s, until finally extirpated by hunters (Carson, 1941). A 1991 restocking effort on the part of Texas Parks and Wildlife Department and the ranch ownership had been deemed sufficiently successful to permit limited hunting in the near future. The stock of 24 animals are of Arizona origin, and a band of three-year-old rams was often within sight of our camp situated at 5.3 mi. N Van Horn. Older rams and ewes with kids were more secretive, and are less often observed. The bighorn is a noted wanderer, and animals recently introduced into the Sierra Diablo and Baylor ranges occasionally wander into the Beach Mountains. One possible threat to the bighorn, and perhaps also to the mule deer (*Odocoileus hemionus*) is the aoudad (*Ammotragus lervia*), an introduced species which is now well established in the Davis Mountains, and which appears to be extending its range in the direction of the Beach Mountains.

DISCUSSION

With limited exceptions, the distribution of Trans-Pecos mammals is only generally understood. Even those regions that have been studied in the past are dynamic situations in which there are ever-changing responses to an increasingly arid environment. Thus, the mammalian fauna over much of the region remains to be documented, and earlier studies are more valuable for the baseline data they can provide to present investigators than as definitive sources of modern distributions (Stangl et al., 1993).

Although a small and isolated range, the Beach Mountains supports a diverse mammalian fauna which is dominated by desert scrub species (that is, *Chaetodipus nelsoni, Dipodomys merriami, Peromyscus eremicus,* and *P. pectoralis*). However, a secure and established desert grasslands fauna (represented by *Chaetodipus hispidus, Reithrodontomys fulvescens, Sigmodon hispidus*) is also present. The ability of these grassland species to survive seems closely related to current land management practices, which follow decades of heavy grazing by domestic sheep, goats, and cattle. Here, as elsewhere in the Trans-Pecos, traditional livestock operations on the marginal grasslands have become less profitable in an increasingly arid environment. Large game species (primarily mule deer and bighorn sheep) are now important cash crops to be conserved and managed. Such operations can only benefit the smaller and less conspicuous nongame species as well, especially those with an affinity for grassland habitats.

Species of hypothetical occurrence

A number of bat species may have escaped our limited collecting efforts. Some, like *Myotis thysanodes*, are probably occasional visitors from the adjacent Sierra Diablo highlands, and migratory bats such as *Lasiurus cinereus, Lasionycteris noctivagans, Tadarida brasiliensis,* and *Nyctinomops macrotis* may well be of seasonal occurrence.

Other species that might be expected to occur in the Beach Mountains include the desert shrew (*Notiosorex crawfordi*) that often eludes collectors, and the spotted skunk (*Spilogale gracilis*), a small and secretive little carnivore that is locally common in the higher woodlands of the Davis and Guadalupe ranges. Among small rodents, *Dipodomys ordii, D. spectabilis, Reithrodontomys montanus*, and *Neotoma micropus* are to be looked for in suitable habitat at lower elevations, as we have taken each of these species within five miles of the Beach Mountains. Particularly deserving of further investigation is the possibility that *Chaetodipus intermedius* occurs in sympatry with *C. nelsoni.*

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GENERAL NOTES

MYOTIS VELIFER IN THE QUITAQUE LOCAL FAUNA, MOTLEY COUNTY, TEXAS

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Dalquest (1964) reported a small but interesting late Pleistocene faunule from Quitaque Creek in Motley Co., Texas. At that time, mollusk shells in the faunule provided an approximate age of 31,400 ± 3,200 radiocarbon years before the present (rybp), indicating an age prior to full Wisconsinan glacial. More recently, a radiocarbon date in "excess of 35,000" rybp for the site was reported by Caran and Baumgardner (in Gustavson, 1986; Dalquest and Schultz, 1992). The Quitaque local fauna included such large mammals as *Megalonyx* sp., *Felis leo*, *Mammuthus columbi, Equus niobrarensis, Camelops* sp., *Odocoileus virginianus*, and *Capromeryx* cf. *furcifer*, as well as several lower vertebrates, rodents, and an unidentified bat (updated faunal list in Dalquest and Schultz, 1992).

The unidentified bat specimen consists of a single upper molar (Midwestern State University vertebrate paleontology collection no. 19233—Fig. 1). This specimen initially was examined by Claude Hibbard, who found it to be unlike all North American bats, and who believed it probably belonged to an undescribed species (Dalquest, 1964; Dalquest and Schultz, 1992).

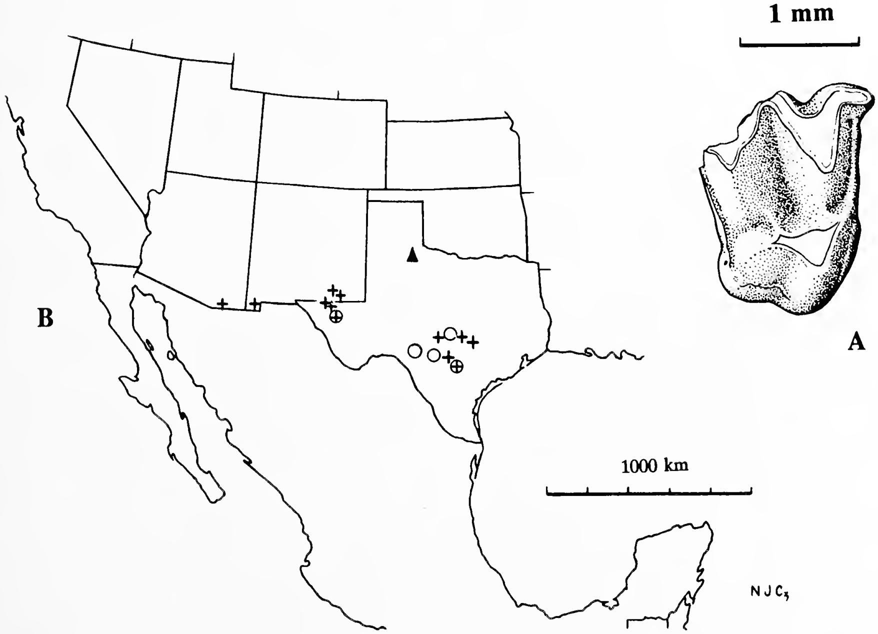

FIGURE 1. A, right M1 of *Myotis velifer* from Quitaque Creek, Motley Co., Texas, in occlusal view. B, distribution of published Quaternary occurrences of *Myotis velifer* in southwestern North America: + = late Pleistocene occurrences; o = Holocene occurrences.

TABLE 1. Quaternary occurrences of *Myotis velifer* in North America.

Taxon listing	Locality	Age (rybp)	References
M. (?) *velifer*	Papago Springs Cave, Arizona	late Pleistocene	Skinner, 1942
M. velifer	U-Bar Cave, New Mexico	35,000 to 13,000	Harris, 1987, 1989
M. velifer	Dry Cave, New Mexico		Harris, 1977, 1985, 1987, 1989
	Bison Chamber	<14,470 and >10,730	
	Harris' Pocket	14,470 ± 250	
	Room of the Vanishing Floor	33,590 ± 1,500	
M. velifer	Muskox Cave, New Mexico	25,500 ± 1,100 to 18,140 ± 200	Logan, 1981
	Texas Localities		
M. v. magnamolaris	Quitaque Creek, Motley Co.	31,400 ± 5,600, >35,000	Dalquest and Schultz, 1992; this paper
M. velifer	Friesenhahn Cave, Bexar Co.	19,000-17,000, also *ca.* 9,000-8,000	Graham, 1987
M. velifer	Longhorn Cavern, Burnet Co.	late Pleistocene	Graham, 1987
M. v. magnamolaris	Fowlkes Cave, Culberson Co.	late Pleistocene	Dalquest and Stangl, 1984
M. v. incautus	Fowlkes Cave, Culberson Co.	pre-Columbian (late Holocene)	
M. velifer	Dust Cave, Culberson Co.	late Pleistocene	Van Devender et al., 1977; Harris, 1985
M. velifer	Lower Sloth Cave, Culberson Co.	11,590 ± 230	Logan, 1983
M. velifer	Upper Sloth Cave, Culberson Co.	11,760 ± 610, 11,060 ± 180, 10,780 ± 140, 10,750 ± 140	Logan and Black, 1979; Harris, 1985
M v. magnamolaris	Schulze Cave, Edwards Co.	9,600; 9,300; middle Holocene	Dalquest and Stangl, 1984; Graham, 1987
M. velifer	Cave Without a Name, Kendall Co.	10,900 ± 190	Lundelius, 1967
M. velifer	Klein Cave, Kerr Co.	early Holocene, "about 8,000 years old"	Roth, 1972; Kurtén and Anderson, 1980
M. velifer	Miller's Cave, Llano Co.	early Holocene, *ca.* 7,300, middle Holocene, *ca.* 3,000	Patton, 1963; Graham, 1987
M. velifer	Zesch Cave, Mason Co.	late Pleistocene	Graham, 1987
M. v. magnamolaris	Laubach Cave (Innerspace Caverns), Travis Co. (type locality of this subspecies)	23,230 ± 450, 15,850 ± 500, 13,970 ± 310	Choate and Hall, 1967; Valastro et al., 1977

At the request of W. W. Dalquest, I reexamined this bat tooth. The specimen, a right M1, is broken in its metastylar area but otherwise is intact. The tooth can be described as follows: ectoloph is typically W-shaped; hypocone is absent but a postprotocrista extends posteriad from the metaconule as a curved sloping ridge with a small talon formed by its base. The trigon basin is deep and is closed off posteriorly by a strong postmetaconule crista (metaloph of Menu, 1985) and anteriorly by a strong postparaconule crista (paraloph of Menu, 1985). The preprotocrista is continuous with a precingulum extending to the parastyle. The lingual cingulum is interrupted on the talon and at the base of the protocone. The posterolingual portion of the cingulum is indented between protocone and talon. The tooth measures 1.90 mm in transverse width (measured from the lingual edge of protocone to the labial edge of tooth at the parastyle) and 1.25 mm in lingual anteroposterior length.

On comparison with all North American species of bats, the specimen is that of a vespertilionid and belongs to *Myotis velifer*, which it matches in size and details of morphology. The only difference I detected between the fossil and M1 in modern specimens of *M. velifer* was the indentation of the posterolingual margin between protocone and talon. Although this configuration was not seen in modern specimens, it nevertheless probably fits within the normal individual variation in the species. The size of the fossil matches M1 of *M. v. magnamolaris*, and the fossil occurrence lies within the modern range of that subspecies.

Myotis velifer is relatively common as a late Pleistocene and Holocene fossil in southwestern North America (Fig. 1, Table 1). Quitaque Creek is the northernmost fossil occurrence of the species. The specimen contributes to an increasing record of the Pleistocene distribution of this species in Texas. In fact, most Pleistocene records of *M. velifer* have originated in what is now Texas. Perhaps more interesting is the unique occurrence of the Quitaque Creek bat in an open site rather than in a cave like all the other fossil records. Also, all previous fossil records are from caves in regions of limestone or dolomite karst. The Quitaque Creek record, although not from a cave, is the first from a region of gypsum karst, the Northwest Texas gypsum karst (Smith, 1971), suggesting that populations of *M. velifer* occupied nearby gypsum caves in the late Pleistocene. I thank W. W. Dalquest for the opportunity to study this specimen.

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DIET OF SOME COMMON INSECTS IN THE SOUTH LLANO RIVER

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Many studies of stream and lake food webs have been prompted by interest in monitoring pollution levels and determining the mode by which pesticides enter and affect ecosystems (Ricklefs, 1973). A more recent thrust in food web studies has been generated by increased interest in biodiversity, conservation, restoration, and management (Cohen et al., 1990; Pimm, 1991; DeAngelis, 1992). Although invertebrate-dominated food webs are prevalent in nature, the vast majority of food webs that have been published are dominated by vertebrates, in part because predator-prey relationships can be established relatively easily for larger conspicuous animals. A remarkable exception is the arthropod dominated below-ground detrital food web studied by Moore et al. (1988).

The South Llano River (SLR) in Kimble County, Texas, has high insect species diversity, with more than 100 taxa (Herrmann, 1992). Two of the most common groups of predators in the benthic food web of the SLR are creeping water bugs (Hemiptera: Naucoridae) and hellgrammites (Megaloptera: Corydalidae). As part of a larger study dealing with the structure and dynamics of the benthic food web of the SLR, a series of feeding trials were performed with three naucorid species; in addition, stomach contents were analyzed for hellgrammites. Herein, we report the results of those investigations.

Table 1. *Prey consumption, as determined by feeding trials, of the three most common species of naucorids from the South Llano River, Kimble Co., Texas. Prey are ranked according to relative size, from the smallest (top) to the largest (bottom).*

Prey taxon	*Limnocoris Lutzi* 6.8 ± 0.11[1]	*Cryphocricos hungerfordi* 8.4 ± 0.13[1]	*Ambrysus circumcinctus* 8.7 ± 0.15[1]
Traverella presidiana	+	+	+
Tricorythodes sp.	+	+	+
Leptohyphes sp.	+	+	
Stenelmis sp.	+		
Thraulodes gonzalesi		+	+
Fallceon guilleri		+	+
Heptagenia sp.		+	+
Chimarra sp.	+	+	+
Macrelmis texanus	+	+	+
Petrophila sp.		+	+
Hydropsychidae		+	+
Isonychia sicca		+	+

[1] Mean total length ± SE (tip of typlus to tip of abdomen, n = 15).

Naucorids.—Although the family Naucoridae consists mostly of tropical aquatic insects, these animals are prominent members of stream communities throughout the southwestern United States (Polhemus, 1984). The SLR harbors the greatest assemblage of naucorids in the United States, totaling eight species. Four of the five genera that occur in this country inhabit the SLR (Sites and Willig, 1991). Abundant species within riffle habitats are *Ambrysus circumcinctus* Montandon, *Cryphocricos hungerfordi* Usinger, and *Limnocoris lutzi* La Rivers (Sites and Willig, 1991). Although naucorids are suspected to be important predators in lotic communities (Stout, 1981), little is known about their ecology and life history (Sites and Nichols, 1990; Sites and Willig, 1991). A European species, *Ilyocoris cimicoides*, is one of the few naucorids for which any report on prey has been published (Venkatesan and Cloarec, 1988). Records of feeding habits of any species of naucorid for the United States are rare (Polhemus, 1984).

Feeding trials were conducted in June and July, 1991, with 15 feeding trials conducted per naucorid species. All specimens used in a trial were collected at the same time from the same locality. In each trial, one adult naucorid was placed in a five-liter aquarium that contained a single large rock (circumference between 15 and 25 centimeters). The naucorid was introduced 30 minutes before the prey, and the feeding trial was terminated 24 hours later. Potential prey species were presented in pairs, and in a minimum of three different trials. Each individual of prey and predator species was used only once. If a naucorid did not consume any prey items, the data from that trial were discarded.

Considerable overlap in prey characterizes the diets of the three naucorids (Table 1). *Limnocoris lutzi* consumed six different prey items in three major taxonomic groups. The first consisted of mayfly nymphs (Ephemeroptera) in three genera (*Traverella, Tricorythodes,* and *Leptohyphes*). The larvae of two riffle beetles (Elmidae) comprised the second group; both (*Stenelmis* and *Macrelmis*) are abundant in riffles. Larvae of the caddisfly *Chimarra* represented the third prey group. The length of the largest prey item that was consumed by *L. lutzi* did not exceed the length of *L. lutzi*. The other two naucorid species (*C. hungerfordi* and *A. circumcinctus*) exhibited similar diets, and unlike the situation for *L. lutzi*, some prey items were larger than the predatory naucorids (Table 1). These larger prey were a lepidopteran larvae (*Petrophila* sp.), a trichopteran larvae (*Hydropsyche* sp.), and a mayfly nymph (*Isonychia sicca*). Venkatesan and Cloarec (1988) found that predation rates for *Ilyocoris*

TABLE 2. *Stomach contents analysis for three size categories [mean length from tip of clypeus to tip of abdomen ± SE (N)] of* Corydalus cornutus *from the South Llano River, Kimble Co., Texas. Numbers indicate the frequency of each prey item in the foregut of each size category of hellgrammites. Prey are ranked according to relative size, from the smallest (top) to the largest (bottom).*

	Size category		
Prey taxon	30.1 ± 2.1 (6)	36.7 ± 3.2 (9)	44.0 ± 2.9 (14)
Fallceon guilleri	3	3	2
Polycentropus sp.		2	1
Hydropsychidae	2	2	
Limnocoris lutzi	1	1	
Cryphocricos hungerfordi		1	1
Ambrysus circumcinctus			3
Petrophila sp.	2		4
Isonychia sicca		2	3
Erpetogomphus sp.			2
Tabanus sp.		2	1

cimicoides decreased with increasing prey size. These authors hypothesized that increases in body size of prey imply an increase in handling time, making the processing of the prey more time consuming. However, larger prey provide more energy, thus requiring fewer prey items. If this hypothesis is correct, then *C. hungerfordi* and *A. circumcinctus* spend less time searching and more time handling prey, whereas *L. lutzi* spends more time searching and less time handling prey.

Corydalids.—The family Corydalidae occurs in a wide variety of aquatic habitats, ranging from spring sweeps and streams, to lakes and ponds. Corydalid larvae are predators of other aquatic invertebrates and small vertebrates. The morphology of the mouth parts, accentuated by robust mandibles, indicates that corydalids are specialized predators. The genus *Corydalus* is an engulfing predator, and in lotic-erosional and depositional streams, this genus is adapted to cling to, and climb among, the substrate (Evans and Neunzig, 1984). The life history and population energetics of *Corydalus cornutus* in central Texas is known (Stewart et al., 1973; Brown and Fitzpatrick, 1978; Epperson and Short, 1987; Short et al., 1987). It exhibits a one-year life cycle with 11 larval instars. Females typically oviposited two egg masses between late May and August. Eclosion occurred some 13 days after oviposition, with larval growth slowing and eventually stopping by November. Considerable inter-stream variation characterizes the development of *C. cornutus*, and this variation is attributed to differences in thermal attributes (Short et al., 1987). Annual production for this species in Texas is one of the highest reported for a predatory species. Estimates ranged between 1.62 and 22.9 grams of dry mass per square meter per year, comparable values to those of primary consumers in desert streams (Epperson and Short, 1987; Short et al., 1987). The diet for a population of *C. cornutus* in the Brazos River, Palo Pinto, Texas, comprised over 20 prey taxa in at least seven insect orders (Steward et al., 1973). The most prevalent groups in the diet were caddisflies (Hydropsychidae) and black flies (Simuliidae).

In the shallow riffles of the SLR, *C. cornutus* is the top arthropod consumer; it feeds at all consumer trophic levels of the food web (Camilo and Willig, unpublished data). Stomach content analysis of 30 individuals (Table 2), corroborates that *Corydalus* consumes prey from a variety of trophic levels, (that is herbivore, *Fallceon guilleri* (Baetidae); intermediate predator, *Cryphocrycos hungerfordi*; and high predator, *Tabanus* sp.). In addition, two individuals were found with algae in the midgut, but this material probably was ingested accidentally, along with other prey. The diet for *C. cornutus* in the SLR overlaps more than 90 percent with that reported from the Brazos River (Stewart et al., 1973) in terms of species compostion. Cannibalism was prevalent in the Brazos River population; however, we did not detect this phenomenon in the SLR. In the Brazos River, as well as in the SLR, *C. cornutus* did not consume the caddisfly *Chimarra*, even though it is common in the study area and easily subdued, given its size. Our observations are consistent with the hypothesis of Moore et al. (1988) that most top predators of arthropod dominated food webs are omnivores. Moreover, naucorids and corydalids are omnivores *sensu* Pimm and Lawton (1978) in that they feed at more than one trophic level. Pimm and Rice (1987) found that prevalent omnivory, like what we observed in the SLR, reduces the system stability (that is return times of population densities after disturbance are greater, thus increasing the probability of extinction). They also concluded that multi-life-stage models (consuming different prey items at different life stages), or life history omnivory, reduces stability, but less so than does strict omnivory. Adults of each species of naucorid consumed a wide array of prey, including primary consumers and higher trophic levels. Different instars of *C. cornutus* consumed the same prey species (Table 1; Stewart et al., 1973), and might be constrained only by prey size (Camilo and Willig, unpublished data).

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RECORDS OF FIVE SPECIES OF SMALL MAMMALS FROM WESTERN TEXAS

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In the course of field work in 1991 and 1992, parties or individuals asssociated with The Museum at Texas Tech University obtained specimens of five species of mammals that are noteworthy from a distributional point of view. These are detailed below.

Cryptotis parva parva (Say, 1823).— A male (testes 4 x 2 mm) of this diminutive shrew (TTU 62341), which was captured in a Sherman live trap set in mesquite grassland at a place 3 mi. S and 5 mi. E Claude on 19 August 1992, provides the first record of *C. parva* from Armstrong County (see Owen and Hamilton, 1986). This specimen, along with a male (TTU 61632, testes 4 x 2 mm) from 13 mi. E. Canyon, Randall County, trapped on 1 July 1992 on rocky substrate near a yucca plant, aids in better defining the known distribution of this relatively rare species on the northern part of the Llano Estacado.

Another least shrew was taken by A. F. Laemmerzahl in a Sherman trap set 3 mi. N and 9 mi. E Justiceburg, Garza County, in open mesquite grassland. This locality, which is not far off the Llano to the east, represents a new county record for *C. parva* and the southernmost along the western edge of its known range in Texas. A female (TTU 61916), this shrew carried five fetuses that measured 6 mm in crown-rump length on 2 August 1992. We took a male (TTU 62373, testes 5 x 3 mm) at this same locality, on 27 August 1992, in mesquite grassland with abundant broomweed and scattered *Opuntia*.

Finally, two specimens from Lubbock County were brought in by house cats as follows: TTU 62339, unknown sex, from 5 mi. E New Deal, taken on 20 July 1992 by Jean Nichols; TTU 62340, male, from 1 mi. W Acuff, obtained on 20 August 1992 by Venita Davis.

Pipistrellus subflavus (F. Cuvier, 1832).—An adult female (nonpregnant) eastern pipistrelle (TTU 60872) was captured on 15 April 1992 in a fraternity house near the Texas Tech University campus in Lubbock, Lubbock County. This specimen is the first of this bat to be recorded from the Llano Estacado proper (the only other specimen from the region was taken in Fissure Cave, Palo Duro Canyon, Armstrong County, along the edge of the caprock some 85 miles northward from Lubbock—Schmidly, 1991), and represents one of the westernmost records of occurrence for the species in North America.

Dasypus novemcinctus mexicanus Peters, 1864—The nine-banded armadillo is known from several localities along the eastern base of the Llano Estacado and has been recorded from Castro, Hale, and Martin counties on the plateau proper (Choate, 1991). A male, salvaged as a cranium and lower jaws (TTU 61558), was found dead on U.S. Hwy. 62-82, 2 mi. S and 1 mi. W Meadow, Terry County, on 16 June 1992. This respresents the westernmost known record of occurrence on the Llano, and is evidence of continued northwestward dispersal by this species.

Reithrodontomys montanus montanus (Baird, 1855).—This species is "the rarest of the harvest mice occurring in the Trans-Pecos" according to Schmidly (1977:99). It is known in that region only from Culberson, El Paso, Jeff Davis, and the extreme northern parts of Brewster and Presidio counties (Schmidly, 1977; Dalquest and Stangl, 1986; Chapman and Spencer, 1987). We took an adult female (nonpregnant) near the northern boundary of Big Bend National Park on 17 March 1992; the actual location of capture was 0.2 mi. N and 1.3 mi. W Persimmon Gap Ranger Station. This specimen (TTU 61337) provides the first record of the plains harvest mouse from the southern part of the Big Bend region.

Our specimen was taken in a Sherman live trap set near a lechuguilla plant in an area otherwise sparsely vegetated mostly with ocotillo, creosote, cactus, and buffalo grass. The substrate was hard and rocky. Mammals trapped nearby included *Perognathus flavus, Chaetodipus nelsoni, Dipodomys merriami, Peromyscus eremicus, P. leucopus,* and *Reithrodontomys megalotis.*

Baiomys taylori taylori (Thomas, 1887).—An adult female (three fetuses, crown-rump length 7 mm) of this pygmy mouse was trapped by J. R. Goetze at a place 9 mi. S and 1 mi. W Juno, Val Verde County, on 20 July 1991. This specimen (TTU 59843) represents the westernmost record of known occurrence of *B. taylori* in the southern part of its range in Texas.

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THE RED BROCKET, *MAZAMA AMERICANA* (ARTIODACTYLA: CERVIDAE), IN EL SALVADOR

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The red brocket, *Mazama americana*, has been recorded from southern Tamaulipas, México, southward through Central American into South America (Hall, 1981). However, previous to this paper the species has not been reported from El Salvador. Owen et al. (1991) speculated that *Mazama* occurs, or historically occurred, in El Salvador, but they did not include it in their annotated checklist of land mammals of that country because its presence had not been substantiated by actual specimens or first-hand observations.

Recently, Owen identified the skull of a male red brocket collected by Victor Hellebuyck in May 1973 and deposited in the collection of the Museo de Historia Natural de El Salvador, San Salvador, El Salvador (MHNELS 239). The skull exhibits typical features of *Mazama americana* including antlers as simple spikes, less than half the length of the head, a more arched facial profile than in *Odocoileus virginiana* from El Salvador, and nearly straight upper borders of the orbits (Hall, 1981). The Salvadorian subspecies is *M. a. cerasina* Hollister, 1914.

Field notes indicate that this specimen was hunted down by dogs in a cloud forest near Hacienda Los Planes de Montecristo, Departamento de Santa Ana. Hacienda Los Planes de Montecristo (14° 24' N, 89° 22' W, 1800 meters elevation) is in the Lower Montane Wet Forest life zone of Holdridge (1975). This Hacienda is part of Cerro Montecristo National Park and Forest Reserve at the convergence of El Salvador, Guatemala, and Honduras, and is the only extensive forest in El Salvador that has escaped widespread destruction (Daugherty, 1972, 1973). It is possible that populations of *Mazama americana* still exist in the Montecristo forest but we know of no recent reports concerning its presence there. Due to widespread habitat destruction and high density human and dog populations in most of El Salvador, the red brocket must be considered an endangered species in that country and is deserving of complete protection.

We thank Victor Hellebuyck for advising Owen on the possibility of a specimen of a red brocket housed in the collection of the Museo de Historia Natural de El Salvador.

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VARIATION IN REPRODUCTIVE CHARACTERISTICS OF *POA PRATENSIS* ACROSS A SUCCESSIONAL CHRONOSEQUENCE

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Many aspects of reproductive behavior of plants are plastic and can vary greatly among individuals of the same species living in different habitats. The number of seeds produced by a plant is generally more plastic than the mean individual seed mass (Harper et al., 1970), although the size of individual seeds has been observed to be influenced by environmental factors such as light, temperature, soil nutrients, and level of competition (reviewed in McGinley et al., 1987; McGinley and Charnov, 1988). Because both biotic and abiotic conditions change during secondary succession, the reproductive behavior of a species may differ among successional stages. Here I report on the effect of successional stage on the number of seeds, the total mass of seeds, and the mean individual seed mass produced by individuals of the introduced grass *Poa pratensis* at Cedar Creek Natural History Area in Minnesota. Soil nutrient availability and plant biomass increase over time, whereas light availability decreases over time during secondary succession at this site (Inouye et al., 1987). Because *Poa pratensis* colonizes fields rapidly, reaches its greatest proportional abundance in intermediate-aged fields, and remains abundant in the oldest fields at this site, it is an important species in all stages of secondary succession at Cedar Creek (Tilman, 1988).

In July, 1989 I collected all seeds produced by 10 individual plants of *Poa pratensis* growing in each of 22 old fields that differed in the length of time since they were last farmed (seven to 62 years—see Inouye et al., 1987 for descriptions of these fields). I chose plants that were clearly identifiable as separate individuals and I collected plants from throughout the entire field to avoid sampling individuals from the same patch. For each individual, I determined the number of filled seeds, the total mass of all seeds, and the mean individual seed mass.

The number of seeds produced by an individual ranged from zero to 544 (mean = 137.19, S.E. = 6.40). Plants in older fields produced significantly more seeds (log seed number = 1.082 + 0.608 (log field age), $N = 220$, $r^2 = 0.054$, $P = 0.0003$). The total mass allocated to seeds ranged from 0 to 110.6 milligrams (mean = 27.16, S.E. = 18.09), whereas the mean individual seed mass ranged from 0.06 to 0.37 milligrams (mean = 0.188, S.E. = 0.003). There was no significant relationship between field age and either the total seed mass (log total seed mass = 0.973 + 0.237 (log field age), $N = 220$, $r^2 = 0.011$, $P = 0.075$) or the mean individual seed mass (log mean mass = -0.848 + 0.072 (log field age), $r^2 = 0.0007$, $P = 0.122$) produced by a plant. The coefficient of variation for seed number per individual (69.23 percent) and total mass per seed (66.61 percent) were more than two and a half times larger than the CV for mean individual seed mass (24.20 percent). Thus, it appears that variation in environmental conditions associated with field age influenced the number of seeds produced by an individual but not the size of individual seeds.

Interestingly, plants that invested a greater total mass in seeds produced significantly larger individual seeds (log mean mass = -0.912 + 0.13 (log total mass), $N = 220$, $r^2 = 0.134$, $P < 0.0001$). This relationship is predicted to occur in conditions where clutch size influences the probability of offspring survival (Parker and Begon, 1986; McGinley, 1989), suggesting that these relationships should be investigated further at this site.

I thank D. Tilman for financial support (NSF/BSR 8811884), the staff at Cedar Creek Natural History Area for logistical support, and M. Stradtmann, J. Borgerding, K. Westover, and the entire 1989 summer field crew for their help with seed collecting, counting, and weighing.

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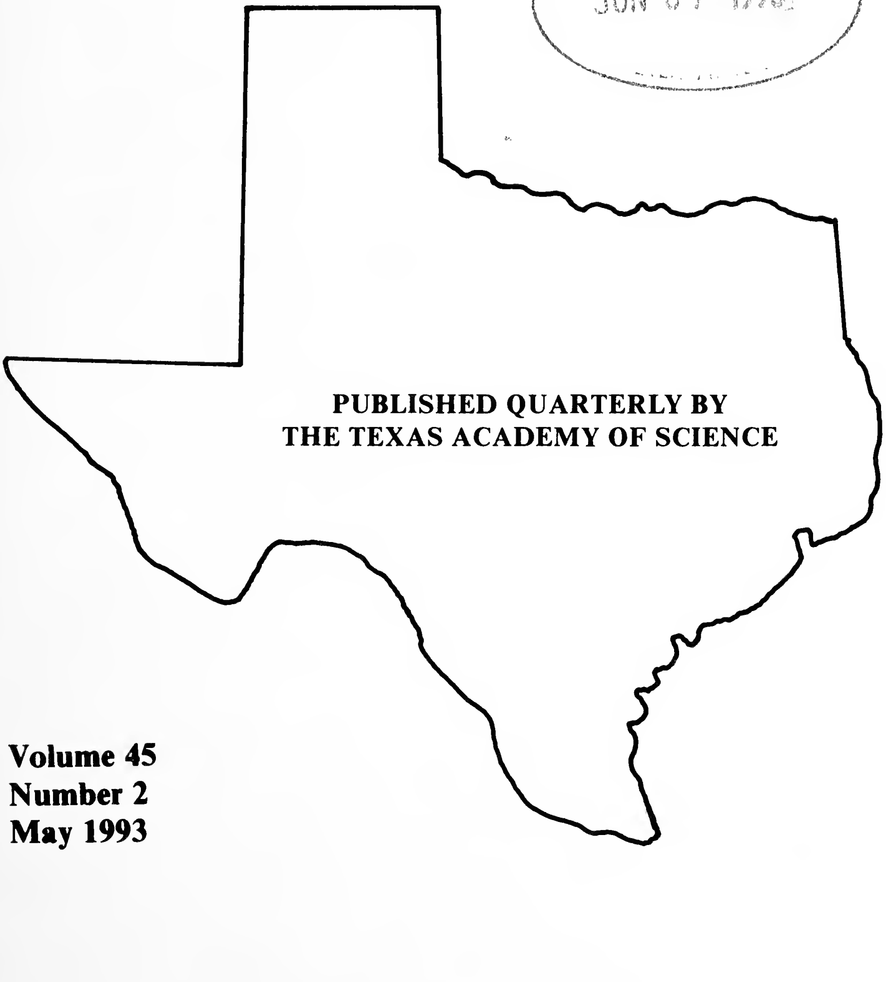

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J KNOX JONES, JR.
DISTINGUISHED TEXAS SCIENTIST, 1992

J KNOX JONES, JR. was born in Lincoln, Nebraska, on 16 March 1929. He received the B.S. in zoology from the University of Nebraska in 1951 and the M.A. (1953) and Ph.D. (1962) in zoology from the University of Kansas.

Dr. Jones served as a Medical Officer in the U.S. Army from 1953 through 1956. During this time, he was stationed in Korea and Japan where he gained extensive knowledge of Asian mammals; the subjects of many of his publications. He joined the faculty at the University of Kansas in 1962 as Assistant Professor in Zoology and Curator of Mammals. He was appointed Associate Director of the Museum in 1967 and Professor of Zoology in 1968.

In 1971, Dr. Jones came to Texas Tech University as Dean of the Graduate School. He was appointed Vice President for Research and Graduate Studies in 1974, a position he held until 1984, when he returned to fulltime teaching and research. Through November 1992, Dr. Jones had authored or edited 360 publications. Several more are still in press and a book is forthcoming from Louisiana State University Press. Dr. Jones directed the graduate programs of 18 doctoral and 15 masters students.

Dr. Jones was President of the American Society of Mammalogists from 1972 to 1974 and he was the recipient of the C. Hart Merriam Award in 1977, the H. H. T. Jackson Award in 1983 and named an Honorary Member in 1992. Indeed, he was known internationally for his research on mammals. In 1985, Dr. Jones won the Barney E. Rushing Award for outstanding research at Texas Tech University and in 1986 he received the university's highest honor when he was named Paul Whitfield Horn Professor of Biological Sciences and Museum Science.

Dr. Jones was a Fellow of the Texas Academy of Science and he was editor of *The Texas Journal of Science* from 1986 until his death on November 15, 1992. Dr. Jones was the recipient of the Texas Academy of Science Distinguished Texas Scientist Award in 1992. The following paper is based on the text of his Plenary Address at the 95th Annual Meeting of the Texas Academy of Science, Wichita Falls, Texas.

THE CONCEPT OF THREATENED AND ENDANGERED SPECIES AS APPLIED TO TEXAS MAMMALS

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Abstract.—Ten species of mammals native to Texas now are extinct there except that three, all artiodactyls, have been reintroduced. One of the 10, the West Indian monk seal, is believed to be extinct throughout its range; remnant to healthy populations of the other nine occur elsewhere than Texas within the natural range of the species. Six land mammals and several marine species are endangered in Texas or its Gulf waters, and others are listed as threatened. Finally, populations of some mammals are so poorly understood that it is unknown if they are threatened, and such species are deserving of timely study. The history of federal and state legislation to protect endangered and threatened biota is briefly reviewed as a prologue to discussion of individual species. *Key words*: mammals; Texas; threatened and endangered species.

The roots of wildlife protection extend back to Roman times, perhaps beyond, when the private landowner was acknowledged to have control over harvest of animals that ranged on his property. In the Middle Ages, with the development of royal forests, preserves, and estates, wildlife became the property of kings and their cronies. Gradually, in England for example, the royal prerogative passed under parliamentary control.

In this country, the several states assumed the responsibility of protecting wildlife, but this activity was confined for many years to animals of economic importance in an attempt to prevent significant decline in numbers or local extinction. The concept of federal control first was manifested in laws governing maritime and freshwater animals—the take of oysters from Atlantic mud flats, for example—with responsibility for the harvest of terrestrial animals left to the states.

The first significant step in federal wildlife law was the Lacey Act of 1900. The major provision of this legislation was the prohibition of interstate transportation of "any wild animals or birds" killed in violation of state law. Thus the principal thrust of the Lacey Act was to enlist the aid of the federal government in the enforcement of state game laws.

It has been only in the past 25 years or so that federal and state laws have been developed to protect nongame animal species, including invertebrates, and also plants. The first federal legislation in this area was the Endangered Species Preservation Act of 1966, in which the Secretary of the Interior was directed to "carry out a program in the United States of conserving, protecting, restoring and propagating selected species of

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A modified version of this paper was presented as the plenary lecture at the 95th annual meeting of the Texas Academy of Science in Wichita Falls on 6 March 1992, in connection with recognition of the author as Distinguished Texas Scientist of the Year by the Academy.

native fish and wildlife." Interior was given authority to acquire land as well as to work with Agriculture and Defense (the other federal departments with large land holdings) in carrying out provisions of the act. A species was to be determined as threatened with extinction upon a finding by the Secretary of the Interior "after consultation with the affected states that its existence is endangered because its habitat is threatened with destruction, drastic modification, or severe curtailment, or because of over exploitation, disease, predation, or because of other facts, and that its survival requires assistance."

While the 1966 Act marked a significant first step in an effort to protect endangered species, it had a number of serious limitations. Among these were: 1) it placed no limits at all on harvest or taking of endangered species—that power remained solely with the states; 2) it did not restrict interstate commerce in endangered species or parts thereof; and 3) it applied only to native wildlife, not to endangered species of foreign origin—spotted cats (furs) or elephants (ivory), for example.

This led to the Endangered Species Act of 1969, which essentially provided protection for species that may be in danger of "worldwide extinction." Importation of such animals or their parts, and subsequent sale in this country, both were prohibited, except for educational, medical, and related purposes, as was interstate commerce in protected species. The 1969 Act also broadened potential coverage to species of "wild mammal, fish, wild bird, amphibian, reptile, mollusk, or crustacean," thus including under the provisions for the first time noneconomically important lower vertebrates and two economically important groups of invertebrates. This act also called for an international meeting of ministers to deal with the problems relating to details and enforcement of laws to protect endangered and threatened wildlife species.

The international conference was held in Washington, D.C., early in 1973 and led to a signing by many countries of the Convention on International Trade in Endangered Species of Wildlife Fauna and Flora (CITES). It was the intent of this convention to restrict international commerce in plant and animal species believed to be endangered by economic exploitation.

Later that year, the Congress passed the Endangered Species Act of 1973, by far the most comprehensive of the three acts. Its principal new provisions were: 1) United States and foreign lists were combined and uniform provisions applied to species on the combined list; 2) categories of "endangered" and "threatened" were defined for the first time; 3) plants and all groups of invertebrates were made eligible for protection, as they were under the CITES provisions; 4) all federal agencies were required to undertake programs for conservation of threatened or endangered species, and were prohibited from actions that might jeopardize such a species or destroy or modify its habitat; 5) broad provisions against taking protected species were authorized, overriding the rights of the several states to set limits or otherwise circumvent the law; 6) cooperative agreements with states became possible using matching federal funds; and 7) additional authority to acquire land to protect affected species was authorized; and 8) implementation of provisions of the CITES treaty was approved.

The 1973 Act has remained more or less intact for the past 20 years, with important amendments in 1978, 1982, and 1988. In 1978 provisions were made to: 1) exempt some situations from the law when a cabinet-level committee convened for that purpose agreed; 2) designate critical habitat concurrent with listing of a species when prudent, taking into consideration economic and other impacts of designating habitat boundaries; and most importantly 3) allow for definition and designation of "populations" of species or vertebrates, as well as any species, subspecies, or variety of plant or invertebrate. Thus for vertebrates, a segment of a species or even of a subspecies—namely a "population"—could be designated as threatened or endangered.

In 1982, the determination of a species considered for listing was required to be based entirely on biological and trade information, and there was additional protection for plants found on federal lands and several provisions for procedures of consideration and listing. In 1988, provisions were added for monitoring the status and recovery of listed species, with periodic reports to the Congress, plus additional protection for plants.

The Endangered Species Act of 1973 expired in 1992. Reauthorization of it surely will engender serious discussions and past experience with application of provisions of the several acts certainly will be considered. The first big case was that of the snail darter, which held up completion of Tellico Dam, a Tennessee Valley Authority project, for almost a decade (until viable populations of the fish were found elsewhere). And we all remember surburban expansion and *Bufo houstonensis* (the Houston toad), more recently the controversy over the spotted owl and logging in forests of the Northwest, and most recently conflict concerning several species of salmon in the Columbia and Snake river drainages.

Before turning to Texas law, the Marine Mammal Protection Act of 1972 should be mentioned. Up to 1972, only eight species of whales threatened with extinction, plus the manatee, the monk seal, the sea otter, and the North Pacific fur seal were federally protected. The remaining marine mammals—all the whales, seals, and their allies—were either protected only by state law or not at all. The Marine Mammal Protection Act removed state authority over all marine mammals, substituting a comprehensive federal program. But provisions were included for the states to re-establish authority with federal assistance and under federal guidelines for operations of their approved management plan. Limited exceptions to protection were carved out for scientific research, public display in aquaria, sea gardens, and the like, and capture incidental to commercial fishing. All this applied to United States territorial waters only, but laid the groundwork for international accords to follow.

STATE LAWS

Why are state laws needed concerning endangered or threatened species? Aren't all species covered by federal law also listed by states in which they occur? The answer is affirmative in that species listed by the U.S. Fish and Wildlife Service (USFWS) are, *de facto*, also included by any state in which they are found. However, state lists allow inclusion of species that, although not endangered or threatened throughout a large part of their range encompassing several or many states or countries, may be rare or have a restricted distribution in one or more states—at the periphery of their overall distribution, for example. Thus, state authorities realistically may feel that protection is needed because of the small area or narrow habitat in which a species may be found there.

The first endangered species legislation in Texas was enacted in 1973, and subsequently has been amended several times. Chapter 68 of the Parks and Wildlife Code provides for the establishment of a list of fish or wildlife threatened with statewide extinction, sets up the procedure to allow the Executive Director of the Texas Parks and Wildlife Department (TPWD) to recommend designation of species for inclusion on the list following public notice, and authorizes procedures for the handling and propagation of endangered species. The statutory definition of fish and wildlife excluded most terrestrial invertebrates from designation as state endangered species.

Legislative authority for the designation of threatened animals is embodied in Chapter 67 of the Code pertaining to nongame species. This legislation authorizes the Parks and Wildlife Commission to adopt a list of protected nongame wildlife following public notice and to regulate the taking and possession of such wildlife. The statutory definition of nongame wildlife does permit the designation of invertebrates as threatened species; however, none has been listed to date.

Chapter 88 of the Code, adopted in 1981 and amended in 1985, set up the designations of endangered, threatened, and protected plants. The Executive Director is authorized to recommend designation of plants for inclusion on any of the lists following public notice, and also to prohibit commercial collection or sale of any listed plant without departmental permits.

Animals and plants are placed on Texas lists of endangered or threatened species by action of the Texas Parks and Wildlife Commission upon recommendation by the Executive Director. Proposed changes and additions must be published in the Texas Register prior to consideration by the Commission.

It should also be pointed out that there are several private organizations and groups that also rank animal or plant species, or both, as to their survival status. On a global scale, the International Union for the Conservation of Nature and Natural Resources (IUCN) ranks species. In Texas, the Texas Organization for Endangered Species (TOES) considers species of both plants and animals as endangered, threatened, or on their "watch list", the latter meaning surveillance from year to year. And the Nature Conservancy, Audubon Society, and others also contribute significantly to the effort of monitoring the well-being of native plants and animals. The real contribution of private organizations to protection of endangered or threatened species lies in the fact that, unencumbered by governmental bureaucracy, whether at the state or federal levels, they can react rapidly to call attention to a recently developed and serious situation, thus bringing public pressure on the various agencies. They also can acquire land through gift or purchase, which later may be turned over to a governmental agency, such as the Harte Ranch addition to Big Bend National Park.

Mammalian Species Extinct in Texas

Ten species of mammals that once occurred in Texas no longer are found there, except for three that were reintroduced, having been driven to extinction within the borders of the state directly or indirectly by humans.

Canis lupus (gray wolf).—Gray wolves once were common in western and central Texas, especially in association with the vast herds of bison that occurred there. This species is listed by USFWS as endangered throughout its distribution in North America except in Alaska and Canada, where reasonably good populations are extant in some areas. Small numbers prevail in the northern Great Lakes states.

The last wolves known to have been taken in Texas were two killed in December of 1970 in Brewster County (Davis, 1974). It is possible that a few individuals still cross over into the Trans-Pecos region from México, but the species is endangered there too. There have been some discussions of reintroducing *C. lupus* to Big Bend National Park, but any action on that proposal is years away and is likely to be strongly questioned by representatives of the livestock industry.

Canis rufus (red wolf).—This species once ranged throughout eastern Texas, northward into Arkansas and southern Oklahoma. None has been taken in Texas since the early 1960s (from Kenedy and Chambers counties—Davis, 1974), and the species is listed as endangered throughout its range in the southeastern United States. Genetic swamping by expanding coyote populations (with which this species is cross-fertile) probably was responsible for much of the decline of the red wolf in Texas.

Fortunately, captive breeding programs for this canine have been remarkably successful, and monitored reintroduction of individuals into the wild now is underway in the Carolinas and Mississippi. If these efforts prove to be successful, reintroduction in eastern and coastal Texas may be possible.

Ursus arctos (grizzly or brown bear).—This species probably occurred sparingly in western Texas from the Panhandle to the Trans-Pecos up until the days of early exploration of the region. However, only one specimen is on record from the state—a large male killed by hunters in October 1890 in the Davis Mountains of Jeff Davis County (Bailey, 1905). The grizzly is regarded as endangered throughout its former range in the conterminous United States and in México.

Mustela nigripes (black-footed ferret).—Closely associated with the vast colonies of black-tailed prairie dogs that once obtained over much of western and central Texas, this mustelid now is extinct in the state and apparently in the wild over its entire former range.

Ferrets were driven to extinction in Texas with the demise of prairie dogs, their principal food source. In one report, it is stated that the last specimen taken in the state was a young animal "3 to 6 weeks old" captured alive in May 1953 in Dallam County, in the extreme northwestern part of the Panhandle. This record, not substantiated by a specimen, seems implausible to me for several reasons; I suspect ferrets disappeared from Texas at least a decade or so earlier.

The last known wild ferrets occurred in Wyoming and died out several years ago from an outbreak of distemper. Fortunately, captive breeding by USFWS has been successful, and reintroductions in Wyoming are scheduled. TPWD is drawing up plans for potential reintroductions in Texas, the only problem being the availability of large enough prairie dog towns to support a breeding population of ferrets. Prairie dogs are widespread and common now, but in small and scattered colonies.

Monachus tropicalis (West Indian monk seal).—This seal rarely occurred in Texas waters, but once was common in the Gulf of Mexico to the south and east. It now may be totally extinct throughout its range.

Panthera onca (jaguar).—The distribution of the jaguar once extended northward well into central Texas, including much of the Edwards

Plateau, as well as all along the southern part of the state. There are many records and sightings that date from the late 1800s and early 1900s, and this large cat actually was regarded as common in some areas. The most recent documented record from the state was in the early 1950s (Tewes, 1990). This species is regarded as endangered throughout its relatively broad range in Central and South America.

Felis wiedii (margay).—The inclusion of this small cat in the fauna of the United States is based on a single specimen taken at (or near) Eagle Pass sometime prior to February 1852 (Goldman, 1943). It presently is known from tropical eastern and western México southward to Paraguay and northern Argentina. One of the smallest of American spotted cats, it is regarded as endangered throughout its range.

Cervus elaphus (wapiti or elk).—This well known species once ranged over parts of northern and western Texas, but there seem to be no actual specimens to document its modern occurrence there. In any event, it was hunted to extinction within the borders of the state before the turn of the last century. Fortunately, good populations remain in several western states. Wapiti were reintroduced into the Guadalupe Mountains National Park in 1928, and a herd that was estimated to number 150 in the late 1970s still occurs there and there also is a small herd in the Davis Mountains area. The reintroductions were not of the native subspecies (*Cervus elaphus merriami*), however, which evidently is extinct.

Bos bison (bison).—This magnificent creature, once numbering in the millions, was hunted to extinction in Texas. It once ranged over most of the state. The last verified report of wild bison was from the northwestern part of the Panhandle (Dallam County) in 1889 (Jones et al., 1988). Though no longer wild-ranging, herds prevail on many national and state sanctuaries in the West. In Texas, bison are kept in captivity on many farms and ranches.

Ovis canadensis (bighorn sheep).—The desert bighorn sheep, which once occurred in the Guadalupe Mountains, on many of the arid ranges in Trans-Pecos Texas, and probably eastward into the rugged lands that form the western edge of the Edwards Plateau proper, was last seen in the Sierra Diablo Mountains, in 1959, when the population was estimated at fourteen (Davis, 1974). After extinction, reintroductions in the Trans-Pecos area, not always of individuals representing the native subspecies, have been successful and bighorn sheep now occur in several mountainous areas in the Trans-Pecos.

In conclusion relative to species extinct in Texas, it should be underscored that of the 10, only the West Indian monk seal is thought to be extinct throughout its range, although the red wolf and black-footed ferret may be extinct in the wild (except for recent reintroductions), the two spotted cats are recognized as endangered, and bison are found only on reservations.

MAMMALIAN SPECIES ENDANGERED IN TEXAS

Six taxa of land mammals currently are considered as endangered in Texas. Four of these, *Leptonycteris nivalis, Felis pardalis, Felis yagouaroundi*, and *Trichechus manatus* appear on both state and federal lists, whereas the black bear (*Ursus americanus*) and the white-nosed coati or coatimundi (*Nasua narica*) are listed as endangered in Texas by TPWD (Table 1).

Leptonycteris nivalis (Mexican long-tongued bat).—This bat acquired its endangered status primarily because it is known in the United States only from the Texas Big Bend. A cave-dwelling species, it is to be looked for elsewhere in the southern Trans-Pecos as well.

Aside from a few records of foraging individuals, *L. nivalis* is known only from a cave on Emory Peak in the Chisos Mountians, where a maternity colony, along with some adult males, is present in spring and early summer, and from the Chinati Mountains in Presidio County (Schmidly, 1991). Several years ago, the Chisos colony was estimated by one investigator to contain 5000 to 6000 individuals, but more recent investigations suggest a lesser number. This is one of a group of Neotropical species that feeds on pollen and nectar of flowering plants, using a long, extensible tongue. It is an important pollenator of some species of agave and cactus.

Ursus americanus (black bear).—This bear once occurred throughout the state. The last native animals were taken in the woods and swamps of eastern Texas in the 1940s, but a stocking program in Louisiana has resulted in a few reports from along the border in recent years. As an aside, the population in Louisiana was pronounced as endangered in 1991 by USFWS even though part of it is descendent from 161 black bears transplanted there in the 1960s from Minnesota.

A small number of black bears, perhaps numbering as many as eight, now occur in Big Bend National Park, presumably from natural invasion from México in the past few years. It is hoped that a breeding population will become reestablished in the park.

Nasua narica (white-nosed coati).—The coatimundi is listed by TPWD as in the endangered category primarily because of its sporadic occurrence along the southern border of the state—from the lower Rio Grande Valley to the Trans-Pecos. It evidently has not been listed as endangered by USFWS because of the relatively good populations extant in southeastern Arizona. It is widespread in México and Middle America. The current status of this procyonid in Texas definitely is in need of serious study.

Felis pardalis (ocelot).—This beautiful spotted cat once ranged over much of southern, eastern, and central Texas, inhabiting dense brushy country. Currently, the population is estimated to be between 80 and 120

TABLE 1. List of endangered and threatened species of land mammals presently extant in Texas as ranked by the U.S. Fish and Wildlife Service and Texas Parks and Wildlife Department.

Species	*Endangered*		*Threatened*	
	USFWS	TPWD	USFWS	TPWD
Leptonycteris nivalis	X	X		
Lasiurus ega				X
Euderma maculatum				X
Plecotus rafinesquii				X
Dipodomys elator				X
Oryzomys couesi				X
Peromyscus truei (*comanche*)				X
Ursus americanus		X		
Nasua narica		X		
Felis pardalis	X	X		
Felis yagouaroundi	X	X		
Trichechus manatus	X	X		

individuals (Tewes, 1990), which are known to occur at a small number of fragmented sites in the lower Rio Grande Valley, especially on the Santa Ana National Wildlife Refuge. Destruction of the dense cover needed by this cat and its prey species has been the principal reason for its decline, and only habitat restoration will enhance its recovery. Its biology in the state presently is under intense study. The ocelot is considered endangered throughout its entire range.

Felis yagouaroundi (jaguarundi).—This cat is known in two color phases—brown and grayish-black. It was never as widely distributed in Texas as the ocelot, but shares the latter's prediliction for brushy country. According to Tewes (1990), the jaguarundi is the rarest of native cats currently extant in the state, being represented in the lower Rio Grande Valley by no more than 15 individuals. With numbers so low, it is doubtful it will survive in the state. Like the ocelot, the jaguarundi has a broad but threatened distribution in Neotropical America. All subspecies occurring from Panamá northward are listed by the USFWS as endangered. The last specimen taken in Texas was a road-killed individual found near Brownsville in 1986 (Tewes, 1990).

Trichechus manatus (manatee).—This is an aquatic mammal of coastal bays and estuaries. Probably the manatee never was especially common along the Texas coast, but reasonably good populations remain in Florida and at some places along the Caribbean Coast of Latin America. Despite this, the manatee is listed as endangered throughout its range by USFWS. The most recent Texas records are a sighting near Corpus Christi in 1979 and a dead animal stranded near the Louisiana border in February 1986 (Fernandez and Jones, 1990).

MAMMALIAN SPECIES THREATENED IN TEXAS

Six species of mammals, three bats and three rodents, are listed as threatened in the state by TPWD (Table 1), but none is thusly recognized on federal lists.

Lasiurus ega (southern yellow bat).—This bat is listed as threatened only because of its limited distribution in the southern part of the state. It is common around Brownsville and in other areas in the lower Rio Grande Valley, and is known northward to Corpus Christi (Schmidly, 1991). Tall palms are necessary roost sites, and this species would really be threatened only if such habitats were destroyed or in danger of destruction.

Euderma maculatum (spotted bat).—This beautiful bat has a wide distribution in western North America, but is not known to be common anywhere within its range. In Texas, it is known only from Big Bend National Park (Schmidly, 1991), but probably will be found elsewhere in the Trans-Pecos region. The restricted range in Texas accounts for the threatened status there. The USFWS has taken the position that much more knowledge is needed about the biology of this widespread western species, which is known from southern Canada to northern México, before listing should be considered.

Plecotus rafinesquii (Rafinesque's big-eared bat).—This bat, which occurs in mountainous and hilly country through the middle part of eastern North America, has a restricted distribution in eastern Texas (Schmidly, 1991), and thus is listed as threatened by TPWD.

Dipodomys elator (Texas kangaroo rat).—The Texas kangaroo rat is unique in that it is the only species of native mammal that is restricted in distribution to Texas. A beautiful kangaroo rat with a banner tail, the species occurs in a band just south of the Red River from Motley County in the west to Montague County in the east, but with substantial populations apparently only in Hardeman, Wichita, and Wilbarger counties. Its status is even more peculiar when it is realized that three specimens of *D. elator* have been reported from Oklahoma, one taken in 1904 and another in 1905 in Comanche County, and the third from Cottle County, just across the Red River from Texas, obtained in 1969. The provenance of the latter specimen is doubtful to me but, in any case, this rat evidently does not occur in Oklahoma at the present time.

Because of its restricted geographic range and because of habitat alteration from time to time for agricultural purposes within that range, this species is justly listed as threatened by TPWD. USFWS has taken a somewhat more cautious view of the status, all the while seeking additional information on *D. elator*. Several state- and federally-sponsored studies of the Texas kangaroo rat have been completed in recent years (see, for example, Jones et al., 1988). It appears that heavily grazed rangeland and the eroded sides of well-worn rangeland roadways may provide optimum habitat for this species—much as overgrazing and trampling by bison may have done in the past (Stangl et al., 1992).

Oryzomys couesi (Coues' rice rat).—This small rat is regarded as threatened in Texas by TPWD only because it is restricted in occurrence to the grasslands along the southern coast and adjacent inland areas in Cameron and Hidalgo counties. It is a common small mammal from México southward to Panamá, where it is in absolutely no danger. Whether it should be continued to be listed in Texas is problematic.

Peromyscus truei (piñon mouse).—TPWD has listed an endemic subspecies of this mouse, *Peromyscus truei comanche*, as threatened. This is sometimes referred to as the Palo Duro mouse because it occurs in Palo Duro Canyon State Park and adjacent areas, including Caprock Canyons State Park, in three Texas counties—Armstrong, Briscoe, and Randall (Jones and Jones, 1992). There it occupies high rocky ledges clothed with juniper along the break of the Llano Estacado. Taking into account the numerous side canyons, identations, and contours along the edge of the Llano caprock within its range, this mouse must have at least 100 miles of more-or-less continuous distribution. Whether it occurs beyond this area to the north or south remains to be determined, but it now is known that supposed records from as far south as Garza and Lynn counties represent misidentifications.

Actually, another subspecies of the piñon mouse, *Peromyscus truei truei*, also occurs in Texas, and is much rarer than *P. t. comanche*. It is known by only four specimens from Guadalupe Mountains National Park and five from along the northern edge of the Llano Estacado, just inside Texas from New Mexico in Deaf Smith County. To be consistent, all known populations in Texas should be regarded as threatened.

Although this mouse is not currently in direct danger from man's activities, it easily could fall victim to major climatic perturbations such as global warming. An upward shift of mean annual temperature of but a degree or two easily could put a competitor, *Peromyscus attwateri* of more southerly overall distribution in the region, at advantage. Elsewhere, the piñon mouse is widespread and common in piñon and yellow pine forests in western North America.

Whales, Dolphins, and Porpoises

Although cetaceans, for several reasons, have not been a main thrust of this manuscript it is noteworthy that there are 20 or so species that occur in Gulf waters near the Texas coast, more than half of which are listed either as threatened or endangered. All are covered under the Marine Mammal Protection Act. The sperm whale and all three baleen whales occurring in the region are recorded as endangered on both federal and state lists. Another seven small cetaceans are listed as threatened by TPWD. The status of many of these species is not accurately known. Current research by marine biologists at Texas A & M University at Galveston is designed to provide much-needed data about the biology and status of several species. There is, of course, some question as to how far off shore TPWD should be concerned about marine life—three miles or perhaps up to 12 miles, which are recognized continental limits, would seem appropriate.

Species Possibly Threatened or Endangered

There are several species of terrestrial mammals, or populations thereof, in Texas that may well warrant protection in the future. Certainly their situation bears watching; in some cases, considerable additional data are needed to establish the facts necessary to arrive at a meaningful and biologically defensible position as to their status. Several of these taxa are listed below by way of example.

There are two bats of the genus *Myotis—lucifugus* and *septentrionalis*—that are known from Texas each by a single specimen, the former from Ft. Hancock in Hudspeth County in the early 1900s and the latter from Winter Haven, Dimmit County, in 1942 (Schmidly, 1991). Probably these represent wanderers and neither species now is a part of the permanent Texas fauna. Similarly, the Mexican long-tongued bat (*Choeronycteris mexicana*) is known only from photographs of a single individual and observations of several others at Santa Ana National Wildlife Refuge in the lower Rio Grande Valley. Are these accidental occurrences or is there a tenuous, seasonal population of this pollen- and nectar-feeding species in southernmost Texas? Of certain accidental occurrence is the one specimen of a hairy-legged vampire bat (*Diphylla ecaudata*) found in a partially inundated railway tunnel in Val Verde County in 1967.

The large mastiff bat, *Eumops perotis*, has a restricted distribution along part of the southern border of the state and is recorded from few localities (Schmidly, 1991). It requires clefts in high, rocky cliffs as roosting sites. The pocketed free-tailed bat, *Nyctinomops femorosaccus*, requires similar habitats and has an even more restricted known range in Texas (southern Big Bend region). Another free-tailed species (*N. macrotis*), although widespread as a transient, is a rare resident of the southwestern part of the state.

Among the rodents, the muskrat subspecies *Ondatra zibethicus ripensis* of the Pecos River or the rock mouse, *Peromyscus nasutus*, which occupies only a few mountainous habitats in the southern and western Trans-Pecos, and which is poorly known ecologically, might be mentioned. One interesting case is that of the prairie vole, *Microtus* *ochrogaster*, known from but three localities in the state—from Hardin County in the southeast and Hansford and Lipscomb counties in the northern Panhandle. The single specimen from Hardin County was taken in 1902 and represents the relictual subspecies *M. o. ludovicianus*, now extinct. It once occurred also in adjacent western Louisiana.

The Panhandle specimens, nine in all, were collected in the late 1980s. They represent a totally different subspecies (*M. o. haydenii*) and are from along the southern border of the range of the species on the Great Plains. With only nine specimens known from but two localities in the Panhandle, it could be argued that this vole ought to be protected somehow, but much more information about where it does or does not occur is needed before any such action should be taken. A relatively large area of potentially suitable habitat still needs to be explored. This points up, once again, the fact that there still is much to learn about distributional patterns and biodiversity in otherwise rather well-studied groups of vertebrates.

Concern has been expressed from time to time about the swift and kit foxes, variously regarded as two species, *Vulpes velox* and *V. macrotis*, or as well-differentiated subspecies of a single species, the current view (Dragoo et al., 1990). These little foxes, which occur throughout much of the western part of Texas, were driven to near extinction by indiscriminate poisoning campaigns directed at wolves and later coyotes. With curtailment of this dastardly practice, the population of plains foxes has rebounded, and no longer are these animals threatened.

Another example involves the two species of spotted skunks in the state, *Spilogale gracilis* in the Trans-Pecos and adjacent regions and *S. putorius* in the east and north. Once relatively common, these two species now are rare in some areas and their current status in the state is unknown. This genus is in need of detailed study in Texas. Because these small skunks consume many insects, some believe populations (particularly those of *putorius*) were decimated by widespread use of chlorinated hydrocarbon insecticides, with the deadly effect passed (and concentrated) up the food chain.

Finally, no account of this kind would be complete without mention of the mountain lion (*Felis concolor*). This large cat occurs, at least sporadically, in many areas of Texas. For example, one was shot in Dallam County in 1985 (Jones et al., 1988) and a young adult male was taken in Irion County in 1987 (Engstrom and Maxwell, 1988). It is most often encountered, however, in the Trans-Pecos mountains and in the roughest parts of the southern Edwards Plateau and brushlands of the Rio Grande Plain.

Tewes (1990) estimated that the population of mountain lions in Texas numbered 300 to 500 animals. If this were not a large and feared predator, surely such low numbers would qualify *F. concolor* for special attention as threatened or endangered in the state.

CONCLUSIONS

Much remains to be learned about biodiversity in Texas, and both governmental and private organizations are urged to support the process of gathering much-needed baseline data about the natural history of plants and animals in the state. Obviously, decisions and actions concerning protection and conservation of animal and plant species will be much a part of our future. I urge all to become familiar with the issues so as to act as responsible citizens as an attempt is made to find the appropriate compromises between man's economic and social needs and the clear need to preserve our natural heritage.

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OBITUARY OF J KNOX JONES, JR.

March 16, 1929 - November 15, 1992

J Knox Jones, Jr., passed away in his home in Lubbock, Texas, on November 15, 1992, from complications from lung cancer. He was born in Lincoln, Nebraska, on March 16, 1929, the eldest of three sons of James Knox and Virginia Bowen Jones. After attending public schools in Lincoln, where he and his brother Hobart were state champions in track and field, he matriculated at the University of Nebraska, graduating in 1951 with a B.S. in Zoology (minors in geology and history), and then attended graduate school at the University of Kansas after some heavy recruiting by Dr. Rollin Baker, who first heard of Knox's trapping expertise in the 1940s. (In fact, family legend has it that Knox started his first vertebrate collection when he was two years old.) Like his old Nebraska buddy Robert L. Packard, Knox's early interest was in birds, but under the tutelage of Dr. Baker, Knox's attention later was focused on mammals. After taking the M.A. in zoology under the directorship of Dr. E. Raymond Hall in 1953 (the year in which he married Janet Glock of Rising City, Nebraska, with whom he had three daughters—Amy, Sarah, and Laura), he joined the U. S. Army as a Medical Officer and served in Korea and Japan, working on a classified project on hemorrhagic fever. This allowed him to gain extensive knowledge (for a westerner) of Asian mammals, the subject of many of his early publications. This service also included stints at the Walter Reed Military Hospital and the Smithsonian Institution.

After returning from active military duty, in 1956 he began doctoral work at KU, taking the degree in 1962 with a major in zoology and minor in paleontology. Recognizing a good thing when they saw it, KU persuaded him to stay on as assistant professor of zoology and curator of mammals at the Museum of Natural History. He rose to the rank of full professor in 1968. He also was appointed Associate Director of the Museum by 1967.

He served in these capacities until nominated by Robert L. Packard to fill the position of Graduate Dean at Texas Tech University, which he joined in 1971. Knox revamped graduate education at Texas Tech and introduced practices in the early 1970s, such as graduate faculty and program reviews, which now are common nationwide but were innovative at the time. He rose to Associate Vice President for Research and Graduate Dean after one year, and was appointed Vice President for Research and Graduate Studies in 1974, a position he filled until 1984, when he returned to fulltime teaching and research. He had numerous other responsibilities, including Acting Director of The Museum at Texas Tech in 1971-72, and oversaw the planning and construction of the

Natural Sciences Research Laboratory, which now holds over 65,000 specimens. One of his favorite stories involved his drawing the floor plan of the NSRL while at his desk in the KU Museum. He also began the museum series of publications—*The Occasional Papers of The Museum, Special Publications of The Museum,* and *Museology*—which are models for major museum publications nationwide.

Knox belonged to many professional organizations, but was most recognized for his work in the American Society of Mammalogists, which he joined while in high school and later served as president from 1972 to 1974. He received the three most prestigious honors of ASM: the C. Hart Merriam Award in 1977 for outstanding contributions to research and education in mammalogy, in 1983 the H. H. T. Jackson Award for outstanding service to the society, and in 1992, the position of Honorary Member in recognition of his career in mammalogy. He is the only person in the history of the society to be honored so.

Later honors included honorary membership in the Texas Society of Mammalogists (of which he was president in 1985), the 1992 Outstanding Scientist award from the Southwestern Association of Naturalists, and the Distinguished Texas Scientist award from the Texas Academy of Science in 1992. He won the Barney E. Rushing Award for outstanding researcher at Texas Tech in 1985 and was given the University's highest honor in 1986, when he was named Paul Whitfield Horn Professor of Biological Sciences and Museum Science.

He was a leader in graduate education in the South, and served as Chairman of the Dissertation and Copyright Committee of the Council of Graduate Schools from 1979 to 1984, as well as serving in other national organizations such as NASULGC, OTS, and AAAS.

Knox's research interests were varied and wide-ranging, as he studied mammals in Asia, Eastern Europe, Central America and the Caribbean, and throughout the central United States. In his later years, he concentrated on the evolution and biogeography of mammals in the Great Plains and the Southwest, and devoted many hours to the editorship of the *Texas Journal of Science*, which he guided to a position of national respect as a scientific publication.

During Knox's teaching career he directed 18 doctoral students and 15 masters students whose careers have reflected well on his training as they serve as museum directors, teachers and researchers at respected institutions; their own students are carrying on the Hall-Jones tradition.

Through November, 1992, Knox had authored and edited 360 publications, with several more still in press and a book forthcoming from LSU Press. He loved being in the field, but he loved even more writing up his findings, often quoting the old saying that "Research without publication is recreation." He was at his desk at home editing one of the forthcoming papers the day before he died. His total commitment to excellence in scientific publication and education informed every aspect of his life and touched the lives of everyone associated with him. After our marriage in 1989, much of our "free" time was spent working on the *Texas Journal of Science.* His impact on science in Texas was far-reaching and will be appreciated in years to come.

On a personal note, I can say that Knox lived life to the fullest and was passionate in his work and his personal relationships. He is greatly missed by his colleagues, his students, his friends, and especially his family, to whom he was devoted and loving father and husband. He has four grandchildren too young to remember much about him and two more expected in the summer of 1993, but he has left a wonderful legacy for them to discover later. All of our lives were enriched by knowing and loving Knox. There will never be anyone like him in Texas science again.

NOTE: Dr. Jones's library and reprints have been donated to the University of Kansas Museum of Natural History, where they will be combined with E. Raymond Hall's to form perhaps the pre-eminent private library in mammalian studies in the world. Knox's full bibliography will be printed with his obituary in *The Journal of Mammalogy.* Marijane R. Davis (Jones), The Graduate School, Texas Tech University, Box 41033, Lubbock, Texas 79409-1033.

PHYTOGEOGRAPHY OF THE WOODY FLORA OF THE LOWER RIO GRANDE VALLEY, TEXAS

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Abstract.—The lower Rio Grande Valley (LRGV) of Texas is delimited by distinct physiographic features and its fauna and flora include many species that do not occur elsewhere in the state. The LRGV native woody flora is comprised of 178 species. Sixty-six species (37.1 percent) reach their northern limit of distribution in southern Texas, and 46 of these species also occur in southern Florida. The LRGV woody flora has its greatest affinity (46.1 percent of the species) with the nondesert woody flora of México, but there is a strong representation (37.6 percent) of woody species from southwestern deserts. These two elements comprise 83.7 percent of the LRGV woody flora. There are no species endemic to the LRGV, but 14 species (7.9 percent of the LRGV woody flora) are endemic to the Tamaulipan Biotic Province. Colonization has mainly been from México and areas of humid tropical America (including the Caribbean), southwestern deserts (especially the Chihuahuan Desert), and the Coastal Plain of temperate North America. Dry fruits are the most common propagules. Birds and other animals are the dominant dispersal agents. *Key words*: phytogeography; Rio Grande Valley; woody plants.

The lower Rio Grande Valley (LRGV) is comprised by Cameron, Hidalgo, Starr, and Willacy counties of southernmost Texas (Fig. 1). The area is delimited by distinct physiographic features. These are the Rio Grande on the south, the Gulf of Mexico on the east, the Bordas Scarp (Clover, 1937) on the west, and eolian sand deposits on the north (Lonard et al., 1991). Dice (1943) included this region in the Tamaulipan Biotic Province (Fig. 2) and Blair (1950) emphasized the distinctiveness of the fauna and flora of the region by naming it the Matamoran Biotic District. Most of the LRGV occurs in the South Texas Plains vegetation area, but Padre Island and a narrow strip of the mainland are in the Gulf Prairies and Marshes vegetation area (Schuster and Hatch, 1990). Muller (1947) characterized the vegetation as Tamaulipan Thorn Shrubland and Tamaulipan Thorn Forest, and he rejected the designation of "chaparral" as applied by Clover (1937).

The flora and vegetation of the LRGV are relatively well known (Clover, 1937; Johnston, 1955, 1963; Vines, 1960; Correll and Johnston, 1970; Judd et al., 1977; Crosswhite, 1980; Lonard and Judd, 1981, 1985, 1991; Richardson, 1990; Vora, 1990; Vora and Messerly, 1990; McLendon, 1991; and Lonard et al., 1991). Lonard et al. (1991) reported that the native woody flora consists of 170 species in 55 families. Despite the data available on the species and communites of woody plants

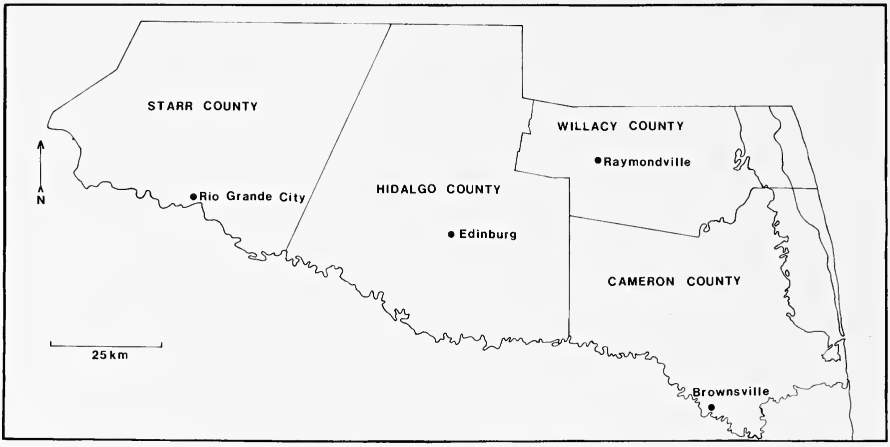

FIGURE 1. Map of lower Rio Grande Valley, Texas.

present, information on the geographic affinities of the woody flora of the LRGV is lacking. Thus, the purposes of this paper are to analyze the phytogeography of the woody plants of the LRGV and to identify the major dispersal agents. This information should facilitate a better understanding of the floristic relationships of the woody plants of the region and contribute to the phytogeographic knowledge of the Tamaulipan Biotic Province.

METHODS AND SOURCE MATERIAL

Descriptions of the area, its climate and soils are provided in Clover (1937), Blair (1950), Judd et al. (1977), Crosswhite (1980), Lonard and Judd (1981), McLendon (1991), and Lonard et al. (1991). The list of woody taxa used in this study was taken from Lonard et al. (1991) except for eight species that were added while their book was in press.

Much of the information on the distribution of the woody species found in the LRGV was obtained from Vines (1960), Correll and Johnston (1970), Stanford (1976), MacRoberts (1984), Mahler (1988), and Powell (1988). Lonard and Judd (1980) was consulted for the distribution of maritime species. Nomenclature follows Hatch et al. (1990).

RESULTS AND DISCUSSION

The native woody flora of the LRGV includes 178 species representing 55 families (Table 1). Nine families, Fabaceae (32), Asteraceae (16), Verbenaceae (11), Euphorbiaceae (10), Boraginaceae (seven), Chenopodiaceae (seven), Malvaceae (seven), Rutaceae (five), and Solanaceae (five) account for 56.1 percent of the woody species richness. Twenty-seven families each are represented by a single species. Forty-eight species (27.0 percent) are armed with spines, prickles, or thorns, which suggests co-evolution between the flora and the herbivorous vertebrate fauna (Janzen, 1986).

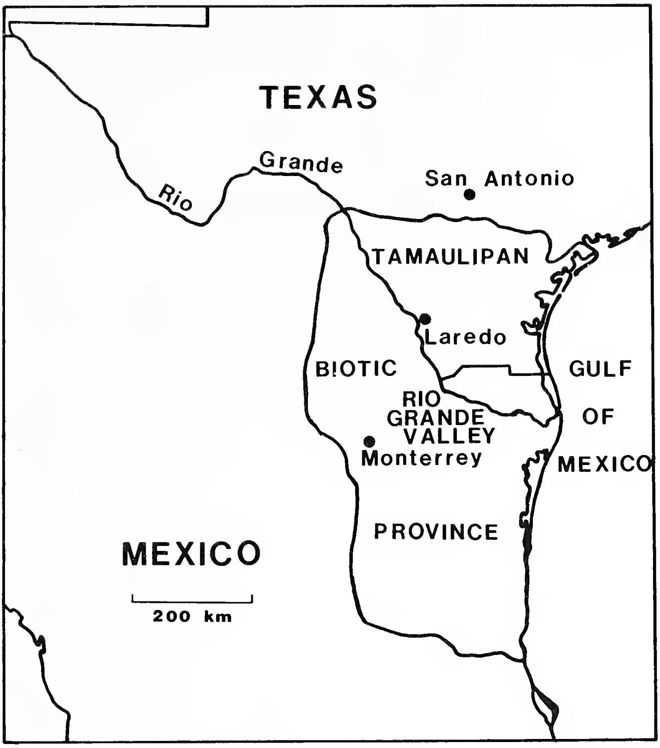

FIGURE 2. Relationship of lower Rio Grande Valley, Texas to the Tamaulipan Biotic Province.

Many tropical and subtropical plant species have been introduced intentionally or inadvertently by man into the LRGV. At least 18 woody species persist in formerly cultivated sites and have spread into disturbed areas (Table 2). Because, we are interested in the native woody flora, these species have not been included in the analyses of geographic affinities and dispersal agents.

Phytogeographic Affinities And Dispersal Agents

Table 3 includes a summary of the phytogeographic affinites of the native woody plants of the LRGV, and Table 4 provides a comparison of the fruit types and dispersal agents of these species among the geographic categories. Because dispersal of woody plant fruits are rarely directly observed, we identified the most probable mechanism(s) based on characteristics of the fruit. Multiple dispersal agents are likely for many species.

Subcosmopolitan.—Taxa that are neither exclusively temperate nor strictly tropical and that are represented on all continents are referred to

TABLE 1. List of native woody species of lower Rio Grande Valley, Texas. Phytogeographic affinity, fruit type, and probable dispersal agent(s) are given for each species, SCP=subcosmopolitan, TTM=tropical and temperate maritime, CES=widespread in central, eastern, southeastern United States and México, MEP=widespread in México, range terminates on Edwards Plateau of Texas, MST=widespread in México, range terminates in southern Texas (TTS is a subdivision of MST and indicates species endemic to the Tamaulipan Thorn Shrubland of México and Texas), SWD=southwestern deserts, B=birds, OA=other animals, WA=water, WI=wind; ach=achene, agg=aggregate, ant=anthocarp, ber=berry, cap=capsule, car=caryopsis, dru=drupe, foll=follicle, leg=legume, nds=naked dry seeds, ntl=nutlets, nut=nut, sam=samara, utr=utricle.

- Taxodiaceae
  - *Taxodium mucronatum* L. MST (nds; WA, B, OA)
- Ephedraceae
  - *Ephedra antisyphilitica* C. A. Meyer SWD (nds; OA, B)
  - *E. pedunculata* Engelm. *ex.* Wats. MEP (nds; OA, B)
- Poaceae (Gramineae)
  - *Phragmites australis* (Cav.) Trin. *ex.* Steud. SCP (car; WA)
- Arecaceae (Palmae)
  - *Sabal mexicana* Mart. MST (TTS) (dru; B, OA)
- Bromeliaceae
  - *Hechtia glomerata* Zucc. MST (TTS) (cap; OA)
- Liliaceae
  - *Smilax bona-nox* L. CES (dru; B)
  - *Yucca constricta* Buckl. SWD (cap; OA)
  - *Y. treculeana* Carr. MST (cap; OA)
- Amaryllidaceae
  - *Agave lopantha* Schiede MST (TTS) (cap; OA)
  - *A. americana* L. SWD (cap; OA)
  - *A. scabra* Salm-Dyck MST (TTS) (cap; OA)
- Salicaceae
  - *Salix exigua* Nutt. SWD (cap; WA, WI)
  - *S. nigra* CES (cap; WA, WI)
- Fagaceae
  - *Quercus virginiana* Mill. CES (nut; OA)
- Ulmaceae
  - *Celtis laevigata* Willd. CES (dru; B, OA)
  - *C. pallida* Torr. SWD (dru; B, OA)
  - *Ulmus crassifolia* Nutt. CES (sam; WI, WA)
- Visaceae
  - *Phoradendron tomentosum* (DC.) Gray CES (dru; B)
- Chenopodiaceae
  - *Atriplex acanthocarpa* (Torr.) S. Wats. SWD (utr; B, OA)
  - *A. canescens* (Pursh) Nutt. SWD (utr; B, OA)
  - *A. matamorensis* A. Nels. MST (TTS) (utr; WA)
  - *Salicornia virginica* L. TTM (utr; WA)
  - *Suaeda conferta* (Small) I. M. Johnst. MST (utr; WA)
  - *S. moquinii* (Torr.) Greene SWD (utr; WA)
  - *S. tampicensis* (Standl.) Standl. MST (utr; WA)
- Amaranthaceae
  - *Celosia nitida* Vahl MEP (utr; B, OA)
  - *Iresine palmeri* (S. Wats.) Standl. MST (TTS) (utr; B)

Table 1. Continued

- Nyctaginaceae
  - *Boerhavia scandens* L. SWD (ant; B)
  - *Pisonia aculeata* L. MST (ant; B)
- Batidaceae
  - *Batis maritima* L. TTM (ber; WA)
- Phytolaccaceae
  - *Petiveria alliacea* L. MST (ach; B, OA)
  - *Rivina humilis* L. CES (dru; B, OA)
- Achatocarpaceae
  - *Phaulothamnus spinescens* Gray MST (TTS) (dru; B, OA)
- Ranunculaceae
  - *Clematis drummondii* T. & G. SWD (ach; WI)
- Menispermaceae
  - *Cocculus diversifolius* DC. SWD (dru; B, OA)
- Capparidaceae
  - *Koeberlinia spinosa* Zucc. SWD (ber; B, OA)
- Rosaceae
  - *Prunus texana* Dietr. MEP (dru; OA)
  - *Rubus riograndis* Bailey CES (agg; B, OA)
- Fabaceae (Leguminosae)
  - *Acacia angustissima* (Mill.) O. Ktze. var. *hirta* (Nutt.) Robins. CES (leg; OA)
  - *A. berlandieri* Benth. SWD (leg; OA)
  - *A. constricta* Benth. SWD (leg; OA)
  - *A. greggii* Gray SWD (leg; OA)
  - *A. rigidula* Benth. SWD (leg; OA)
  - *A. roemeriana* Scheele SWD (leg; OA)
  - *A. schaffneri* (S. Wats.) Herm. var. *bravoensis* Isley MST (leg; OA)
  - *A. smallii* Isley CES (leg; OA)
  - *A. wrightii* Benth. *ex.* Gray SWD (leg; OA)
  - *Caesalpinia caudata* (Gray) Fisher MST (TTS) (leg; OA)
  - *C. mexicana* Gray MST (leg; OA)
  - *Calliandra conferta* Benth. in Gray SWD (leg; OA)
  - *Coursetia axillaris* Coult. & Rose MST (TTS) (leg; OA)
  - *Dalea scandens* (Miller) Clausen var. *paucifolia* (Coult.) Barneby MST (leg; B,OA)
  - *Erythrina herbacea* L. CES (leg; OA)
  - *Eysenhardtia texana* Scheele MEP (leg; B,OA)
  - *Leucaena pulverulenta* (Schl.) Benth. MST (leg; OA)
  - *Mimosa pigra* L. var. *berlandieri* (Gray) B. L. Turner MST (leg; B,OA)
  - *M. texana* (Gray) Small MST (leg; B, OA)
  - *Parkinsonia aculeata* L. CES (leg; B, OA)
  - *P. texana* (Gray) S. Wats. MEP (leg; B, OA)
  - *P. texana* (Gray) S. Wats. var. *macra* (I. M. Johnst.) Isely MST (TTS) (leg; B, OA)
  - *Pithecellobium flexicaule* (Benth.) Coult. MST (leg; B, OA)
  - *P. pallens* (Benth.) Standl. MST (leg; B, OA)
  - *Prosopis glandulosa* Torr. SWD (leg; B, OA)
  - *P. reptans* Benth. var. *cinerascens* (Gray) Burkhart TTM (leg; OA, WA)
  - *Senna bauhinioides* (Gray) Irwin & Barneby SWD (leg; OA)
  - *S. lindheimeriana* (Scheele) Irwin & Barneby SWD (leg; OA)
  - *Sesbania drummondii* (Rydb.) Cory CES (leg; WA)
  - *Sophora secundiflora* (Ort.) DC. SWD (leg; B)
  - *S. tomentosa* L. var. *occidentalis* (L.) Isely TTM (leg; WA)

TABLE 1. Continued

- Krameriaceae
  - *Krameria ramosissima* (Gray) S. Wats. SWD (ach; OA)
- Zygophyllaceae
  - *Guaiacum angustifolium* Engelm. SWD (cap; B, OA)
  - *Larrea tridentata* (DC.) Cov. SWD (cap; OA)
- Rutaceae
  - *Amyris madrensis* S. Wats. MST (dru; B, OA)
  - *A. texana* (Buckl.) P. Wils. MST (dru; B, OA)
  - *Helietta parvifolia* (Hemsl.) Benth. MST (sam; WI)
  - *Zanthoxylum fagara* (L.) Sarg. MST (foll; B, OA)
  - *Z. hirsutum* Buckl. CES (foll; B, OA)
- Simaroubaceae
  - *Castela texana* (T. & G.) Rose SWD (dru; B, OA)
- Malpighiaceae
  - *Malpighia glabra* L. MST (dru; B, OA)
- Euphorbiaceae
  - *Adelia vaseyi* (Coult.) Pax & Hoffm. MST (TTS) (cap; B, OA)
  - *Bernardia myricifolia* (Scheele) S. Wats. MEP (cap; B, OA)
  - *Croton ciliatoglandulosus* Ortega SWD (cap; B, OA)
  - *C. cortesianus* Kunth in H.B.K. MST
  - *C. fruticulosus* Torr. SWD (cap; B, OA)
  - *C. humilis* L. CES (cap; B, OA)
  - *C. incanus* Kunth in H.B.K. SWD (cap; B, OA)
  - *C. punctatus* Jacq. TTM (cap; B, OA)
  - *Euphorbia antisyphilitica* Zucc. SWD (cap; B, OA)
  - *Jatropha dioica* Cerv. MEP (cap; B, OA)
- Celastraceae
  - *Maytenus texana* Lundell MST (cap; B, OA, WA)
  - *Mortonia greggii* Gray MST (ach; B, OA)
  - *Schaefferia cuneifolia* Gray SWD (ber; B, OA)
- Sapindaceae
  - *Sapindus drummondii* Hook. & Arn. CES (dru; WA, B)
  - *Serjania brachycarpa* Gray MST (sam; B, OA)
  - *S. incisa* Torr. MEP (sam; B, OA)
  - *Urvillea ulmacea* Kunth in H.B.K. MST (sam; B, OA)
- Rhamnaceae
  - *Colubrina greggii* Gray MST (cap; B, OA)
  - *C. texensis* (T. & G.) Gray SWD (cap; B, OA)
  - *Condalia hookeri* M. C. Johnst. MEP (dru; B, OA)
  - *C. spathulata* Gray MEP (dru; B, OA)
  - *Karwinskia humboldtiana* (Schult.) Zucc. SWD (dru; B, OA)
  - *Ziziphus obtusifolia* (T. & G.) Gray SWD (dru; B, OA)
- Vitaceae
  - *Ampelopsis arborea* (L.) Koehne CES (ber; B, OA)
  - *Cissus incisa* (T. & G.) Des Moulins CES (ber; B, OA)
- Malvaceae
  - *Abutilon abutiloides* (Jacq.) Britt. & P. Wils. MST (cap; B, OA)
  - *A. hulseanum* (T. & G.) Chapm. MST (cap; B, OA)
  - *A. hypoleucum* Gray MEP (cap; B, OA)
  - *A. trisulcatum* (Jacq.) Urban MST (cap; B, OA)
  - *Allowissadula lozanii* (Rose) Bates MEP (cap; B, OA)

TABLE 1. Continued

  - *Hibiscus martianus* Zucc. SWD (cap; B,OA)
  - *Malvaviscus arboreus* Cav. var. *drummondii* (T. & G.) Schery. CES (ber; B, OA)
- Sterculiaceae
  - *Ayenia limitaris* Cristobal MST (cap; B, OA)
  - *Melochia pyramidata* L. SWD (cap; B, OA)
  - *M. tomentosa* L. MST (cap; B, OA)
  - *Waltheria indica* L. MST (ach; B, OA)
- Frankeniaceae
  - *Frankenia johnstonii* Correll MST (cap; B, OA)
- Flacourtiaceae
  - *Xylosma flexuosa* Kunth in H.B.K. MST (ber; B, OA)
- Turneraceae
  - *Turnera diffusa* Willd. *ex.* Schult. var. *aphrodisiaca* (Ward.) Urban SWD (cap; B, OA)
- Loasaceae
  - *Cevallia sinuata* Lag. SWD (ach; B, OA)
- Cactaceae
  - *Cereus pentagonus* (L.) Haw. MST (ber; B,OA)
  - *C. poselgeri* (Lem.) Coult. MST (ber; B, OA)
  - *Opuntia leptocaulis* DC. SWD (ber; B, OA)
  - *O. lindheimeri* Englelm. var. *lehmannii* L. Benson SWD (ber; B, OA)
- Lythraceae
  - *Heimia salicifolia* (Kunth in H.B.K.) Link MST (cap; B, OA)
- Plumbaginaceae
  - *Plumbago scandens* L. MST (cap; B, OA)
- Sapotaceae
  - *Bumelia celastrina* Kunth in H.B.K. MST (dru; B, OA)
- Ebenaceae
  - *Diospyros texana* Scheele MEP (ber; B, OA)
- Oleaceae
  - *Forestiera angustifolia* Torr. SWD (dru; B, OA)
  - *Fraxinus berlandieriana* DC. in A. DC. SWD (sam; WA, WI)
- Loganiaceae
  - *Buddleia sessiliflora* Kunth in H.B.K. SWD (cap; B, OA, WA)
- Apocynaceae
  - *Macrosiphonia macrosiphon* (Torr.) Heller SWD (foll; B, OA, WI)
- Boraginaceae
  - *Cordia boissieri* A. DC. MST (dru; B, OA)
  - *C. podocephala* Torr. MEP (dru; B, OA)
  - *Ehretia anacua* (Teran. & Berl.) I. M. Johnst. MEP (dru; B, OA)
  - *Heliotropium confertifolium* (Torr.) Gray SWD (ntl; B, OA)
  - *H. torreyi* I. M. Johnst. SWD (ntl; B, OA)
  - *Tiquilia canescens* (DC.) A. Richards. SWD (ntl; B, OA)
  - *Tournefortia volubilis* L. MST (dru; B, OA)
- Avicenniaceae
  - *Avicennia germinans* (L.) L. TTM (cap; WA)
- Verbenaceae
  - *Aloysia gratissima* Juss. SWD (dru; B, OA)
  - *A. macrostachya* (Torr.) Moldenke MST (dru; B, OA)
  - *Citharexylum berlandieri* Robins. MST (dru; B, OA)
  - *C. brachyanthum* (Gray) Gray MST (TTS) (dru; B, OA)
  - *C. spathulatum* Moldenke & Lundell MST (TTS) (dru; B, OA)

TABLE 1. Continued

Lantana frutilla Moldenke MST (dru; B, OA)
  L. horrida Kunth in H.B.K. SWD (dru; B, OA)
  L. macropoda Torr. MST (dru; B, OA)
  L. microcephala A. Rich. MST (dru; B, OA)
  Lippia alba (Mill.) N.E. Br. MST (dru; B, OA)
  L. graveolens Kunth in H.B.K. SWD (dru; B, OA)
Lamiaceae (Labiatae)
  Salvia ballotiflora Benth. SWD (ntl; B, OA)
Solanaceae
  Capsicum annuum L. var. *aviculare* D'Arcy & Esbaugh SWD (ber; B, OA)
  Lycium berlandieri Dunal. SWD (ber; B, OA)
  L. carolinianum Walt. var. *quadrifidum* (Dun.) C. L. Hitchc. TTM (ber; B, OA)
  Solanum erianthum D. Don MST (ber; B, OA)
  S. triquetrum Cav. SWD (ber; B, OA)
Scrophulariaceae
  Leucophyllum frutescens (Berl.) I. M. Johnst. SWD (cap; B, OA)
Acanthaceae
  Tetramerium platystegium Torr. MEP (cap; B, OA)
Rubiaceae
  Cephalanthus occidentalis L. SCP (cap; B, OA, WA)
  C. salicifolius Humb. & Bonpl. MST (cap; B, OA, WA)
  Chiococca alba (L.) Hitchc. MST (dru; B, OA)
  Randia rhagocarpa Standl. MST (dru; B, OA)
Asteraceae (Compositae)
  Aster spinosus Benth. SWD (ach; B, OA)
  Baccharis neglecta Britt. SWD (ach; B, WA, WI)
  B. salicifolia (R. & P.) Pers. SWD (ach; B, WA, WI)
  B. texana (T. & G.) Gray SWD (ach; B, WA, WI)
  Borrichia frutescens (L.) DC. TTM (ach; B, OA, WA)
  Clappia suaedifolia Gray SWD (ach; B, OA)
  Ericameria austrotexana M. C. Johnst. MST (TTS) (ach; B, OA, WI)
  Gochnatia hypoleuca (DC.) Gray MST (ach; B, OA, WI)
  Gymnosperma glutinosum (Spreng.) Less. SWD (ach; B, OA)
  Isocoma coronopifolia (Gray) Greene SWD (ach; B, OA, WI)
  I. drummondii (T. & G.) Greene MST (ach; B, OA)
  Trixis inula Cranz. MST (ach; B, OA, WI)
  Varilla texana Gray SWD (ach; B, OA)
  Viguiera stenoloba Blake SWD (ach; B, OA)
  Wedelia hispida H.B.K. SWD (ach; B, OA)
  Zexmenia brevifolia Gray SWD (ach; B, OA)

as subcosmopolitan (Thorne, 1972). Only two species, comprising 1.1 percent of the woody flora of the LRGV, have subcosmopolitan distributions (Tables 1 and 3). Thorne (1972) stated that the number of subcosmopolitan species is low and that only 125 genera worldwide exhibit this type of distribution.

Most subcosmopolitan species are aquatic and this holds true for both species occurring in the LRGV. *Phragmites australis* (common reed)

TABLE 2. Woody species introduced into the lower Rio Grande Valley of Texas by man. Some of these species have escaped cultivation and are spreading into disturbed sites.

Scientific name	Common name
Aloe barbadensis	Aloe vera
Arundo donax	Giant reed
Bougainvillea glabra	Bougainvillea
Ipomoea carnea ssp. fistulosa	Shrubby morning glory
Lantana camara	West Indian lantana
Leucaena leucocephala	Popinac
Melia azedarach	Chinaberry
Morus alba	White mulberry
Nerium oleander	Oleander
Nicotiana glauca	Tree tobacco
Phoenix canariensis	Ornamental date palm
P. dactylifera	Date palm
Ricinus communis	Castor bean
Sapium sebiferum	Chinese tallow
Tamarix aphylla	Athel tamarisk
T. gallica	Salt cedar
Washingtonia filifera	Washington palm
W. robusta	Washington palm

occurs along the Rio Grande, irrigation canals, resacas, and on barrier and spoil islands (Lonard et al., 1991). Its propagules are dispersed by water. *Cephalanthus occidentalis* (common buttonbush) is infrequent along drainage ditches and resaca banks near the Rio Grande (Lonard et al., 1991). Its fruits are carried by water and dispersed by waterfowl.

In addition to *Phragmites australis* and *Cephalanthus occidentalis*, four other LRGV woody species have widespread distributions in Texas. The

TABLE 3. Comparison of species distribution among phytogeographic groups of the woody flora of the lower Rio Grande Valley, Texas.

Phytogeographic affinity	Number of species	Percent of LRGV woody flora
Subcosmopolitan	2	1.1
Tropical and temperate maritime	8	4.5
Widespread in central, eastern, southeastern United States and México	19	10.7
Widespread in México; range terminates on Edwards Plateau of Texas	16	9.0
Widespread in México; range terminates in southern Texas	66	37.1
(endemic to Tamaulipan Thorn Shrublands)	(14)	(7.9)
Southwestern deserts	67	37.6.

TABLE 4. Comparison of fruit types and dispersal agents among phytogeographic categories of the woody flora of the lower Rio Grande Valley, Texas, (B=birds, OA=other animals, WA=water, WI=wind).

Fruit type	No. species	Percent flora	Dispersal agents
	Subcosmopolitan		
Dry fruits			
capsule	1	0.56	B, WA
caryopsis	1	0.56	WA
	Tropical and temperate maritime		
Dry fruits			
achene	1	0.56	B, WA
capsule	2	1.12	B, WA
legume	2	1.12	B, WA
utricle	1	0.56	WA
Fleshy fruits			
berry	2	1.12	B
	Widespread in central, eastern and southeastern United States and México		
Dry fruits			
capsule	2	1.12	B, OA, WA, WI
follicle	1	0.56	B
legume	5	2.81	B, OA, WA
nut	1	0.56	OA
samara	1	0.56	WA, WI
Fleshy fruits			
aggregate	1	0.56	B, OA
berry	3	1.68	B, OA
drupe	5	2.81	B, OA
	Widespread in México; range terminates on Edwards Plateau of Texas		
Dry fruits			
capsule	5	2.81	B, OA
legume	2	1.12	B, OA
samara	1	0.56	B, OA
utricle	1	0.56	B, OA
no fruit, dry seeds	1	0.56	B, OA
Fleshy fruits			
berry	1	0.56	B, OA
drupe	5	2.81	B, OA
	Widespread in México; range terminates in southern Texas		
Dry fruits			
achene	7	3.93	B, OA, WA, WI
anthocarp	1	0.56	B, OA
capsule	16	8.99	B, OA, WA
follicle	1	0.56	B, OA
legume	13	7.30	B, OA, WA
no fruit, dry seeds	1	0.56	B, WA
samara	3	1.68	B, OA, WI
utricle	3	1.68	B, OA, WA, WI

Table 4. Continued

Fleshy fruits			
berry	6	3.37	B, OA
drupe	16	8.99	B, OA, WA
	Southwestern deserts		
Dry fruits			
achene	13	7.30	B, OA, WA, WI
anthocarp	1	0.56	B, OA
capsule	16	8.99	B, OA, WA
follicle	1	0.56	WI
legume	11	6.18	B, OA
no fruit, dry seeds	1	0.56	B, OA
nutlets	4	2.25	B, OA
samara	1	0.56	WA, WI
utricle	2	1.12	B, OA, WA

two subcosmopolitan species and *Prosopis glandulosa* (honey mesquite), *Sapindus drummondi* (jaboncillo), *Cissus incisa* (ivy treebine), and *Solanum triquetrum* (Texas nightshade), occur in all vegetational zones of the state.

Tropical and temperate maritime.—Eight species (4.5 percent of the native woody flora) are widely distributed in tropical or temperate maritime zones (Tables 1 and 3). These species are derived from pantropical beaches, New World tropical coastlines, or temperate coastlines that include the Gulf of Mexico and amphi-Atlantic coasts (Lonard and Judd, 1980). Six species—*Avicennia germinans* (black mangrove), *Batis maritima* (maritime saltwort), *Borrichia frutescens* (sea ox-eye), *Croton punctatus* (beach croton), *Prosopis reptans* (dwarf screw bean), and *Sophora tomentosa* (yellow sophora)—have tropical affinites. Two species, *Lycium carolinianum* (Carolina wolfberry) and *Salicornia virginica* (woody glasswort), have temperate distributions.

Except for *Borrichia frutescens*, the ranges of these species do not extend inland. In the LRGV, *B. frutescens* occurs in saline sites adjacent to the Rio Grande inland to La Joya, Hidalgo County, approximately 160 kilometers from the Gulf coast. Most of the species are dispersed primarily by oceanic drift, and the propagules of some species are subsequently carried by birds. *Prosopis reptans*, for example, likely has this dispersal sequence.

Widespread in central, eastern and southeastern United States and México.—There are 19 species comprising 10.7 percent of the woody flora in this category (Tables 1 and 3). This temperate zone element presumably has been derived through spread from the continental United States into the LRGV and México. Species in this category include some of the characteristic trees, shrubs, and woody vines of the eastern North

American deciduous forest and particularly elements of the Coastal Plain forest, such as *Ampelopsis arborea* (pepper-vine), *Celtis laevigata* (Texas sugarberry), *Cissus incisa* (ivy treebine), *Erythrina herbacea* (coral bean), *Phoradendron tomentosum* (mistletoe), *Quercus virginiana* (live-oak), and *Ulmus crassifolia* (cedar elm) (Benson, 1979; MacRoberts, 1984).

Comparisons with other deciduous floras show that 28 of the LRGV woody species (15.7 percent) are common to the Eastern Deciduous Forest element identified by MacRoberts (1984) in the Louisiana flora. And, a similar number of species (23) are common to the woody flora of north-central Texas (Mahler, 1988). Most of these deciduous species lose their leaves during the dry winter season in the LRGV, whereas the majority of species with tropical affinities retain their leaves in winter. The deciduous species are usually present in mesic to aquatic sites in the LRGV and their propagules are represented almost equally by dry and fleshy fruits (Tables 1 and 4).

Widespread in México; range terminates on Edwards Plateau of Texas.—Sixteen species comprising 9.0 percent of the woody flora of the LRGV are widely distributed in tropical México and extend northward to the Edwards Plateau of Texas (Tables 1 and 3). All but *Cordia podocephala* are common in the LRGV.

There is a great deal of similarity in the woody floras of the LRGV and the Edwards Plateau. Indeed, 84 of the woody species from the LRGV (47.2 percent) occur in the flora of the Edwards Plateau identified by Stanford (1976). The similarity in woody species probably reflects similarity in precipitation patterns, amounts, and winter temperatures. However, because freezing temperatures usually occur each winter on the Edwards Plateau, the establishment of many species with tropical affinities is prevented. And, the absence of acid soils south of the Balcones fault-line likely inhibits the invasion of many temperate, mid-continental species into southern Texas and LRGV (Blair, 1950).

Widespread in México; range terminates in southern Texas.—Sixty-six species comprising 37.1 percent of the woody flora of the LRGV have tropical distributions in México, Central America, or the Caribbean and do not extend farther northward into the continental United States than southern Texas (Tables 1 and 3). Fourteen (7.9 percent of these species are endemic to the Tamaulipan Biotic Province delimited by Blair (1950) and the Tamaulipan Thorn Shrubland of Muller (1939). At least 36 species (20.2 percent) are shared with subtropical areas of Florida (counties adjacent to Lake Okeechobee and southward). Thirty-one species (17.4 percent) are shared with the Caribbean region, specifically the islands of Cuba, Hispaniola, Jamaica, Puerto Rico, and Bahamas.

Tropical and subtropical coasts of the Gulf of Mexico and Caribbean have been emergent since Pleistocene times. These coasts share summer precipitation peaks and dry winters. Colonization of the LRGV by species with tropical and Caribbean affinities has occurred during Pleistocene and Recent times. Birds have been the most common dispersal agents for these phytogeographic elements and 67.2 percent of the species have dry fruits as propagules (Tables 1 and 4).

Southwestern deserts.—Sixty-seven species representing 37.6 percent of the LRGV woody flora have affinities with Southwestern deserts (Tables 1 and 3) and primarily with Texas Chihuahuan Desert species (Powell, 1988). Similarity in temperatures and rainfall patterns are important factors contributing to the phytogeographic similarity of the woody floras of the LRGV and the wetter portions of the Chihuahuan Desert. Greater rainfall contributes to the greater density and luxuriance of shrubs and low trees in the LRGV. Common shrubs of the LRGV that are important elements of the Chihuahuan Desert are *Acacia berlandieri, A. greggii, A. roemeriana, Celtis pallida, Citharexylum brachyanthum, Condalia spathulata, Jatropha dioica,* and *Koeberlinia spinosa* (Muller, 1939, 1947; Powell, 1988).

The LRGV desert woody flora element includes an interesting group of North-South America disjunct taxa—for example, the genera *Castela, Condalia,* and *Guaiacum* and the species *Celtis pallida* and *Koeberlinia spinosa* (Rzedowski, 1973). *Koeberlinia spinosa* is widely distributed in the LRGV and northern México and has a disjunct range in a dry area of Bolivia (Johnston, 1940). Genera with closely related species pairs in North and South American deserts include *Prosopis, Ephedra, Acacia, Caesalpinia, Condalia,* and *Lycium.* Dry fruits comprise the propagules of 75.8 percent of the LRGV desert woody species (Tables 1 and 4). Achenes, capsules, legumes and other dry fruits are resistant to water loss. Birds and other animals are the probable dispersal agents for most species.

CONCLUSIONS

The LRGV woody flora most closely resembles the nondesert woody flora of México (46.1 percent of the LRGV woody species), but woody species from the southwestern deserts are strongly represented (37.6 percent of the species). Together, these elements make up 83.7 percent of the LRGV woody flora.

There are no species endemic to the LRGV, but 14 species (7.8 percent of the LRGV woody flora) are endemic to the Tamaulipan Biotic Province of México and Texas. Eighty-four of the LRGV woody species (47.2 percent) also occur on the Edwards Plateau of Texas. Temperate deciduous forest species comprise 10.6 percent of the LRGV woody flora.

Woody plant colonization of the LRGV has occurred during Pleistocene and Recent times and has come from three main sources: 1) humid, tropical America, including the Caribbean, 2) southwestern deserts, especially the Chihuahuan Desert, and 3) the temperate deciduous forest of the North American Coastal Plain. Dry fruits are the most common propagules. Birds and other animals are the most frequent dispersal agents.

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EFFECT OF CARBON SOURCES ON THE PRODUCTION OF EXTRACELLULAR CELL WALL DEGRADING ENZYMES BY *EXSEROHILUM ROSTRATUM*

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Abstract.—The extracellular cellulases of *Exserohilum rostratum* and the effect of different carbon sources on the production of these enzymes were investigated. Production of cellobiohydrolase, endoglucanase and xylanase was induced by all carbon sources tested. Maximum production of these enzymes was induced when carboxymethyl cellulose (CMC) was used as carbon source and enzyme inducer. Results of this study suggest that *E. rostratum* produces constitutively small amounts of these cell wall degrading enzymes. *Key words: Exserohilum*, enzymes, cellulases.

Direct penetration of susceptible hosts by the infective hyphae of phytopathogenic fungi is facilitated by the production of cutinases (Agrios, 1988), followed by softening or disintegration of host tissues by cell wall degrading enzymes produced by the pathogen (Kenaga, 1974; Agrios, 1988). Production of these enzymes is induced in many plant pathogenic fungi when these organisms are grown on media containing various sugar polymers (Cooper and Wood, 1973; Pegg, 1981; Ortega, 1990).

Exserohilum rostratum (Dreschler) Leonard & Suggs (Leonard and Suggs, 1974), attacks many gramineous species of plants, including some hosts of economic importance. *E. rostratum* causes foliage blight of sugar cane seedlings (Byther and Steiner, 1972), leaf disease of corn (Cook, 1981), stalk rot of corn (Kucharek, 1973; Nyvall, 1989) and leaf blight of sorghum (Sprague, 1950). These crops are intensively cultivated in the lower Rio Grande Valley of southern Texas.

The main objectives of this work were to determine the components of extracellular cell wall degrading enzymes of *E. rostratum* and to determine the effects of the carbon source on the production of these enzymes by the test fungus.

Materials and Methods

Organism and Culture Conditions

Stock cultures of *E. rostratum* were maintained on PDA slants (Difco, B13). The fungus was previously grown in 250-milliliter flasks with 125 milliliters of a medium containing: 0.02 percent $MgSO_4.7H_2O$, 0.01 percent Ca $(NO_3)_2.4H_2O$, 0.1 percent Peptone, 0.2 percent yeast extract, 2.0 percent glucose in Na-citrate buffer at pH 4.8. After four days growth at 26°C, five milliliters of mycelium inoculum was washed twice in distilled water and used to inoculate the cellulolytic growth medium. The medium for the production of cellulases contained: 0.15 percent NH_4NO_3, 0.24 percent K_2PO_4, 0.08 percent $MgSO_4$, 0.08 percent Ca $(NO_3)_2.4H_2O$, 0.72 ppm Fe $(NO_3)_3.9H_2O$, 0.44 ppm $ZnSO_4.7H_2O$, 2.0 ppm $MnSO_4.4H_2O$, 0.40 ppm $ZnCl_2$, 0.1 percent Peptone, 0.1 percent yeast extract, 1.0 percent carbohydrate. The carbohydrates used as carbon sources and cellulase inducers were: sodium carboxymethyl cellulose (CMC, Aqualon Company, type 7HF), microcrystalline cellulose (Sigma Chemical Company, type 50), and xylan (Aldrich Chemical Company). The control cultures had glucose as the sole carbon source. The pH of the growing medium was adjusted to 4.8 with citric acid. Incubation of the cultures was carried out for seven days in covered 250-milliliters flasks on an orbital shaker at 100 rpm and 26°C.

Enzyme Preparation and Assays

Culture fluids were collected after seven days of growth by centrifugation (4500 rpm, 30 minutes, 10°C). The supernatant was subsequently used for the determination of extracellular enzyme activity. For simplification, the collected supernatant is hereafter referred to as the enzyme. All tests were replicated four times.

Cellobiohydrolase (1,4-B-D-glucan cellobiohydrolase, EC 3.2.1.91). Cellobiohydrolase activity was measured by combining in separate test tubes one milliliter of enzyme with 20 milligrams of microcrystalline cellulose in one milliliter of 0.05 M sodium citrate buffer (pH 4.8) and incubating the reaction mixture for two hours at 50°C. The tubes were stirred several times during incubation. After centrifugation, the concentration of reducing sugar in the supernatant was determined by the dinitrosalicylic acid method of Miller (1959).

Endoglucanase (CM-cellulase, carboxymethyl cellulase, EC 3.2.1.4). Endoglucanase activity was measured by combining one milliliter of enzyme with one milliliter of 0.8 percent carboxymethyl cellulose in 0.05 M sodium citrate buffer, pH 4.8. The reaction mixture was incubated at 50°C for 30 minutes. The concentration of reducing sugar in the reaction mixture was determined by the dinitrosalicylic acid method of Miller (1959).

Xylanase (EC 3.2.1.32). Xylanase activity was measured by combining 10 milligrams of xylan in one milliliter of 0.05 M sodium citrate buffer, pH 4.8, with one milliliter of enzyme. The reaction mixture was incubated at 50°C for 30 minutes. After centrifugation, the concentration of reducing sugars in the supernatant fluid were determined by the dinitrosalicylic acid method of Miller (1959).

Protein Determination

Extracellular protein in the crude supernatants was determined with the BCA reagent (Pierce Chemical Company) using bovine serum albumin as standard.

Data Analysis

All enzyme activity tests and protein determinations were replicated four times. The results were expressed as units of specific enzyme activity and represent means plus or minus the standard deviation of four replications. One unit of specific activity (U) will liberate 1.0 microgram of glucose or its reducing sugar equivalent per minute per milliliter of enzyme per milligram of extracellular protein at pH 4.8 at 50°C. Statistical analyses of experimental data were made with Student's *t*-tests.

Results and Discussion

Cellobiohydrolase

Production of cellobiohydrolase was induced in all cultures. Maximum cellobiohydrolase activity (9.85 U) was measured in fluids from cultures with CMC as carbon source and enzyme inducer (Table 1). This activity was significantly higher ($p \leq 0.001$) than the activities of the enzyme measured in fluids from cultures with microcrystalline cellulose, xylan or glucose as the carbon sources. Cellobiohydrolase activities measured in

TABLE 1. Effect of different carbon sources on the specific activities[1] of extracellular cell wall degrading enzymes produced by *Exserohilum rostratum*.

	Enzymes			
Carbon source	Cellobio-hydrolase	Endoglucanse	Xylanase	Extracellular protein[2]
Microcrystalline cellulose	5.10±0.10	20.81±1.12	9.82±0.10	0.209±0.002
CMC	9.85±0.71*	34.91±1.68*	39.80±3.59*	0.268±0.009
Xylan	4.71±0.21	22.23±1.93	13.80±1.80	0.483±0.005*
Glucose	2.38±0.16	14.58±0.55	8.97±0.08	0.444±0.002

[1] ug of glucose or its reducing sugar equivalent/min/ml/mg of protein. Mean ± SD of four replications.

[2] mg/ml.

* Using Student's *t*-test, significantly ($p \leq 0.001$) different from control (glucose).

fluids from cultures with microcrystalline cellulose, xylan or glucose as carbon sources were 52.0, 47.9 and 23.4 percent, respectively, of the activity measured in fluids from cultures with CMC (Table 1). The activities of this enzyme measured in the fluids from cultures containing microcrystalline cellulose or xylan (5.10 U and 4.71 U, respectively) were significantly higher ($p \leq 0.001$) than the activities measured in fluids from cultures containing glucose (2.38 U, Table 1). The difference (0.39 U) between the cellobiohydrolase activity measured in fluids from cultures containing microcrystalline cellulose and the activity determined in fluids from cultures with xylan source was not statistically significant (Table 1). The lowest cellobiohydrolase activity was recorded in fluids with glucose as carbon source (Table 1). Apparently, *E. rostratum* produces small amounts of cellobiohydrolase in a constitutive manner. It was found before (Ortega, 1990), that production of this enzyme is induced in cultures of *Fusarium oxysporum* f. sp. *lycopersici* with CMC as carbon source.

Endoglucanase

Maximum endoglucanase activity (34.91 U) was measured in the culture fluids of *E. rostratum* when the fungus was grown in media containing CMC as carbon source and enzyme inducer (Table 1). This activity was significantly higher ($p \leq 0.001$) than the activities measured in fluids containing microcrystalline cellulose, xylan or glucose, respectively. Endoglucanase activities measured in fluids from cultures with microcrystalline cellulose, xylan or glucose were 59.6, 63.6 and 41.7 percent, respectively, of the activity measured in fluids from cultures with CMC (Table 1). Endoglucanase activities measured in the fluids from cultures containing microcrystalline cellulose or xylan (21.81 U and 22.23 U, respectively) were significantly higher ($p \leq 0.001$) than the activities measured in fluids from cultures containing glucose (14.58 U, Table 1). The difference (1.42 U) between the endoglucanase activity measured in fluids from cultures containing microcrystalline cellulose and the activity determined in fluids from cultures with xylan source was not statistically significant (Table 1). The lowest endoglucanase activity (14.58 U) was measured in cultures that had glucose (Table 1). Probably, the endoglucanase recorded in the control medium is a component of the complex of cellulolytic enzymes that is produced constitutively. It was found before (Ortega, 1990) that *Fusarium oxysporum* f. sp. *lycopersici* cultivated under similar conditions, produced constitutively a small amount (0.45 IU) of endoglucanase. Cooper and Wood (1973) have shown that *F. oxysporum* f. sp. *lycopersici* and *Verticillium albo-atrum* grown with the proper enzyme inducers produce endoglucanase, galactosidase and polygalacturonase.

Xylanase

Production of xylanase by the test fungus was induced in all cultures (Table 1). Maximum production of this enzyme (39.80 U) was found in the cultures that had CMC as the carbon source and enzyme inducer. This activity was significantly higher ($p \leq 0.001$) than the activities measured in fluids from cultures containing microcrystalline cellulose, xylan or glucose, respectively. Xylanase activities measured in fluids from cultures with microcrystalline cellulose, xylan or glucose were 24.6, 34.6 and 22.5 percent, respectively, of the activity measured in fluids from cultures with CMC (Table 1). The activity of this enzyme measured in fluids from cultures containing xylan (13.80 U) was higher ($p \leq 0.01$) than the activities measured in fluids from cultures containing microcrystalline cellulose or glucose (9.82 U and 8.97 U, respectively, Table 1). The difference (0.85 U) between the xylanase activity measured in fluids from cultures containing microcrystalline cellulose and the activity determined in fluids from cultures with glucose was not statistically significant (Table 1). The lowest xylanase activity (8.97 U) was measured in cultures that had glucose (Table 1). Probably, the xylanase recorded in the control medium is a component of the complex of cellulolytic enzymes that is produced constitutively. It has been shown (Robson et al., 1989) that *Rhizoctonia solani*, another phytopathogenic fungus, produces xylanase in a constitutive manner. It was found before (Ortega, 1990) that CMC induces the production of xylanase by *Fusarium oxysporum* f. sp. *lycopersici*. Cooper and Wood (1973) used D-xylose to induce the production of xylanase in cultures of *F. oxysporum* f. sp. *lycopersici* and *V. albo-atrum*.

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DESCRIPTION OF A NEW SPECIES OF *EIMERIA* (APICOMPLEXA: EIMERIIDAE) FROM *HELODERMA SUSPECTUM* (SAURIA: HELODERMATIDAE)

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Abstract.—A new species of coccidian, *Eimeria becki*, is described from the feces of 3/3 Gila monsters, *Heloderma suspectum* (Helodermatidae), housed at the Dallas Zoo. Oocysts of this new eimerian are cylindroid, 31.0 × 18.4 (29.6-33.4 × 17.6-19.2) μm; shape index (length/width) 1.69 (1.62-1.82). Micropyle and oocyst residuum absent, single polar granule present. Sporocysts are ellipsoid to cylindroid, 11.9 × 7.7 (10.4-12.8 × 7.2-8.2) μm; shape index 1.55 (1.33-1.73). Sporozoites each with spheroid, rarely ellipsoid, posterior refractile body. This represents the first coccidian to be described from a member of the family Helodermatidae. *Key words: Heloderma suspectum*; Helodermatidae; Gila monster; coccidia; *Eimeria*; Dallas Zoo.

The Gila monster, *Heloderma suspectum* Cope, 1869 is a large, heavy bodied venomous lizard that ranges from extreme southwestern Utah to northern Sinaloa, México (Stebbins, 1985). It inhabits shrubby, grassy, and succulent desert, arroyos, canyon bottoms, and occasionally oak woodland. The Gila monster feeds on small mammals, eggs of ground-nesting birds and reptiles, lizards, insects, and carrion (Beck, 1990). Although considerable information is available on helminth parasites of the Gila monster (Smith, 1910; Hannum, 1941; Ryerson, 1949; Stabler and Schmittner, 1958; Chabaud and Frank, 1961a, 1961b; Mahrt, 1979; Griner, 1983; Goldberg and Bursey, 1990, 1991), nothing has been published on coccidia from this lizard. Below we present a description of a new species of coccidian from captive Gila monsters at the Dallas Zoo.

Materials and Methods

Fecal samples were collected between July and August, 1992 from three captive female *H. suspectum* (310-350 mm snout-vent length) housed at the Dallas Zoo. The lizards had been originally confiscated by the U.S. Fish and Wildlife Service in May 1982 and 1986. Although the exact origin from which the lizards were illegally collected is not known, it is believed that they probably came from Arizona. Samples were placed in 2.5 percent (w/v) aqueous potassium dichromate solution and, following a brief microscopic examination of portions of the samples, shipped to Kansas State University. Oocysts in feces were concentrated by flotation in an aqueous sucrose solution (sp. gr. 1.30), and examined and photographed using Nomarski interference-contrast microscopy.

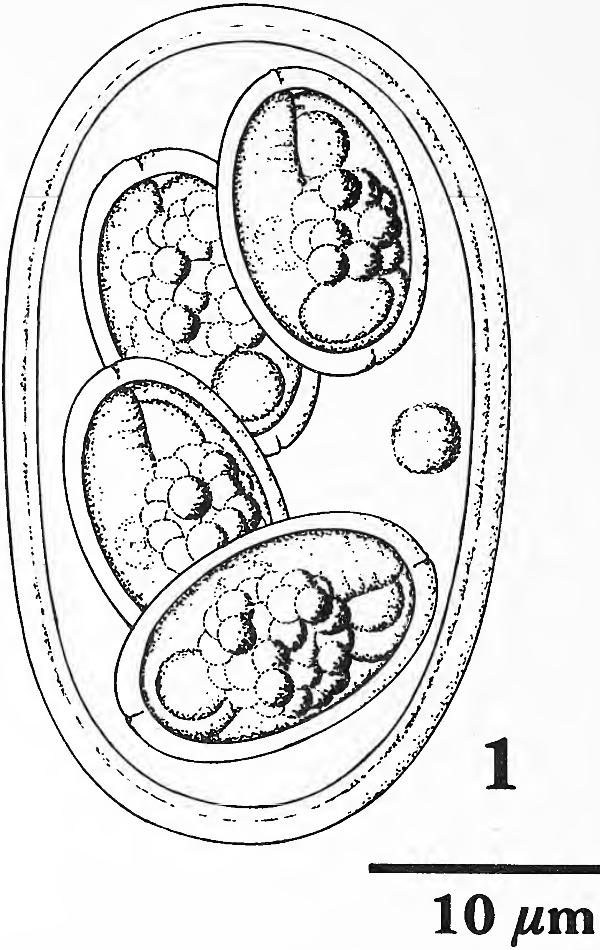
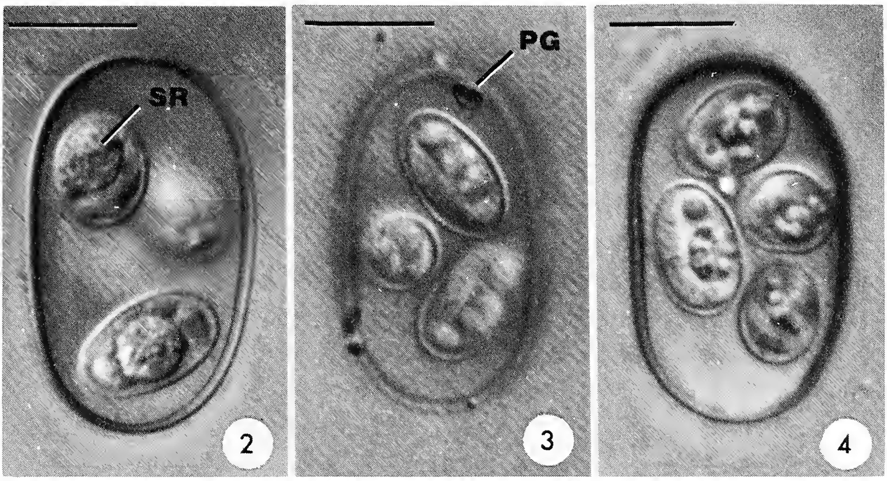


Figure 1. Composite line drawing of oocyst of *Eimeria becki*, new species.

Measurements were made in micrometers (μm) using a calibrated ocular micrometer and are reported as means, followed by the ranges in parenthesis.

Eimeria becki, new species (Figs. 1-4)
(Apicomplexa: Eimeriidae)

Oocysts cylindroid, 31.0 × 18.4 (29.6-33.4 × 17.6-19.2) (N=25), with a smooth, bilayered wall ca 1.4 thick; shape index (length/width) 1.69 (1.62-1.82). Micropyle and oocyst residuum absent; single polar granule present. Sporocysts ellipsoid to cylindroid, 11.9 × 7.7 (10.4-12.8 × 7.2-8.2) (N = 18), with smooth, single-layered wall ca 0.5 thick and



FIGURES 2-4. Nomarski interference-contrast photomicrographs of sporulated oocysts of *Eimeria becki* new species. Scale bars = 10 μm. Abbreviations: PG, polar granule; SR, sporocyst residuum.

composed of two valves joined by suture; Stieda and substieda bodies absent; shape index 1.55 (1.33-1.73). Sporocyst residuum present, composed of numerous coarse granules in spheroid mass, 4.7 (4.0-5.8) (N = 12). Sporozoites elongate, 13.8 × 2.6 (12.8-16.0 × 2.2-2.8) (N = 12), laying parallel to the length of the sporocyst and in opposite directions to one another. Anterior refractile body absent; posterior refractile body present, spheroid (rarely subspherical), 2.3 (2.0-2.6) (N = 12). Nucleus lies anterior to refractile body.

Type host.—*Heloderma suspectum suspectum* Cope, 1869, "reticulate Gila monster" (Sauria: Helodermatidae); adult female, #865G07, 350 mm snout-vent length, acquired May, 1986, currently alive and housed at the Dallas Zoo.

Other hosts.—Two additional female Gila monsters at the Zoo were also found to be passing oocysts of this new species.

Type locality.—Unknown. The infected animal was confiscated in May, 1986 by the U.S. Fish and Wildlife Service. The exact origin of the lizard remains unknown.

Site of infection.—Unknown. Oocysts recovered from feces. Oocyst shape suggests that this species may infect the biliary epithelium.

Sporulation.—Exogenous. All oocysts were passed fully sporulated.

Etymology.—The specific epithet is given in honor of Dr. Daniel David Beck, Albuquerque, New Mexico, in recognition of his numerous contributions to the ecology of helodermatid lizards.

Remarks.—This represents the first report of a coccidian from any member of the family Helodermatidae. Oocysts of this new species are morphologically distinguishable from other eimerians described from lizards, and only a handful of species appear similar. Oocysts of *Eimeria turcicus* Upton, McAllister, and Freed, 1988 are larger and the sporocysts stouter (Upton et al., 1988). Oocysts of *E. gehyrae* Cannon, 1967 are more robust than the form we report here and have stouter sporocysts (Cannon, 1967). Oocysts of *E. rochalimai* Carini and Pinto, 1926, *E. flavidiridis* Setna and Bana, 1935, and *E. sexlineatus* McAllister, Upton, and Trauth, 1991 are smaller and, again, have stouter sporocysts (Cannon, 1967; McAllister et al., 1991; Setna, 1933; Setna and Bana, 1935; Upton et al., 1992). The most similar species, *E. beccari* Upton and Freed, 1990, was reported from *Varanus prasinus beccari* from the Aru Islands. Oocysts of this species are slightly larger and are often attenuated at one end, which we never observed for the new form presented here (Upton and Freed, 1990).

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ON THE ROOTS OF LINEAR TRANSFORMATIONS

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ABSTRACT.—Let $A = UD$ be the polar decomposition of the linear transformation A on a unitary space of dimension n. One may conjecture that, if we get the p-th root of U and the non-negative p-th root of D, then a p-th root of A can be obtained. We shall partially solve the conjecture. *Key words*: Polar decomposition.

DEFINITIONS AND NOTATION

We shall use standard notations of linear algebra. An n-dimensional unitary space over the field of complex numbers will be denoted by E_n and over the field of real numbers will be denoted by R_n. Linear transformations will be denoted by capital letters. Let $\mathscr{B}$ be a basis in E_n. The matrix of a linear transformation A on E_n with respect to $\mathscr{B}$ is denoted by $[A]_B$. When there is no confusion, we only write $[A]$. In what follows, the *standard basis* of E_n refers to an orthonormal basis $\{\epsilon_1, \ldots, \epsilon_n\}$, where ϵ_j is $(\delta_{1j}, \ldots, \delta_{ij}, \ldots, \delta_{nj})$, and δ_{ij} is the Kronecker δ, i. e., $\delta_{ij} = 1$ if $i = j$, and $\delta_{ij} = 0$ if $i \neq j$. We denote scalars by Latin letters $a, b, c, \ldots$ and vectors by Greek letters $\alpha, \beta, \gamma, \ldots$. The *adjoint* A^* of a linear transformation A on E_n is defined by $(A\xi, \eta) = (\xi, A^* \eta)$. It is well known that the matrix of A^* is the conjugate transpose of the matrix of A, whenever the same orthonormal basis is considered. A linear transformation U is called *unitary or an isometry* if $(U\xi, U\eta) = (\xi, \eta)$ for all $\xi, \eta \epsilon E_n$. A Hermitian transformation A is called *positive* if $(A\xi, \xi) > 0$ for all $\xi \neq 0$, and A is *non-negative* if $(A\xi, \xi) \geqq 0$ (Amir-Moéz, 1990; MacDuffee, 1933).

ROOTS OF AN ISOMETRY

Let U be an isometry on E_n. Then there exists an orthonormal basis with respect to which the matrix of U is

$$[U] = \begin{pmatrix} e^{\theta_1} & 0 & \cdots & 0 \\ 0 & e^{\theta_2} & & \vdots \\ \vdots & & & 0 \\ 0 & \cdots & & e^{\theta_n} \end{pmatrix}.$$

Clearly, for each e^{θ_k}, $k = 1, 2, \ldots, n$, we can obtain p different p-th roots, and therefore we get p^n isometries, call one of them V, such that V^p

$= U$. As a result, the solution V is not unique. Since the proper spaces of V and U are identical, all the p-th roots of U may be obtained in this way. If the matrix of V with respect to the orthonormal basis is $[V]$, then $[V]^p = [U]$.

THE NON-NEGATIVE p-th ROOT OF A NON-NEGATIVE TRANSFORMATION

Let A be a non-negative linear transformation on E_n. It is well known that the proper values of A are real and non-negative.

Let $a_1, a_2, \ldots, a_n$ be the proper values of A. There exists an orthonormal basis $\mathscr{B}$ in E_n such that the matrix of A with respect to $\mathscr{B}$ is

$$[A] = \begin{pmatrix} a_1 & 0 & \ldots & 0 \\ 0 & a_2 & & \vdots \\ \vdots & & \ddots & 0 \\ 0 & \ldots & 0 & a_n \end{pmatrix}.$$

We can find the unique real non-negative p-th root b_k of each a_k. Let

$$[B] = \begin{pmatrix} b_1 & 0 & \ldots & 0 \\ 0 & b_2 & & \vdots \\ \vdots & & \ddots & 0 \\ 0 & \ldots & 0 & b_n \end{pmatrix}.$$

Then $[B]$ is non-negative and $[B]^p = [A]$. Thus $[B]$ is the matrix of the linear transformation B with respect to $\mathscr{B}$, and clearly $B^p = A$. Since each b_k is unique, B is the unique non-negative p-th root of A.

ROOTS OF NORMAL TRANSFORMATION

Let A be a normal transformation of rank m on E (i.e., $A^*A = AA^*$). Let $A = DU$ be the polar decomposition of A, where U is an isometry and $D = \sqrt{A^*A}$ is non-negative.

Since A is normal, there exists an orthonormal basis with respect to which the matrix of A is of the form

$$[A] = \begin{pmatrix} a_1 e^{\theta_1} & & & \dots\ 0 \\ 0 & & & \\ \vdots & \ddots & & \vdots \\ 0 & a_m e^{\theta_m} & & 0 \\ & & 0 & \\ \vdots & & \ddots & \vdots \\ 0 & \dots & & 0 \end{pmatrix}$$

$$= \begin{pmatrix} a_1 & \dots & 0 \\ 0 & & \\ \vdots & \ddots & \vdots \\ 0 & a_m & 0 \\ \vdots & 0 & \vdots \\ 0 & \dots & 0 \end{pmatrix} \cdot \begin{pmatrix} e^{\theta_1} & & \dots\ 0 \\ 0 & & \\ \vdots & \ddots & \vdots \\ 0 & e^{\theta_m} & 0 \\ \vdots & \ddots & 0 \\ 0 & \dots & 1 \end{pmatrix} = [D]\,[U].$$

Notice that $[D]$ and $[U]$ form a polar decomposition of $[A]$. We have filled out the diagonal of U to make it an isometry.

Using the methods described in previous sections, we find a p-th root of the isometry U, call it V, and the non-negative p-th root of D, call it C. Note V is an isometry and C is non-negative. It is easily shown that $[V]\,[C] = [C]\,[V] = [B]$, where $[B]^p = [A]$. Notice the ones inserted along the diagonal of $[U]$ do not affect $[B]$ therefore, we obtain only p^m roots of A.

Example: Let

$$[A]_{\mathscr{B}} = \frac{1}{2} \begin{pmatrix} 1 + 4i & -1 + 4i \\ -1 + 4i & 1 + 4i \end{pmatrix}$$

be the matrix of a normal transformation on E_2 with respect to the standard basis $\mathscr{B}$ in E_2. The characteristic equation of A is

$$m^2 - (1 + 4i)m + 4i = 0.$$

Thus the proper values of A are 1 and $4i$, and we choose corresponding proper vectors $(1/\sqrt{2}, 1/\sqrt{2})$ and $(-1/\sqrt{2}, 1/\sqrt{2})$, respectively. Let $\mathscr{A} = \{(1/\sqrt{2}, 1/\sqrt{2}), (-1/\sqrt{2}, 1/\sqrt{2})\}$ be a basis in E_2. The matrix

$$V = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 & -1 \\ 1 & 1 \end{pmatrix}$$

changes basis $\mathscr{A}$ to $\mathscr{B}$. Then $V^*[A]_{\mathscr{B}}V = [A]_{\mathscr{A}}$ will be a diagonal form; i.e.,

$$\frac{1}{\sqrt{2}} \begin{pmatrix} 1 & 1 \\ -1 & 1 \end{pmatrix} \cdot \frac{1}{2} \begin{pmatrix} 1+4i & -1+4i \\ -1+4i & 1+4i \end{pmatrix} \frac{1}{\sqrt{2}} \begin{pmatrix} 1 & -1 \\ 1 & 1 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 4i \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & i \end{pmatrix} \cdot \begin{pmatrix} 1 & 0 \\ 0 & 4 \end{pmatrix}.$$

The matrix of a square root of A with respect to $\mathscr{B}$ is

$$\begin{pmatrix} 1 & 0 \\ 0 & \frac{1+i}{\sqrt{2}} \end{pmatrix} \begin{pmatrix} 1 & 0 \\ 0 & 2 \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & 2\frac{(1+i)}{\sqrt{2}} \end{pmatrix}.$$

We shall leave the change to the basis $\mathscr{A}$ to the reader.

In general, if A can be diagonalized, one can obtain a linear transformation B such that $B^{\mathrm{P}} = A$. But one can not use the polar decomposition of A and A^{P}.

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MIDDLE ALBIAN AMMONITES FROM EL MADERO, WEST-CENTRAL CHIHUAHUA

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ABSTRACT.—A small ammonite fauna is herein reported from Cerro Madero, west-central Chihuahua. It includes species of the genera *Beudanticeras* Hitzel, *Desmoceras* Zittel, *Lyelliceras* Spath, and *Tegoceras* Hyatt. The latter genus has not been reported previously from North America, and the other three genera only rarely. The fauna is from a Cretaceous inlier in the eastern edge of the volcanics of the Sierra Madre Occidental, is Middle Albian, and emphasizes that the many inliers of Cretaceous rocks along the eastern edge of the Sierra Madre Occidental should be examined much more closely. *Key words:* ammonites; Cretaceous; west-central Chihuahua, México.

Approximately 25 years ago, I traded some rudists to Geological Enterprises of Ardmore, Oklahoma, for a small collection of Albian ammonites. The ammonites were obtained from a collector in Ciudad Juárez, who claimed they came from Cerro Madero, about 75 miles northwest of Ciudad Chihuahua. El Madero (a village) is about 2.5 kilometers northwest of Mesa del Huracan (another village) at the end of an abandoned railroad near El Gato. El Madero is at 29° 41′ N, 108° 16.5′ W; it does not appear in the gazetteer of Hendrickson and Straw (1976), but neither do the villages of Madera and Nueva Madera of the Madera 1/250,000 sheet (Dirección General de Geografía del Territorio Nacional, 1982). El Madero is approximately 80 kilometers west-northwest of Ciudad Chihuahua, straight line (Fig. 1). This agrees reasonably with the estimate of distance by the collector. Cerro Madero is a small mountain near the village of El Madero.

Although Cretaceous rocks are shown to crop out farther west according to the geologic map of the Madera sheet (Dirección General de Geografía del Territorio Nacional, 1982), such rocks are not shown to crop out in this area. However, Peter Megaw and David Wark informed me that there are indeed Cretaceous shales beneath the volcanics of the Sierra Madre Occidental at El Madero.

When dealing with purchased collections one must always be careful. I at first doubted the authenticity of the locality of this collection. However, more detailed study revealed that the collection contains South American, perhaps Arizonan, and European affinities. Therefore, I have concluded that the Chihuahua locality is reasonable, and that more attention should be paid to the many inliers of Cretaceous rocks that occur along the eastern, northern, and western margins, of the volcanic terrain of the Sierra Madre Occidental.

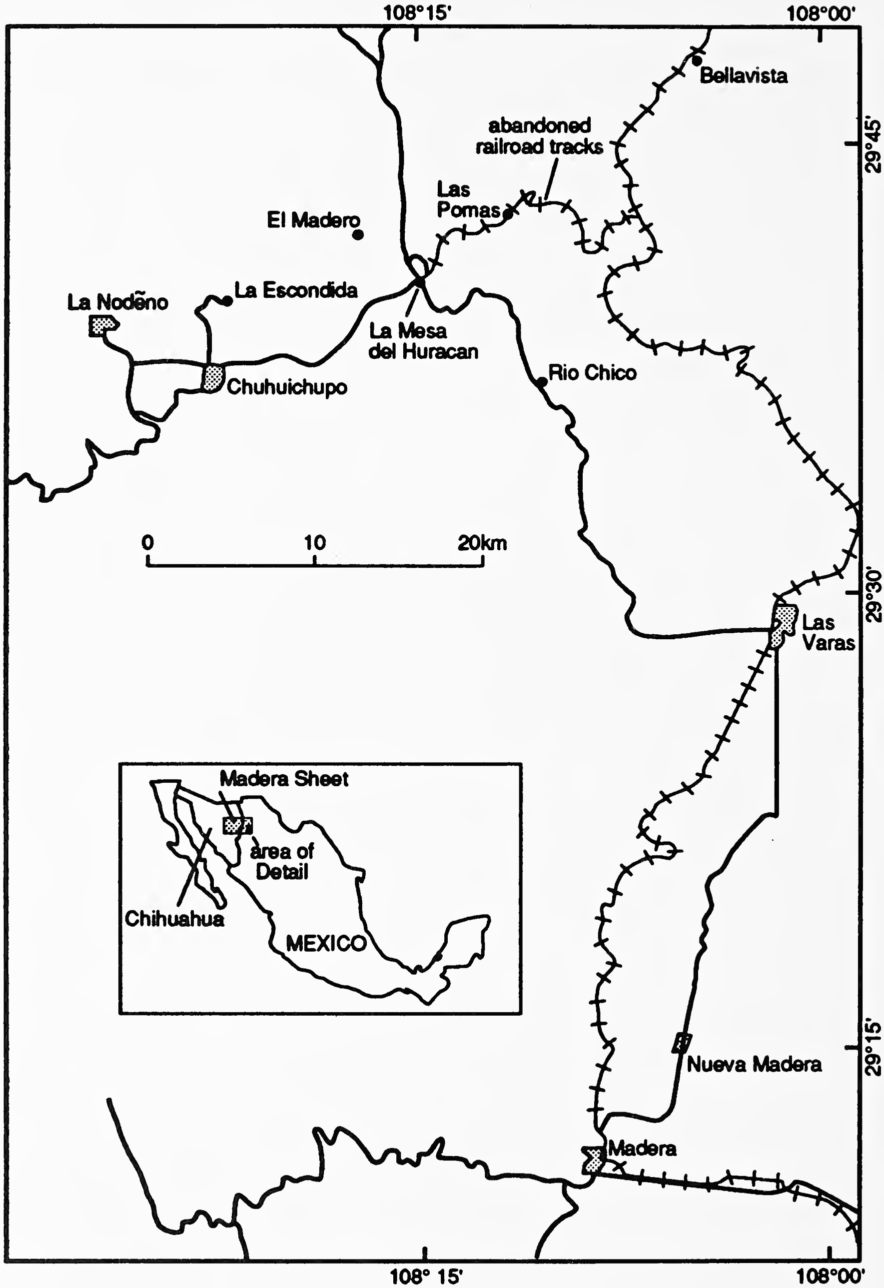


FIGURE 1. Location of El Madero in the eastern half of the Madera Sheet, Chihuahua, México. From Dirección General de Geografía del Territorio Nacional, 1982.

TAXONOMY

Measurements are in millimeters, with percentages of D in parentheses. D is diameter of conch, U is width of umbilicus, H is whorl-height, and W is whorl-width. H/W is a ratio.

Order AMMONOIDEA
Suborder AMMONITINA Hyatt, 1889
Superfamily DESMOCERATACEAE Zittel, 1895
Family DESMOCERATIDAE Zittel, 1895
Subfamily BEUDANTICERATINAE Breistroffer, 1953

Genus *Beudanticeras Hitzel, 1902*

Type species.—Ammonites beudanti Brongniart, 1822.

Beudanticeras cf. *hatchetense* Scott, 1940

Figs. 2:4-6, 14, 15; 3:5, 7.

Material.—One specimen, UT-8294, from Middle Albian shale at Cerro Madero, Chihuahua.

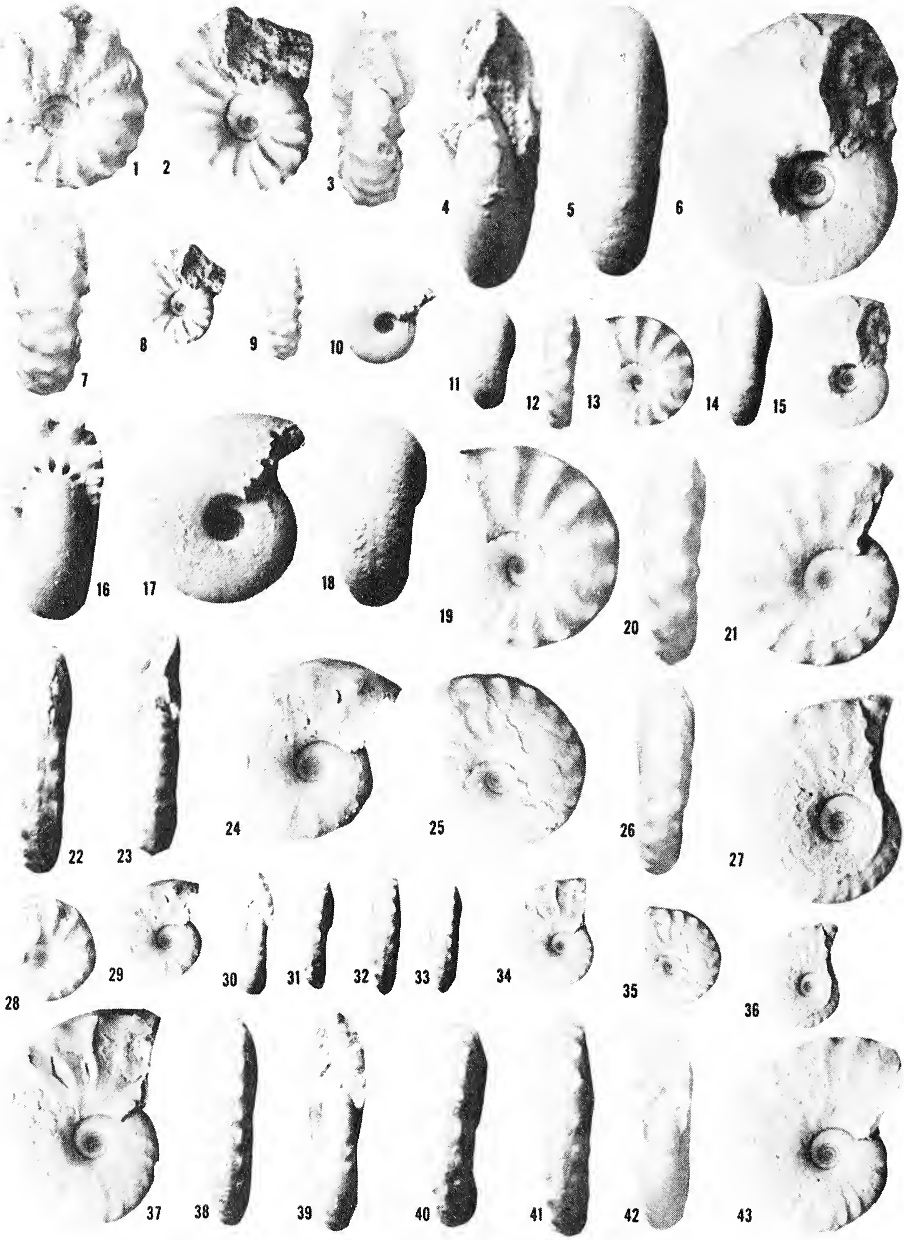
Remarks.—UT-8294 is a high-whorled ammonite with about 12 shallow, sigmoid constrictions per whorl at a diameter of 20 mm. Constrictions extend from the umbilical wall across the venter and are not as strong as on some species of *Beudanticeras.* There are faint, incomplete ribs intercalated between constrictions; most of the ribs do not extend onto the venter nor to the umbilicus. The whorl-section is oval with flanks tapering only slightly ventrad. The umbilical wall is vertical, and the conch is near involute, each whorl overlapping nearly all of the preceding whorl. The specimen is septate throughout.

Measurements.—D, 20.8 (100); U, 4.8 (23.0); H, 9.2 (44.2); W, 7.1 (34.1); H/W, 1.30.

Comparisons.—Most species of *Beudanticeras*, like *B. beudanti* (Brongniart) are higher-whorled than is UT-8294. Exceptions include some interpretations of *Beudanticeras dupinianum* (d'Orbigny) (see Spath, 1923, text figs. 4a-d), *B. besairiei* Breistroffer in Besairie (1936:pl. 15, figs. 17-18), *B. convergens* (Jacob, 1907: pl. 2, figs. 24-26), *B. victoris* Stoyanow (1949:pl. 18, figs. 18-21), *B. arduennense* Breistroffer (Casey, 1961:pl. 27, figs. 9-11), and *B. hatchetense* Scott (1940:pl. 56, figs. 3-5).

Beudanticeras dupinianum (d'Orbigny) is usually, but not always, more strongly ornamented than UT-8294, and as illustrated by Avram et al. (1988:pl. 5, figs. 1a-b), Föllmi (1989:pl. 9, figs. 13a-b), and Casey (1961:pl. 26, fig. 11) the constrictions are more strongly projected on the venter, and the umbilicus is more open. *B. besairiei* Breistroffer has ribs extending across the venter during at least part of the ontogeny.

B. convergens (Jacob) has the narrow umbilicus of UT-8294, and has a similar conformation, but constrictions and ornament do not show, at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least on his illustrations (1907: pl. 2, figs. 24-26). *B. victoris* Stoyanow has a slightly more open umbilicus than UT-8294, but the ornamentation is similar. *B. arduennense* Breistroffer seems to be slightly higher-whorled, but otherwise comparable. Although the form illustrated by Avram et al. (1990:pl. 4, fig. 7), as *B.* cf. *arduennense*, has a comparable whorl-section to UT-8294, it has much deeper constriction than UT-8294, and it lacks umbilical nodes. *B.* cf. *laevigatum* (Sowerby) in Avram et al. (1990:pl. 4, figs. 5-6), is higher-whorled than UT-8294. *B. hatchetense* Scott also may be a little higher-whorled, but ornamentation and umbilicus are comparable.

Scott (1940) thought that *B. hatchetense* was from the *Douvilleiceras* zone. According to Föllmi (1989), *B. arduennense* is Middle Albian. *B. victoris* Stoyanow is from the *nolani* zone, and *B. convergens* (Jacob) is Aptian, both too old to occur with *Lyelliceras.*

Subfamily DESMOCERATINAE Zittel, 1895

Genus *Desmoceras* Zittel, 1884

Type species.—Ammonites latidorsatus Michelin, 1838, subsequently designated by Boule et al. (1906).

Synonymy.—See Arkell et al. 1957.

Desmoceras cf. *latidorsatum* (Michelin, 1838)

Figs. 2:10-11, 16-18; 3:1.

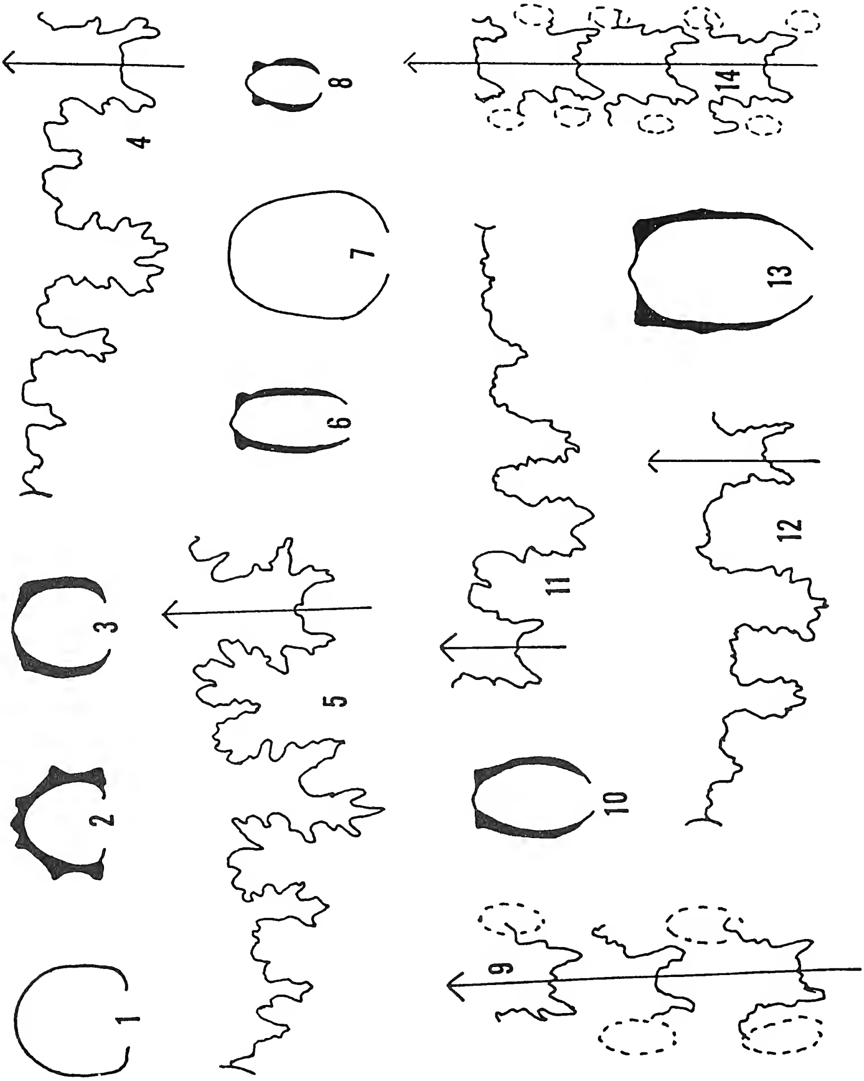
Material.—One specimen, UT-8292, from Middle Albian shale at Cerro Madero, Chihuahua.

Remarks.—UT-8292 is a specimen about 15.2 mm in maximum diameter. It is septate throughout. The conch is regularly expanding, nearly involute with a moderately narrow umbilicus. The whorl-section is almost circular and the height-width ratio is slightly less than 1.0. There is no ornamentation on the pyritized internal mold. A suture was not recovered.

Measurements.—D, 14.1 (100); U, 3.1 (22.0); H, 6.2 (43.9); W, 7.1 (50.4); H/W, 0.87.

⟵

FIGURE 2. *1-3, 7-9.—Lyelliceras* aff. *carvajalorum* Etayo-Serna, 1979. UT-8290; *1-3, 7* X 1.8; *8, 9,* X 0.9. *4-6, 14, 15.—Beudanticeras* cf. *hatchetense* Scott, 1940. UT-8294; *4-6,* X 1.8; *14, 15,* X 0.9. *10, 11, 16-18.—Desmoceras* cf. *latidorsatum* (Michelin, 1838). UT-8292; *10, 11,* X 0.9; *16-18,* X 1.8. *12, 13, 19-21.—Tegoceras* sp. no. 1. UT-8296; *12, 13,* X 0.9; *19-21,* X 1.8. *24, 28, 29.—Tegoceras* n. sp. aff. *gladiator* (Bayle, 1878). UT-8293; *24,* X 1.8; *28, 29,* X 0.9. *22, 23, 25-27, 30-43.—Tegoceras maderoense,* n. sp. UT-8295; *22.* UT-8295-A; *23, 34, 37, 41.* UT-8295-C, the holotype; *25, 26, 31, 35, 40, 42, 43.* UT-8295-E; *27, 36.* UT-8295-B; *30, 32, 33, 38, 39. 22, 23, 25-27, 37-43,* X 1.8; *30-36,* X 0.9.
All specimens are Middle Albian and are from an unnamed shale formation near the village of El Madero, central-western Chihuahua.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Comparisons.—Desmoceras latidorsatum (Michelin, 1838) var. *media* Wiedmann and Dieni (1968:pl. 12, figs. 8a-b) has a slightly more rapidly expanding conch than does UT-8292, and there are faint ribs on the flank that do not appear to cross the venter. It is Upper Albian. UT-8292 is intermediate between the two dimorphs illustrated by Jacob (1907:pl. 4, figs. 10-13), and the forms illustrated by Boule et al. (1906:pl. 2, figs. 4, 4a-b, 5) appear to be similar to Jacob's less obese dimorph, which has an height-width ratio of about 1.0. Spath's (1923:pl. 2, figs. 2a-b) specimen from an unknown Folkstone level is much more like UT-8292, with no observable ornament and a height-width ratio of less than 1.0. *D. latidorsatum* (Michelin) in Marek et al. (1989:pl. 44, figs. 2a-b) is similar to UT-8292, except the umbilicus may be narrower. Stoliczka's (1865:pl. 59, figs. 14a-b) has a more squarish whorl-section, whereas the specimen of his figures 13a-b has the greatest width much more dorsad than is that of UT-8292. Kossmat's (1898:pl. 19, figs. 6a-c, 7a-b) and Crick's (1907:pl. 14, figs. 2, 2a, 3, 3a) specimens also have the greatest width much more dorsad. *D. latidorsatum* (Michelin) *complanata* Jacob in Avram et al. (1990:pl. 4, fig. 2) is not as fully rounded on the flanks as UT-8292, and is older. Anderson's (1938: figs. 3, 3a) illustrations of Stoliczka's species are more involute than either Stoliczka's specimen or UT-8292. Spath (1923:42) cited *D. latidorsatum* (Michelin) as ranging from Lower Albian into the Cenomanian.

Family Lyelliceratidae Spath, 1921

Genus *Lyelliceras* Spath, 1921

Type species.—Ammonites lyelli Leymerie in d'Orbigny, 1841

Lyelliceras aff. *carvajalorum* Etayo-Serna, 1979

Figs. 2: 1-3, 7-9, 3: 2.

Material.—One specimen, UT-8290, from the Middle Albian of Cerro Madero, Chihuahua.

←

Figure 3. *1.—Desmoceras* cf. *latidorsatum* (Michelin, 1838). UT-8292; whorl-section X 2.9 at D = 14.1 mm. *2.—Lyelliceras* aff. *carvajalorum* Etayo-Serna, 1979. UT-8290; whorl section X 1.95 at D = 11.0 mm. *3, 4.—Tegoceras* n. sp. aff. *gladiator* (Bayle, 1878), UT-8293; *3*, whorl-section X 1.75 at D = 14.8 mm; *4*, suture, X 4.75 at D = 17.5 mm. *5, 7.—Beudanticeras* cf. *hatchetense* Scott, 1940, UT-8294; *5*, whorl-section X 2.25 at D = 20.8 mm; *7*, suture X 5.0 at D = 17.5 mm. *6, 8-11.—Tegoceras maderoense*, n. sp., *6, 11*, UT-8295-C, the holotype, *6*, whorl-section X 2.25 at D = 17.0 mm, and *11*, suture X 5.9 at D = 13.8 mm; *8, 9*. UT-8295-A, *8*, whorl-section X 1.95 at D = 15.0 mm, and *9*, suture X 6.5 at D = 17.0 mm, the suture varying in position at mid-venter according to the position of the large ventrolateral clavae; *10*, UT-8295-E, whorl-section X 1.45 at D = 13.6 mm. *12-14.—Tegoceras* sp. no. 1, UT-8296; *12*, suture X 4.8 at D = 15.0 mm, *13*, whorl-section X 2.45 at D = 15.1 mm, and *14*, three successive ventral saddles X 4.4 at D = 15.0±, illustrating the asymmetry of the ventral lobe to the mid-line.

Remarks.—UT-8290, the only specimen from the Chihuahuan locality, is moderately involute, but the umbilicus widens a little during growth, overlap being to about half of the flank at a diameter of 15 mm. Interrib height-width ratio is about 1.2 at a diameter of 13 mm.

There are about 15 rectiradiate ribs at a diameter of 15 mm, of which some are faintly sigmoid. There are more ventral tubercles than there are ribs, but less than two ventral tubercles per rib. Most species of *Lyelliceras* show four lateral tubercles per rib, plus the ventral tubercle, but UT-8290 has only three tubercles per rib, plus the ventral tubercle.

Measurements.—D, 13.0 (100); U, 4.1 (31.5); H, 4.5 (34.6); W, 3.8 (29.2); H/W, 1.18.

Comparisons.—Most of the species of *Lyelliceras* of which I am aware have four tubercles at some part of the growth stage in addition to the ventral tubercle. The single exception is *L. carvajalorum* Etayo-Serna (1979:figs. 8h-i and pl. 11, fig. 5). Therefore I have compared UT-8290, with three lateral tubercles on each flank and one ventral tubercle, to Etayo-Serna's specimen, but on UT-8290 the umbilical tubercles are at the umbilical shoulder instead of removed therefrom as in Etayo-Serna's species. *L. pseudolyelli* (Parona and Bonarelli, 1896) in Benavides-Caceres (1956:pl. 52, fig. 3) also has only three lateral tubercles, but their disposition is different and the specimen is more flat-sided than UT-8292. *L. pseudolyelli* (Parona and Bonarelli, 1896:pl. 14, figs. 1 and 2) also has umbilical tubercles removed from the umbilical shoulder. The same can be said for *Ammonites lyelli* Pictet and Campiche (1858-1864:pl. 14, figs. 7a-b, only), which would appear to be a *Prolyelliceras.*

According to Etayo-Serna (1979:16), if I read him correctly, *L. carvajalorum* should represent some part of the Middle Albian above the lower zone.

Genus *Tegoceras* Hyatt, 1900

Type species.—Ammonites mosensis d'Orbigny, 1841.

Remarks.—The whorl-sections (Fig. 3) are drawn as though the ribs were opposed across the venter. This is for convenience, because opposite ribs, of course, alternate in ventral view in the genus *Tegoceras.*

Tegoceras n. sp. aff. *gladiator* (Bayle, 1878)

Figs. 2:24, 28, 29; 3:3, 4.

Material.—One specimen, UT-8293, from Middle Albian shale, Cerro Madero, Chihuahua.

Remarks.—This specimen is moderately involute for the genus *Tegoceras*, with sloping umbilical wall poorly delineated from the flank. There are about 17 ribs in the outer whorl. Ribs are well spaced with interribs wider than ribs. Ribs are generally rectiradiate with no sinuosity.

There are low shoulder clavae that do not rise ventrad of the venter, and there are low, umbilical swellings at the umbilical ends of the ribs. The height-width ratio is about 1.0.

Measurements.—D, 14.5 (100); U, 4.3 (29.7); H, 4.8 (33.1); W, 4.8 (33.1); H/W, 1.00.

Comparisons.—Although perhaps related to *Tegoceras gladiator* (Bayle, 1878), UT-8293 has a number of distinct differences, including interribs that are wider than ribs, much smaller umbilical swellings on the ribs, and a less accentuated zigzag pattern of the alternating ventrolateral clavae in ventral view. Furthermore these clavae are not as well developed, so that there is no recession of the height of the ribs at the mid-flank position. The first lateral saddle is relatively less wide than is that of the specimen illustrated by Casey (1978: fig. 238f), but this could result from the small size of UT-8293. Etayo-Serna (1979:83) compares the specimen figured by Benavides-Caceres (1956:pl. 52, fig. 3) as *Lyelliceras pseudolyelli* (Parona and Bonarelli) to his species, emphasizing that the whorl-section of the specimen of Benavides-Caceres is unlike the Parona and Bonarelli (1896) specimen.

Tegoceras sp. 1

Figs. 2:12, 13, 19-21; 3:12-14.

Material.—One specimen, UT-8296, from Middle Albian shale, Cerro Madero, Chihuahua.

Remarks.—A relatively high-whorled species of *Tegoceras* with H/W around 1.6. The specimen is relatively involute and shows a small node just ventrad of mid-flank. There are approximately 17 ribs on the outer whorl, and ribs and interribs are about the same width. Width of ribs and interribs expands equally ventrad, and each rib ends in a strong ventrolateral clava. Ventro-lateral clavae alternate on opposite flanks. The suture does not have exceptionally wide saddles or lobes.

Measurements.—D, 15.1 (100); U, 5.4 (35.8); H, 6.0 (39.7); W, 3.6 (23.8); H/W, 1.66.

Comparisons.—UT-8296 has a height-width ratio similar to the specimen of diverse *Ammonites lyelli* of Pictet and Campiche (1858-1864: pl. 24, figs. 8a-d) and probably the specimen of *Tegoceras benavidescaceresi* Etayo-Serna (1979:pl. 11, fig. 8). Etayo-Serna's species and the illustrations of Pictet and Campiche mentioned above also have the minor node at mid-flank, but otherwise the specimen of *Tegoceras benavidescaceresi* is much too large to compare readily with UT-8296. The specimens (figs. 8a-d) illustrated by Pictet and Campiche (1858-64) have a much more evenly tabulate venter than does UT-8296, and the ribs do not start as early in the ontogeny, but this could be due to artistic license in Pictet and Campiche. On UT-8296 ventrolateral nodes are more pronounced and the venter, therefore, appears to vary in width, unlike the specimen illustrated by Pictet and Campiche.

Tegoceras maderoense, n. sp.

Figs. 2:22, 23, 25-27, 30-43; 3:6, 8-11.

Material.—Five specimens, UT-8295-C, the holotype, and four paratypes (UT-8295) from Middle Albian shale, Cerro Madero, Chihuahua.

Remarks.—Suite UT-8295 represents a widely involute (overlap is more than one-half of the flank), more densely costate (20 to 24 ribs per whorl) species. Ribs are markedly sigmoid, and on the ventral half of the flank interribs are much wider than ribs. Interribs widen markedly ventrad, whereas ribs are about the same width across the flank. H/W ranges from about 1.6 to over 2.0, but the higher figures may be due to preservation. However, the species is relatively high-whorled. There appears to be the remnant of a ventral tubercle on all specimens. The suture is typical of those species of *Tegoceras* with the narrower first lateral saddles. Four specimens show an asymmetry of the ventral saddle according to its position in relation to the ventrolateral clavae, a condition most markedly expressed by UT-8295-A (fig. 3.9). Only one specimen, UT-8295-D, does not show this asymmetry.

Measurements.—UT-8295-A: D, 17.8 (100); U, 5.1 (28.7); H, 6.7 (37.6); W, 4.0 (22.5); H/W, 1.67. UT-8295-B: D, 15.9 (100); U, 3.6 (22.6); H, 7.1 (44.7); W, 3.2 (20.2); H/W, 2.22. UT-8295-C: D, 17.0 (100); U, 4.2 (24.7); H, 6.6 (38.8); W, 3.3 (19.4); H/W, 2.00. UT-8295-D: D, 15.9 (100); U, 4.1 (25.8); H, 6.0 (37.7); W, 3.5 (22.0); H/W, 1.71. UT-8295-E: D, 13.6 (100); U, 4.0 (29.4); H, 5.2 (38.2); W, 3.3 (24.3); H/W, 1.58.

Comparisons.—*Tegoceras maderoense*, n. sp., is more densely costate than other high-whorled species of *Tegoceras*, except for *T. benavidescaceresi* Etayo-Serna (1979:pl. 11, fig. 8), which has even more ribs, upwards of 26 per volution, but they are rectiradiate. *T. maderoense*, n. sp., differs from *T. benavidescaceresi* in the markedly sigmoid ribbing of the former. The sutures are similar to the group of *T. gladiator* (Bayle), although the specimens are small, which may account for their narrower first lateral saddles.

ACKNOWLEDGMENTS

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GENERAL NOTES

NEW HOST RECORD FOR *ORCHOPEAS LEUCOPUS* FROM THE EASTERN PIPISTREL, *PIPISTRELLUS SUBFLAVUS*

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Orchopeas leucopus is a common flea, primarily associated with various *Peromyscus* spp. in eastern North America (Benton, 1980; Holland, 1985). It is frequently encountered throughout the year (e.g. Benton and Altmann, 1964; Jackson and DeFoliart, 1976) and has been collected from a large number of hosts, many of which are undoubtedly accidental: *Didelphis, Sorex, Blarina, Glaucomys, Spermophilus, Tamias, Tamiasciurus, Sciurus, Sigmodon, Ondatra, Dipodomys, Perognathus, Neotoma, Onychomys, Reithrodontomys, Microtus, Clethrionomys, Synaptomys, Napaeozapus, Mus, Erethizon,* and various carnivores (Morlan, 1955; Benton, 1980; Haddow et al., 1983; Holland, 1985). There is even a record of *O. leucopus* from the Saw-Whet Owl, *Aegiolus acadicus* (Holland, 1985).

On June 15, 1989, while collecting bats from Brown's Cave, 2.2 mi. SW Evans, Douglas County, Missouri, a male *O. leucopus* was found on the back of an adult female *Pipistrellus subflavus* (RMP 2546). This record is the first from *P. subflavus,* or any Chiroptera, for that matter. It was almost certainly an accidental association, where a suitable host probably nested nearby, though no evidence of other small mammals were observed in the cave. The specimen of *P. subflavus* is deposited in the Texas Cooperative Wildlife Collection (TCWC). The specimen of *O. leucopus* is deposited in the J. B. Wallis Museum of Entomology, Department of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada.

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A SECOND CONFIRMED POPULATION OF THE RARE MEXICAN RATTLESNAKE, *CROTALUS TRANSVERSUS* (SERPENTES: VIPERIDAE)

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The Mexican cross-banded mountain rattlesnake, *Crotalus transversus*, has been rarely collected and remains known from fewer than 20 individuals. Previously, all known specimens have been found at or near the type locality of the Lagunas de Zempoala (sometimes spelled Cempoala) in the state of Morelos near the Morelos-México boundary (Campbell, 1988).

During a survey of the herpetofauna of the Jiquipilco region in the state of México, a second population of *Crotalus transversus* was discovered. Two specimens were collected near Los Tachos, 12 km. E Jiquipilco, at an elevation of about 3000 meters. This locality lies to the northwest of the Valley of México and is about 62 kilometers airline from the type locality; it lies at about 99° 36′N, 19° 33′W. The climate is temperate with summer rains and a relatively dry winter (García, 1978). These specimens confirm the presence of *Crotalus transversus* in the northern Sierra Ajusco in the state of México (this portion of the range is referred to as the Sierra de Monte Alto or the Sierra de Las Cruces on some maps). The highest point in this range reaches 3650 meters.

One snake is an adult male obtained on 13 July 1992, which is currently being maintained alive. It was encountered beneath a small rock just before a heavy rain. Another specimen (ENEPI 3817) is a female neonate taken on 20 August 1992 with a rattle consisting of a single button. The neonate was encountered while actively crawling in a small rocky, grassy area within the forest. A second neonate was also observed about two meters from the first but escaped into a small burrow.

Our specimens of *C. transversus* from near Jiquipilco agree in most respects with the descriptions provided by Taylor (1944), Klauber (1952), Campbell (1988), and Campbell and Lamar (1989). The neonate is 150 mm in snout-vent length, 164 mm in total length, and has 21-21-17 dorsal scale rows, 3 preventrals, 136 ventrals (umbilical scar on ventrals 123-126), 20 subcaudals, 8 rattle-fringe scales, 9/9 supralabials, 9/8 infralabials, 2/2 preoculars, 2/2 suboculars, 2/2 postoculars, a single loreal on each side, 17 interrictals, 40 dorsal crossbands on the body and 7 on the tail. The anterior part of the snout is covered with a large flat pair of internasals and a pair of prefrontals (the latter may be interpreted as canthals). A single large azygous scale in the frontal region separates the supraoculars. The parietal region is mostly covered by four large, somewhat irregular flat scales. The loreal on the right side contacts the first and second supralabials. Foveals are absent except for one scale on the left side that precludes contact of the loreal with the supralabial series. The presence of only 4 (versus 5-6) scales in the internasal-prefrontal region, the single (versus 2-3) intersupraocular, and 136 (versus 141-152) ventrals amplifies the variation known in this species (Campbell and Lamar, 1989). Of these characters, the low number of ventrals in a female is particularly significant.

The habitat surrounding Jiquipilco is similar to that of the type locality near Lagunas Zempoala and covered by coniferous forest (Rzedowski, 1978) containing species of pines and *Abies religiosa*. Mostly the same species of amphibians and reptiles inhabit the two localities, including *Hyla eximia, Pseudoeurycea cephalica, Chiropterotriton chiropterus, Rhyacosiredon altamiranoi, Eumeces copei, Barisia imbricata, Sceloporus aeneus, S. grammicus, Thamnophis scalaris,* and *Storeria storerioides*. Many of these species were reported from several sites lying at slightly lower elevations (2500-2750 meters) to the north of Jiquipilco by Ramírez-Bautista et al. (1992), but *C. transversus* was absent from their collections.

The date of capture of the neonate in July corresponds with the period during which juvenile *Sceloporus grammicus* make their appearance. This abundant lizard is known to be prey for *C. transversus* (Campbell, 1988); our neonate specimen was maintained in the laboratory for a short time and fed readily on this species of lizard.

The distribution of *C. transversus* is still poorly understood. With one exception, all specimens have been obtained from the highland area bordering the south and west of the Valley of México. These highlands are continuous, but *C. transversus* is almost certainly distributed in a series of localized, disjunct populations along the higher parts of the range. The only record of *C. transversus* possibly occurring elsewhere is that of a specimen (FMNH 39115) from the Cerro de Tancítaro in the state of Michoacán (Campbell, 1982). This specimen was previously identified as *C. intermedius* (Klauber, 1952), but this allocation is almost certainly in error. Whether this specimen represents *C. transversus* or is a novel taxon awaits confirmation by further collecting on Tancítaro.

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NOTEWORTHY RECORDS OF BATS FROM HONDURAS

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This paper presents a summary of specimens obtained during a collecting trip to the Republic of Honduras in August 1991. Included are distributional comments for seven species of bats and the first published karyotype of *Tonatia evotis*. Bats were collected at five localities representing lowland tropical areas near the Atlantic and Pacific Coasts. These localities included scrub woodland and adjacent mangrove swamps of the Pacific Coast (8.5 mi. SSW, San Lorenzo, Departmento de Valle; 8.0 mi. S, 1.0 mi. E, San Lorenzo, Departmento de Valle; 0.2 mi. S, Los Mangles, Departmento de Choloteca) and from abandoned mines near open broadleaf deciduous forest and cultivated plots (1.3 mi. S, 8.4 mi. W, Nacaome, Departmento de Valle). Lancetilla, Departmento de Atlántida, on the Atlantic Coast, is characterized by pristine broadleaf forest (Lancetilla National Botanical Gardens) adjacent to banana plantations. Voucher specimens have been deposited in The Museum of Texas Tech University. We would like to thank R. Van Den Bussche and R. J. Baker for their critical reviews of earlier drafts of the manuscript. This project was supported by an Alfred and Alma Shadle Award to R. D. Bradley and by NSF grant BSR-90-06797 to R. J. Baker.

Saccopteryx leptura Schreber, 1771.—Greenbaum and Jones (1978) reported one male of this species netted 10 mi. SSW Nacaome, Departmento de Valle, in 1975, the only previous record from the country. Three specimens, one female and two males, were taken in a mango orchard 8.5 mi. SSW, San Lorenzo, Departmento de Valle. Additionally, two males were caught at 8.0 mi. S, 1.0 mi. E, San Lorenzo, Departmento de Valle, and six specimens (two females and four males) were collected from 0.2 mi. S, Los Mangles, Departmento de Choloteca. Additional species collected from both localities included: *Pteronotus parnellii mesoamericanus, Phyllostomus discolor verrucosus, Glossophaga soricina handleyi, Carollia brevicauda, Carollia perspicilata azteca, Carollia subrufa, Sturnira lilium parvidens, Desmodus rotundus murinus, Artibeus inopinatus, Artibeus lituratus intermedius, Artibeus jamaicensis richardsoni, Dermanura phaeotis phaeotis, Chiroderma salvini salvini, Uroderma bilobatum convexum, Eptesicus furinalis gaumeri, Myotis keaysi pilosatibalis*, and *Rhogeessa tumida.*

Peropteryx macrotis macrotis Wagner, 1843.—Goodwin (1942) reported three specimens from Sabana Grande, and one from La Flor Archaga, both in Departmento de Francisco Morazán. These localities are mountainous and range from 350 to 1700 meters in elevation. We collected eleven specimens in abandoned mines in tropical lowlands 1.3 mi. S, 8.4 mi. W, Nacaome, Departmento de Valle. Additional species taken from these mines included: *Pteronotus parnellii mesoamericanus, Glossophaga soricina handleyi*, and *Artibeus inopinatus.*

Leptonycteris curasoae yerbabuenae Miller, 1900.—Lee and Bradley (1991) reported the first record of *L. c. yerbabuenae* for Honduras based on three specimens collected from abandoned mines 1.3 mi. S, 8.4 mi. W, Nacaome, Departmento de Valle. We collected two males from this same locality. Multiple collections at this site (1983 and 1991) may indicate that a permanent colony of *L. c. yerbabuenae* resides there. These records also extend the range of *L. c. yerbabuenae* eastward into Honduras from the distribution noted by Jones et al. (1988).

Micronycteris schmidtorum Sanborn, 1935.—A male of this species was collected at Lancitilla, Atlántida. This provides a second record of occurrence of this species from Honduras and an extension of the range northeastward approximately 150 kilometers from the nearest previous record (Davis et al., 1964; Hall, 1981). Other species of bats collected at Lancitilla included: *Phyllostomus discolor verrucosus, Glossophaga soricina handleyi, Carollia perspicilata azteca, Sturnira lilium parvidens, Desmodus rotundus murinus,*

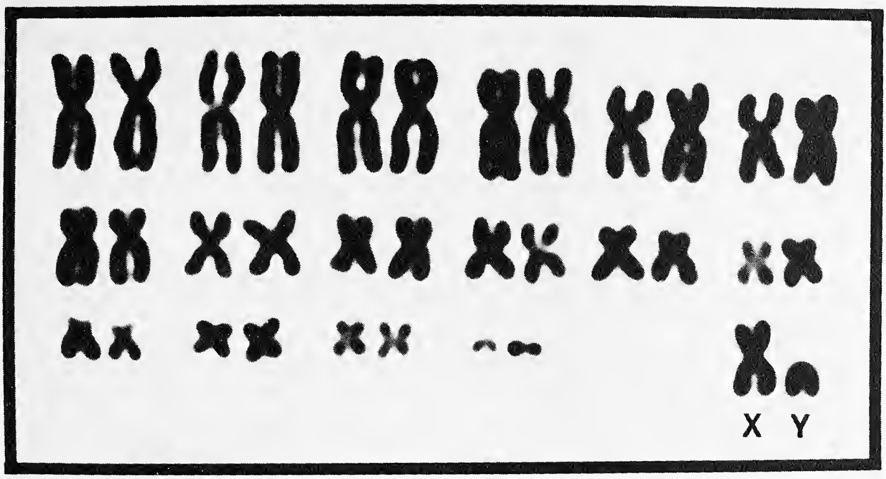

Figure 1. Standard karyotype of a male *Tonatia evotis* (TTU 70593) from Lancitilla, Atlántida, Honduras.

Artibeus jamaicensis richardsoni, Artibeus lituratus intermedius, Dermanura phaeotis phaeotis, Uroderma bilobatum molaris, Vampyressa pusilla thyone, Vampyrops helleri, Eptesicus furinalis gaumeri, and *Rhogeessa tumida.*

Phyllostomus hastatus panamensis Allen, 1904.—Lee and Bradley (1991) reported the first record of this species for Honduras from 2.4 mi. SW, Dulce Nombre de Culmi, Departmento de Olancho. We collected 26 individuals from Lancitilla, Atlántida, of which nine (four females and five males) were prepared as voucher specimens. This documents the second record of this species for Honduras and may indicate that this species is widespread throughout much of central Honduras.

Vampyrum spectrum Linnaeus, 1758.—A male collected at Lancitilla, Atlántida provides the second specimen of this species from Honduras, the first having been reported by Lee and Bradley (1991) from the same locality. This species probably has a restricted distribution in Honduras due to habitat fragmentation.

Tonatia evotis Davis and Carter, 1978.—A single specimen of this species was reported by Davis and Carter (1978) from Puerto Lempira, Departmento de Gracias a Dios. A male netted at Lancitilla, Atlántida, represents a second record for Honduras and a range extension of 390 kilometers westward from the nearest previous locality of known occurrence. The standard karyotype of a male *Tonatia evotis* consisting of 30 biarmed and two acrocentric autosomes is illustrated here for the first time (Fig. 1). *Tonatia silvicola*, a closely related species, has a similar karyotype, 2n=34.

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EFFECTS OF DROUGHT ON AMERICAN ALLIGATORS (*ALLIGATOR MISSISSIPPIENSIS*) IN TEXAS

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Most knowledge regarding the American alligator (*Alligator mississippiensis*) during dry weather refers to the annual dry season regime in southern Florida (Hines et al., 1968) or to droughts in Louisiana (Chabreck, 1965). In this paper, we present a compilation of observations made on alligators at Brazos Bend State Park, Fort Bend County, Texas during a drought that extended from spring 1988 through spring 1989.

Brazos Bend State Park consists of 1,982 ha located less than 32 km southwest of the Houston city limits. Prominent aquatic areas in the park consist of a freshwater marsh (Pilant Lake), three lakes (Elm, Forty Acre, Creekfield), three oxbows (Old Horseshoe, New Horseshoe, Hale), and a slough (Pilant Slough). Hiking/biking trails border portions of the aquatic areas, and sometimes serve as the only separation between adjacent impoundments. Big Creek flows through the park and the Brazos River forms the eastern park boundary. These water courses serve as potential dispersal routes.

During 1988 the total rainfall for the Houston area was 58.24 cm, which was the driest year since 1917 when the rainfall total was less than 45 cm (Houston Area National Weather Service, pers. comm.). The total rainfall for 1989 was 133.84 cm, which is misleading unless the rainfall on a per month basis is examined. The dry conditions actually persisted through May 1989 when 34.44 cm of precipitation were recorded, bringing the water levels to within normal limits. In June 1989 a total of 41.35 cm of rainfall was noted, and these extremely high consecutive rainfall totals for the two months were due to three tropical storms that passed through the area.

Concurrent with reduced rainfall was the draining of the 191 ha Pilant Lake to create earthen mounds for alligator basking and nesting, and to improve conditions for waterfowl. Pilant Lake was drained during a three-week period in February 1988. Borrow ditches along the southern side of Pilant Lake still contained water after the draining of the lake proper, as did areas in association with alligator holes and a few scattered low-lying areas. Forty Acre, Elm, Old Horseshoe, and New Horseshoe lakes experienced a lowering of water levels as well as varying exposure of the lake bed. Water levels continued to recede throughout the summer, reached a low by August 1988, and remained critically low until May 1989.

Drought-related data were collected during other research activities on alligators at Forty Acre Lake and Elm Lake and at the southern and western portions of Pilant Lake. From 1985 to 1989, data from diurnal basking censuses were collected; these data included the sizes (total length = TL, estimated to nearest 0.1 m) and numbers of alligators sighted at locations along a designated route. The number of nests and their locations were monitored from 1986 to 1990. Additionally, Old Horseshoe and New Horseshoe lakes were checked periodically to see what portions of the lakebeds were devoid of water and if alligator holes and dens were exposed. Nests and dens located in areas with little water and accessible by foot were visited up to several times per week to check for the presence, number, and size of alligators. A few observations were based on reports by park visitors which were investigated and validated by park personnel when possible.

Adult alligators were more common during the 1988-1989 drought than during 1985-1987 in the central portion of Elm Lake. An extensive egret rookery existed for the first time in 1988 at the southern portion of Elm Lake instead of at Pilant Lake. The change of location apparently resulted from the draining of Pilant Lake. Jones (1988) noted alligators lunging at trees in the rookery and eating young birds that were grabbed, or fell, from the nests. Juvenile alligators were present in greater numbers than usual at the south side of Elm Lake and especially at the east side of Forty Acre Lake. Basking census data for 1985-1989 revealed a dramatic increase in the number of animals sighted (from <60 to >140 animals) during 1988 and 1989; this increase was due to greater densities at Elm and Forty Acre lakes. Nocturnal censuses by personnel of the Texas Parks and Wildlife Department (TPWD, pers. comm.) corroborated these findings.

A substantial number of alligator dens became partially or completely exposed at Pilant Lake, Pilant Slough, Elm Lake, Old Horseshoe Lake, and New Horseshoe Lake. When water levels surrounding the dens were very low or dry, the perimeters of "alligator holes" were clearly delineated as water-filled or waterless depressions in front of the dens. Inhabitants of the holes ranged from a lone adult to pods of juveniles.

If the alligator's den site was dry, but there was water in the vicinity, the larger animals (>2.4 m TL) moved past other animals' dens to use any water that was nearby. One large male (3.0 m) moved back and forth between Elm Lake and an area with almost no water. Almost every hole that was nearly or completely dry and not close to abundant water had one or more alligators in the hole or in the adjacent den. Guardian females at nests remained in the nest vicinity even if there was little water in the immediate area. They were found in their den, in the hole associated with the den, or by the nest. Females with young also remained in their den/pond area. One female with two yearling offspring inhabited two adjacent dens alternately, and the juveniles stayed inside the same den with her.

Adults and juveniles in open water areas appeared to display normal behavior when in water or on land. This contrasted greatly with the actions of adults and juveniles in areas that had little to no water. Such adults became highly agitated and hissed loudly when approached, while juveniles tended to be extremely wary, submerging if sufficient water was available or else moving quickly into their dens. Undisturbed alligators were inactive, remaining nearly motionless.

The presence of numerous tail drags on the footpath between Pilant and Forty Acre lakes, coupled with nocturnal census data (TPWD, pers. comm.) for Forty Acre Lake when Pilant Lake was dry, indicated that nocturnal trips were made to Forty Acre Lake by at least a portion of the adult alligators in Pilant Lake. There was no way to gauge the frequency of the trips or number of participants in these movements to water, which presumably functioned as feeding excursions in addition to dehydration avoidance.

Cannibalism was observed on three occasions in spring and summer 1988. On 30 May at 1500 h a 2.7 m female seized a 1.4 m alligator near her den site. She carried it by the head and violently shook it for at least 1 h until it was dead. At approximately 1700 h she began to eat it, and at 1730 h a 3.0 m male chased and mated with her. Copulation lasted for five min with the female completely submerged and exhibiting signs of stress. She then shook her prey violently, growled at the male, and crawled out of the water to the top of the bank where she resumed eating. She almost had the alligator's head bitten off, and continuously crushed the anterior half of the body in her jaws, beginning with the head, going posteriorly down the body, and then starting over again by shaking the head and then biting it. At 2000 h, when darkness began to obscure visibility, she was still eating the alligator. On 31 May at 1007 h, her mate (identified by his size and distinctive head shape) was observed picking the alligator carcass out of the water and attempting to eat it. Only the posterior half of the carcass remained, and it was identified as a male from the protruding penis.

We noted another incident of cannibalism at the fishing pier on the southwest side of Forty Acre Lake in which a 2.4 m alligator ate a 1.2 m conspecific. A third instance of cannibalism was documented at Elm Lake by fishermen who reported one alligator eating another, but were unsure of the sizes of either animal. Both incidents occurred in late June 1988.

In May 1988 the breeding season began as usual with frequent bellowing, increased movements between lakes, and alligators congregating together. The draining of Pilant Lake greatly affected nest building except in borrow ditches at the southeastern part of the lake. The remainder of the lake had only one nest (as opposed to three or more in past years). This nest was located on the west side and contained 46 eggs, 45 which were viable to full term. The eggs were sacrificed for a sex ratio study, thus no survivorship data were available. The total number of eggs laid by the 2.7 m female at the southeast side of Pilant Lake is unknown. However, at the predicted hatching time she was observed with approximately 15 hatchlings which gradually dwindled to about four within two months.

In 1989, almost no bellowing was heard and mating activity was minimal, although water levels had returned to normal by the onset of the breeding season. Nests were found only at the perimeters of Elm and Forty Acre lakes. In an examination of nest data for 1987-1990, the trend was for fewer nests during the drought years of 1988 and 1989. The number of nests sighted during 1988 and 1989 was six and four respectively, compared to eight for 1987 and 11 for 1990 for the same nest-census route. The pattern of nesting for 1990 appeared normal except at the western portion of Pilant Lake where there were no nests.

No animals in areas without water were known to have died from dehydration or starvation, and no carcasses were found. There was no evidence of emaciation or illness in inhabitants of holes containing little to no visible water. All individuals appeared to be in good condition. It appears that alligators were able to either "wait out" the drought, possibly relying on fat reserves, or they were able to obtain sufficient food to maintain body condition.

However, the drought may have indirectly contributed to a winter kill of approximately 12 adult alligators at Elm Lake in December 1989. Though a severe freeze (-13.9°C on 23 December) might have caused mortality by itself, Elm Lake was the only location in the park where freeze-related deaths were noted. An increased number of animals within the lake could result in a higher mortality if all animals were unable to occupy areas that provided maximal protection from the cold. Lang (1989) noted that crocodilians defend winter sites, and at Elm Lake the less dominant animals may have been restricted to shallow areas affording less protection from freezing temperatures.

In agreement with our observations, Lang (1987) observed that crocodilians may group together at permanent water during drought. Chabreck's (1965) assertion that females remain at their dens while males and immature alligators seek deeper water apparently agrees with our observations, although nocturnal movements of females are a possibility. Our data suggest that females with nests or young tend to remain in their established territories, and that hatchling viability and survival may have been adversely affected by the drought.

The apparent decrease in nesting at Brazos Bend during the drought agrees with the observations of Joanen and McNease (1975, 1978, 1989) on alligators during dry periods in Louisiana. Since the drought had just started at the beginning of the breeding season in 1988, there was little change in the amount of bellowing and mating behavior observed from previous years. In 1989, the drought had ended by the time of the onset of the spring mating season, but bellowing and mating behavior were depressed compared with previous years and nests were present only at the perimeters of lakes retaining substantial areas of permanent water. Guillette et al. (pers. comm.) observed via blood plasma levels of estradiol and vitellogenin that female alligator reproductive activity began in the fall rather than spring. Thus, the critical time for the onset of female reproduction for the 1989 nesting season was in fall 1988 when the alligators were still affected by the drought. By 1990, mating and nesting activities had returned to normal levels.

Pilant Lake was nearly devoid of visible plant and animal life when it refilled with water in 1989; but in 1990 it supported a variety of aquatic plants and animals. Alligators (in addition to those that remained during the drought) reinhabited the marsh, but did not reach the population densities that existed prior to the draining of Pilant Lake until summer 1991. The lack of nesting in 1990 at the west side of Pilant Lake (as opposed to normal nesting patterns elsewhere) also suggests that the marsh had not completely recovered until summer 1991 when nesting resumed there. It appears that the draining of Pilant Lake caused immediate changes that were more drastic and prolonged than those caused by the gradually decreasing water levels in areas affected by drought alone.

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VALUE OF THE LEAST INTERORBITAL BREADTH IN THE DISCRIMINATION OF SOME PROBLEMATIC SPECIES OF *PEROMYSCUS* AND *REITHRODONTOMYS*

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A variety of characters serve to distinguish congeneric species of *Peromyscus* and *Reithrodontomys*. However, where the range of the white-footed mouse (*P. leucopus*) overlaps with that of the deer mouse (*P. maniculatus*), and where the western harvest mouse (*R. megalotis*) occurs in sympatry with the plains harvest mouse (*R. montanus*), specific identifications sometimes can be troublesome. This is particularly true when researchers have only incomplete materials at their disposal.

Fusions early in life of the cranial elements associated with the interorbital breadth afford a measurement that, for many small rodents, is comparable among older juveniles and adults of all ages, and one that is highly repeatable. This fused or tightly articulated interorbital region usually remains intact long after other bones of the skull have loosened or become completely disarticulated, rendering most other cranial measurements inaccurate if not impossible to obtain. We have consistently found this to be true among the indigestible skeletal material recovered from regurgitated owl pellets, and sometimes even from skulls found in the sediments of river terraces or cave floors dating to the latest Pleistocene in age.

Selected series of *Peromyscus leucopus*, *P. maniculatus*, and *Reithrodontomys megalotis*, and *R. montanus* were chosen from the Midwestern State University Collection of Recent Mammals on the basis of certain identification, taxonomic (subspecific) diversity, and broad geographic representation from Texas and nearby states of Colorado, Kansas, New Mexico, and Oklahoma. According to the range maps of Hall (1981), our samples included three subspecies of *P. leucopus* (*leucopus, texanus,* and *tornillo*), six of *P. maniculatus* (*blandus, rufinus*, and the diminutive races of *luteus*, *nebrascensis*, *ozarkarium*, and *pallescens*), three of *R. megalotis* (*aztecus, dychei,* and *megalotis*), and two of *R. montanus* (*griseus* and *montanus*).

Individual variation among sampled populations of each species was slight (coefficients of variation [CV] = 1.60-5.19), except for a series of nine *P. leucopus* from Childress County, Texas (CV = 12.15). Geographic variation for the interorbital breadth measurement was negligible, except for *P. maniculatus*, where the larger western subspecies (*blandus* and *rufinus*, respective means of 4.08 and 4.12) averaged greater than the more diminutive subspecies, whose range of means from six localities was 3.81-3.96. The range of means for *P. leucopus* from thirteen localities was 4.16-4.30; for *R. megalotis* from five localities, 3.16-3.29; and for *R. montanus* from eight localities, 2.90-2.99.

While there were considerable overlaps of the interorbital breadth measurements between congeneric species, discrimination at the 99% confidence

TABLE 1. Comparisons of least interorbital breadth between two species each of *Peromyscus* and of *Reithrodontomys*. Among the *P. maniculatus*, the "A" sample is comprised of the larger *P. m. rufinus* and *P. m. blandus*. The "B" sample is comprised of examples of the more diminutive races (see text). Descriptive statistics are sample size (N), mean, standard deviation (SD), range, and 99% confidence intervals.

Taxon (N)	Mean ± SD (Range) 99% confidence interval
Peromyscus leucopus (130)	4.247±0.165 (3.81-4.72) 4.21-4.28
P. maniculatus - A (19)	4.099±0.132 (3.84-4.27) 4.02-4.18
P. maniculatus - B (66)	3.869-0.172 (3.53-4.26) 3.81-3.92
Reithrodontomys megalotis (67)	3.204±0.119 (2.87-3.57) 3.17-3.24
R. montanus (85)	2.946±0.124 (2.60-3.14) 2.19-2.98

level (Table 1) should provide an acceptable alternative to identifications restricted to the generic level.

For useful comments, we thank Clyde Jones and Richard Manning.

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A NEW STATE RECORD FOR THE GIANT WHIPTAIL LIZARD, *CNEMIDOPHORUS SACKI* WIEGMANN, IN VERACRUZ, MEXICO

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Duellman and Zweifel (1962) restricted the name *Cnemidophorus sacki* Wiegmann ". . . to the large, finely scaled (species) with small postantebrachials . . ." that occurs in southern México (type locality Oaxaca, Oaxaca). Also, they recommended that *C. gigas*, described by Davis and Smith (1952), be treated as a subspecies of *C. sacki* because the only apparent

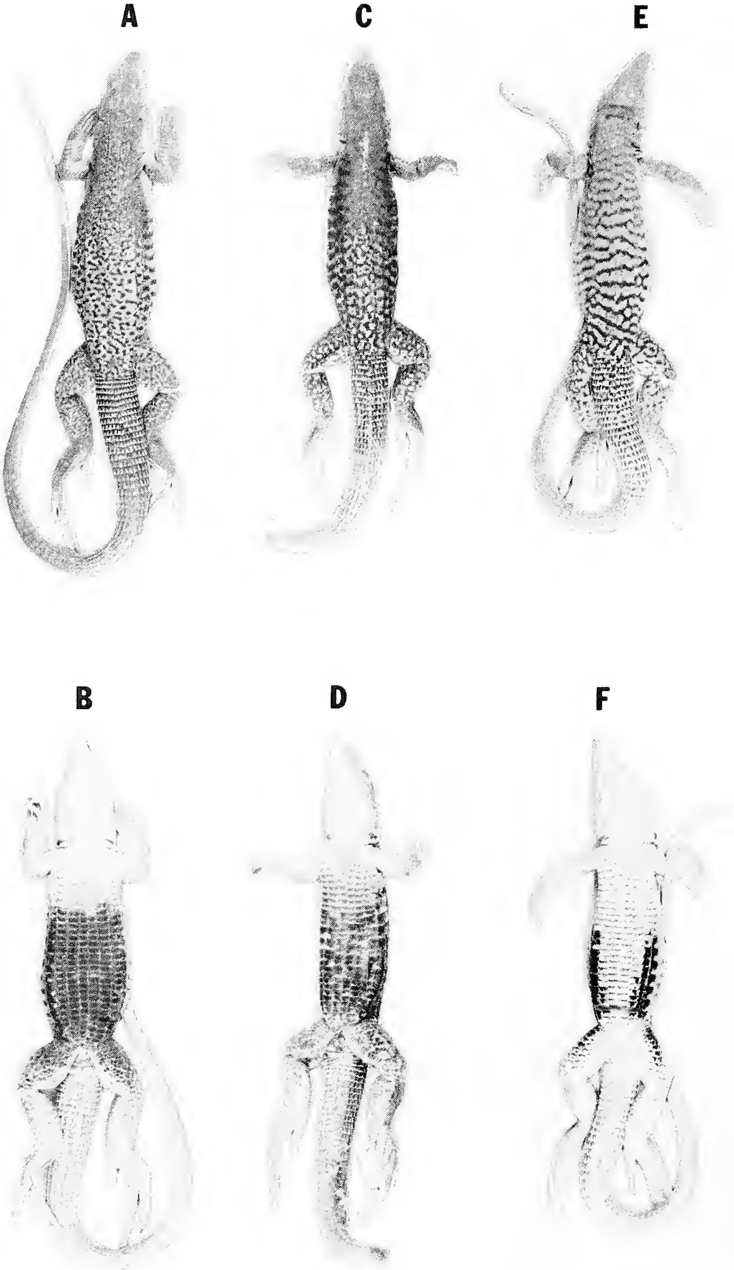

FIGURE 1. Comparison of *Cnemidophorus sacki gigas* (A-B, SVL-snout vent length 134 mm, UCM 49822) from Guerrero, new state record for *C. sacki gigas* (C-D, SVL 128 mm, CAS 135700) from Veracruz, and *C. sacki sacki* (E-F, SVL 133 mm, UCM 38872) from Puebla (all specimens are males).

difference between the two is in dorsal coloration. Based on records provided by Duellman and Zweifel (1962) and Walker (1981), *C. s. sacki* occurs in semiarid valleys from southeastern Puebla to central Oaxaca; based on records provided by Davis and Smith (1952), Pianka and Smith (1959), Davis and Dixon (1961), and Duellman and Zweifel (1962), *C. s. gigas* occurs in the upper Balsas basin in Guerrero, Morelos, and Puebla. The purpose of this paper is to record the presence of *C. sacki* in the state of Veracruz. Specimens utilized in this study are deposited in the collections of the California Academy of Sciences (CAS) and the University of Colorado Museum (UCM).

A specimen of *C. sacki*, bearing the number CAS 135700, is catalogued as having been collected at Cuautlapan, Veracruz, on 23 December 1972. The only map known to us that includes the town of Cuautlapan (97° 01′ N, 18° 52′ W), which can be reached approximately 48 kilometers east of the Puebla state border by a highway turning east off México 150 several kilometers east of Orizaba, was published by the Instituto Nacional de Estadistica Geografía e Informatica (Orizaba E14-6).

Specimen CAS 135700 is a male with a snout vent length (SVL) of 128 mm. There are 130 granules around midbody, 212 granules from occiput to rump, 48 femoral pores summed, 32 subdigital lamellae on the longest toe of the left pes, 11 circumorbital scales summed, 16 lateral supraocular granules on the left side, 16 enlarged mesoptychial scales, and 4-4 supraocular scales. The mesoptychial scales at the edge of the gular fold are abruptly enlarged, the postantebrachial scales are small (though not granular), and the circumorbital scales extend anteriorly to near the middle of the third supraocular scales. Counts for the granules around midbody and femoral pores for CAS 135700 lie within the ranges of variation in these characters reported for both *C. s. sacki* and *C. s. gigas* (Duellman and Zweifel, 1962). However, the count for the number of granules from occiput to rump is much lower in CAS 135700 (212) than in five specimens of *C. s. sacki* (counts of 244-275) from Puebla (UCM 38857, 38864, 38872, 38898, 38905) and four specimens of *C. s. gigas* (counts of 249-272) from Guerrero (UCM 49822, 49830-49832) available to us. That CAS 135700 is a specimen of *C. s. gigas* rather than *C. s. sacki* is apparent on the basis of color pattern, as well as geographic provenance. Adults of *C. s. gigas* have a dorsal reticulum of black and brown, pink throat, and purple-black on the abdominal region (Fig. 1A-B, 134 mm snout vent length), whereas adults of *C. s. sacki* have dark brown dorsal cross bars, tan throat, and purple-black in the abdominal region (Fig. 1 E-F, 133 mm snout vent length). The dorsal and ventral color patterns of the Veracruz specimen (Fig. 1C-D) are similar (if not identical) to those in the comparative material from Guerrero (for example, Fig. 1A-B), and specimens shown in Duellman and Zweifel (1962: pl. 26) from Morelos.

We are grateful to Robert Drewes, California Academy of Sciences, and Shi-Kuei Wu, University of Colorado Museum, for the loans of specimens of *Cnemidophorus* in their care. The location of Cuautlapan, Veracruz, was made possible through maps provided by Ricardo Torres Carreto, Instituto Nacional de Estadistica, Geografía e Informatica, México.

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A NEW RECORD OF THE CHONDRICHTHYAN FISH *PHYSONEMUS MIRABILIS* FROM THE UPPER PENNSYLVANIAN OF TEXAS

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Part of a large chondrichthyan fin spine from Middle Pennsylvanian deposits of Illinois was described and named *Xystracanthus mirabilis* by St. John and Worthen (1875). Eastman (1917) considered *Xystracanthus* to be a synonym of *Physonemus* M'Coy, 1884. However, when Moore (1929) discovered a similar large ichthyodorulite in uppermost Pennsylvanian sediments in Eastland County, Texas, he named it a new species, *Xystracanthus grandis.* Zidek (1977) reported a relatively complete spine from Tulsa County, Oklahoma, and referred it to *Physonemus mirabilis.* The following year Chorn and Frailey (1978) placed *Xystracanthus grandis* Moore in the synonomy of *Physonemus mirabilis* (St. John and Worthen), and this appears to be the proper taxon for the fish.

The nomenclature of *Physonemus mirabilis* seems clear but its taxonomic status is less so. Zidek (1977) included it in the Family Ctenacanthidae. Most recently Carroll (1988) listed it in the Order Symmoriidae and also under "Presumed Elasmobranchii Remains Not Identifiable to Order". *Physonemus* remains a form genus, of a large chondrichthyan fish of late Paleozoic marine waters, known only from its fin spines.

While collecting marine invertebrate fossils from Upper Pennsylvanian deposits near Jacksboro, Jack County, Texas, one of us (P. B-S) found fragments of a large *Physonemus* spine that fit together to form an almost complete ichthyodorulite (Fig. 1) that, in life, was probably in excess of 50 cm in length. An estimated 4 cm has been lost at the distal tip, one edge of the broad, proximal end is missing, and the remaining proximal edge is raggedly broken where an unknown, but probably small amount of dentine is missing. When found, the spine was broken across into seven sections of approximately equal length.

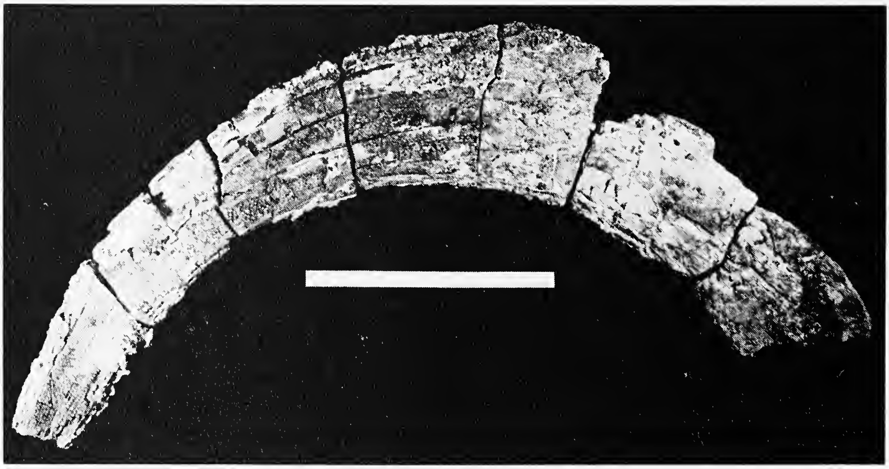

Figure 1. Fin spine of *Physonemus mirabilis* from Jack County, Texas. White bar = 15 cm.

Our spine is approximately as complete as other specimens of *Physonemus* that have been discovered in Pennsylvanian deposits of the Midwest. As in other specimens, the distal, pointed tip is missing. The flattened, presumably inserted, proximal part is mostly present. There is some minor crushing along the margin external to the arc of curvature, probably resulting from weakness caused by the internal medullary cavity (Fig. 2). A shallow depression in the proximal, inserted, portion is present on one side only, but the dentine here does not appear to be crushed. There are a few longitudinal cracks on the surface exposed to weathering and some bits of dentine with covering ornamentation have been broken away. The opposite surface, partly buried in shale matrix when discovered, is heavily coated with gypsum and quite fragile. An area of 40 mm^2 was cleaned, with some minor damage to the surface, to show that the ornamentation is similar to that of the exposed side. Some individual variation in spine structure of *Physonemus* is to be expected, but specimens figured from the midwestern United States are almost alike in size, shape and ornamentation.

The ornamentation of our spine (Fig. 3a) is more worn than that of most. Rows of denticles are more numerous proximally than distally, but damage prevents an accurate count. We estimate that there are about 22 rows that extend parallel to the length of the spine near its tip and perhaps twice that many proximally, where the ornamentation ends. There is a secondary, less exact, orientation in oblique, transverse rows. Longitudinal rows average nine per two centimeters of breadth. Most denticles are about one millimeter in diameter (Fig. 3b) but the denticles along the edge of the arc of curvature are enlarged, and in any row some denticles are enlarged. Each larger denticle in a row is followed by several smaller ones. Denticles have a slight but definite proximal inclination (Fig. 3c).

Enlarged, the denticles are seen to be strongly fluted, each with a major keel that extends from the base over the rounded apex and down the opposite side. There may be five to eight minor carinae between the major keels. Surfaces exposed where denticles have been broken across show an internal structure of osteodentine and pallial dentine (Fig. 3d).

Measurements of our spine are in millimeters (see Fig. 4 for methods): greatest length as preserved, 450; estimated original overall length, 470; maximum curvature as preserved, 130; anteroposterior diameter where indicated in Fig. 4, 112; inserted part of spine in excess of 65.

The specimen was found 11 km. South and 6 km. West of Jacksboro, Jack County, Texas, 250 meters West of County Road No. 4 (land not surveyed in sections), in the lower part of the Finis Shale Member of the Graham Formation, Upper Pennsylvanian (lower Virgilian). The specimen reported by Moore (1929) was taken from the Wayland Shale, the topmost Member of the Graham Formation, "midway between the towns of Eastland and Graham" Where our specimen was taken, the black Finis Shale is exposed in several small knolls. The base of the shale is not exposed. The exposed shale, ca. three meters thick, slopes steeply to base level, is capped and protected from weathering by a layer of the hard, ferruginous Jacksboro Limestone, and is gullied with numerous small erosion channels and littered with limestone fragments. The spine lay mostly exposed on weathered shale beneath the limestone.

The basal, black part of the Finis Shale was deposited in deep but not abyssal water. The shale is phosphatic and almost free of fossils except for scarce specimens of *Ammodiscus* and *Endothyra*, foraminifera with broad ranges of tolerance to environmental conditions. Strata immediately above and beneath the Finis Shale are moderately to strongly fossiliferous. Conditions in the black shale must have been anoxic (Haekel, 1977; Boardman et al., 1984; Boston, 1988). The discovery of the *Physonemus* spine in the deep-water deposit does not prove that the fish lived there but it does suggest deep-water association. Moore's (1929) specimen was found in direct association with a large invertebrate fauna (Moore, 1928).

Authors (Eastman, 1917; Moore, 1929; Baird, 1957; Chorn and Frailey, 1978) have speculated as to the function of the *Physonemus* spine. All agree that the spine is of the dorsal fin and that in life the concave margin was directed anteriorly, the tip pointing forward. All are of the opinion that the spine must have been used in some fashion during copulation.

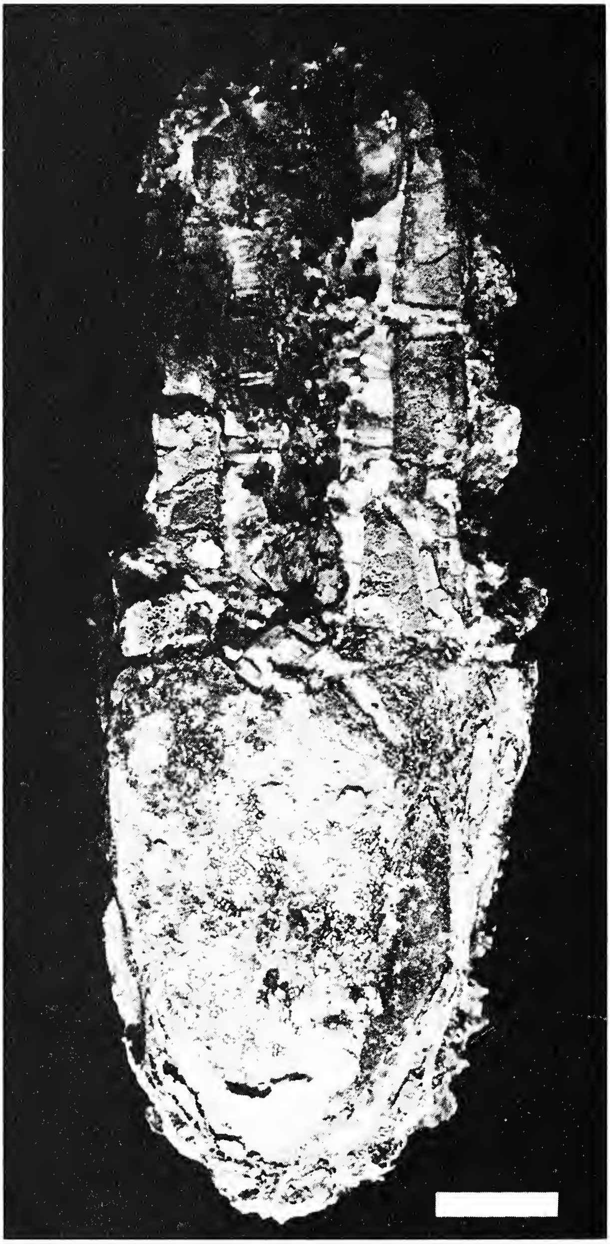

FIGURE 2. Cross-section (natural break) across spine near where indicated in Fig. 4. The medullary cavity (top) is filled with gypsum crystals.

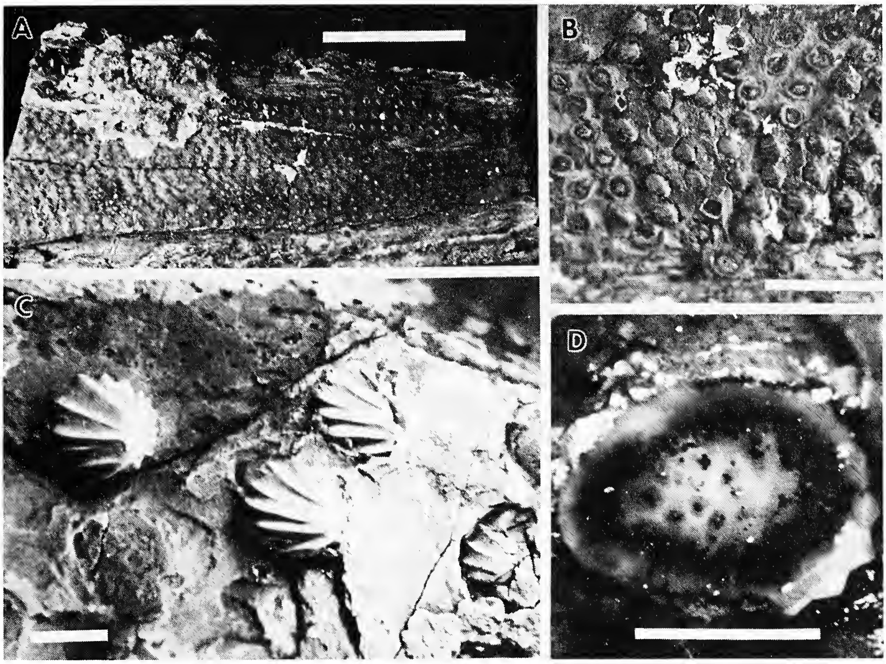

Figure 3. Details of denticulation. A, distal tip of preserved part of spine. Note variations in size of denticles and major orientation parallel to axis of spine; bar = 15 cm; B, enlarged view of spine surface, showing major orientation and secondary, oblique-vertical orientation of denticle rows; bar = 3 cm; C, enlarged view of denticles showing carina and inclination of denticles; proximal to right; bar = 1 mm; D, section across fractured denticle showing complicated internal structure; bar = 0.3 mm.

Hopefully, a *Physonemus* spine will be found in association with other body parts that will aid in understanding this enigmatic fish.

We searched the site where the fin spine was discovered but no spine fragments of other vertebrate remains were found. Screen washing of ca. 20 kilograms of the black shale yielded no fish remains. We were permitted to examine a private collection of some 20 teeth of chondrichthyans taken in gray Finis Shale some 20 kilometers from where the spine was found, but whether any of these might have come from fish like *Physonemus* we cannot say.

We are deeply indebted to Dr. Jiri Zidek, New Mexico Bureau of Mines and Mineral Resources, for identification of our fossil and other favors. Our investigation was supported, in part, by a grant from the Charles and Elizabeth Prothro Distinguished Professorship of Geological Sciences, endowed by the Perkins-Prothro Foundation and funds supplied by the Midwestern State University Research Committee.

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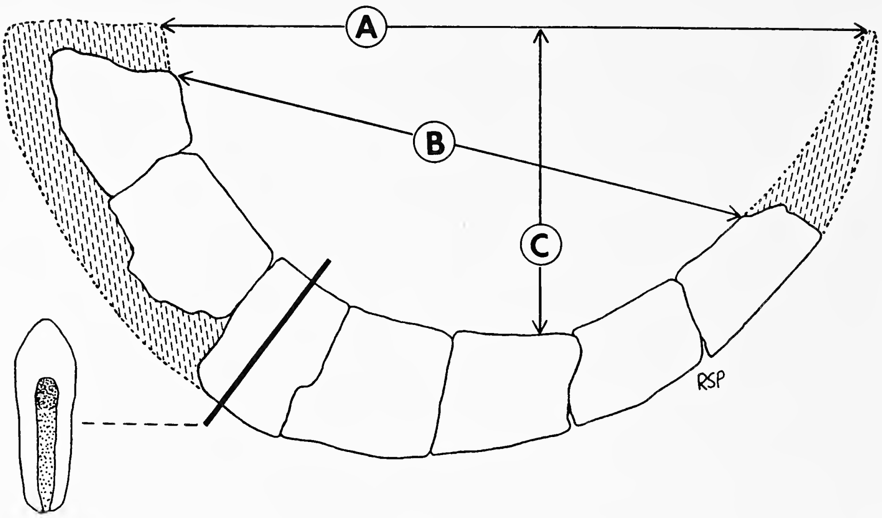

FIGURE 4. Method of measurements of fin spine; A, estimated total length; B, length of specimen as preserved; C, curvature = greatest vertical distance from estimated greatest length to posterior edge of spine; inset shows site, slightly offset, where cross-section was measured.

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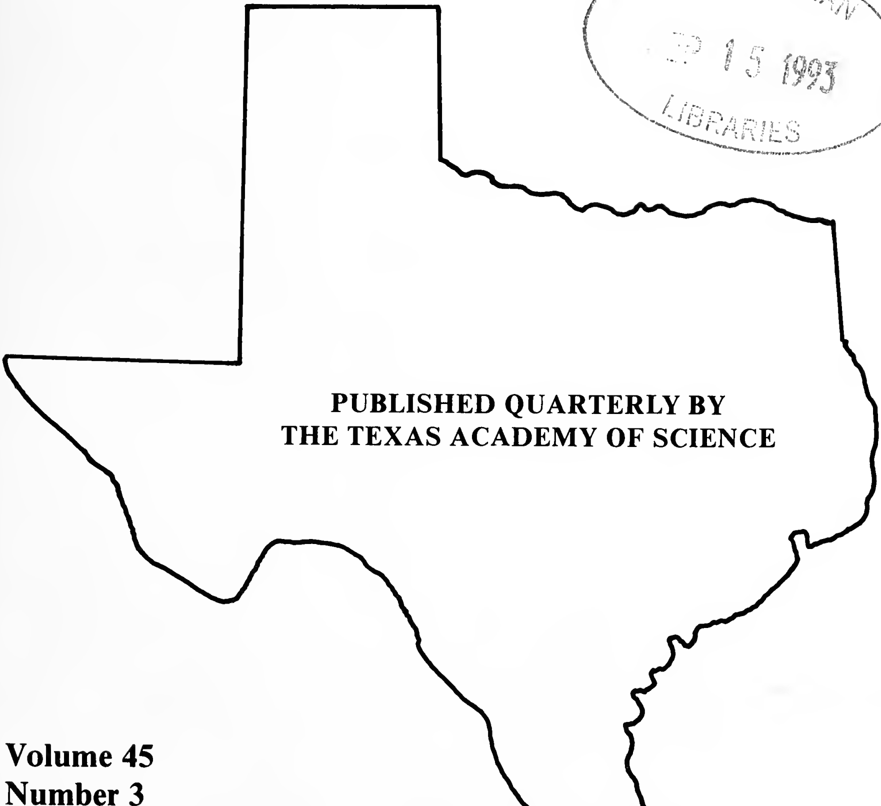

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SIZE DISTRIBUTION PATTERNS AND POTENTIAL POPULATION CHANGE OF SOME DOMINANT WOODY SPECIES OF THE EDWARDS PLATEAU REGION OF TEXAS

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Abstract.—Little documented information is available to demonstrate changes in plant populations of the Edwards Plateau Region of Texas. Photographic documentation is presented to show a lack of *Juniperus ashei* seedlings in an Edwards Plateau evergreen woodland and a high number of *J. ashei* seedlings in heavily grazed Edwards Plateau grasslands. Population size distribution analyses of four of five *J. ashei* stands examined showed a non-normal distribution and suggested a negative exponential population structure, which may be indicative of a species with an expanding population. Inspection of the structure of the fifth stand suggested the self-thinning stage of population growth, with a lack of recruitment into the population. Population structure of *Quercus texana*, *Q. glaucoides* and *Taxodium distichum* stands also suggested the self-thinning stage and a lack of recruitment into the population. Reasons for changes are varied and depend on the community type, but little actual proof is available. High density of *J. ashei* seedlings in grasslands appears to be related to low grass biomass caused by heavy grazing and a concomitant reduction in fire frequency. Lack of recruitment of *J. ashei* seedlings into an apparently mature *J. ashei* stand may be due to seedling shade intolerance. Low recruitment of *Quercus* seedlings in deciduious woodland communities is more than likely due to an increased density of large herbivores. Lack of seedlings of *T. distichum* in riparian forest communities may be caused by light limitations in the understory or lack of safe sites for seedlings. *Key words:* Edwards Plateau; woody plants; plant population change; population structure.

In spite of almost 300 years of settlement by European man, the basic biology and ecology of most plant species found in the Edwards Plateau Region of Texas are essentially unknown. The limited published literature is reviewed in Amos and Gehlbach (1988). Many authors consider the Edwards Plateau Region a separate physiographic unit because of its distinct flora (Tharp, 1939; Blair, 1950; Gould, 1969; Correll and Johnston, 1970; Amos and Gehlbach, 1988). Several endemics occur in the area, and there is a major center of endemism in the southeastern section of the Plateau (Amos and Rowell, 1988). Many eastern species have their western limits on the flood plains of the region, and several southwestern species may be found on the dry ridges of the Plateau, but not much farther north or east (Palmer, 1920; Blair, 1950; Correll and Johnston, 1970).

The Edwards Plateau Region occupies approximately ten million hectares (Gould, 1969). Physiographically it may be divided into the relatively level upper part, and the rough, eroded, heavily dissected section located in the south and southeastern third of the region (Sellards et al., 1932). Geologically, the parent rock is limestone or dolomite except in the central granitic basin (Sellards et al., 1932). Exposed surface formations are Cretaceous in age and relatively level. Formations are frequently composed of alternating beds of hard limestone and softer shales and marls. Area soils are usually shallow except on some of the river terraces, and most are underlain by limestone or caliche (Gould, 1969).

Climatographically, the area is dry, subhumid to semiarid, and mesothermal (Thornthwaite, 1948). A moisture gradient occurs across the region, with approximately 51 centimeters/year falling in the west and 76 centimeters/year in the east, with considerable variation from year to year (Arbingast et al., 1976). Rainfall peaks occur in May and September with approximately 15 percent of the yearly rainfall occurring in each month. A temperature gradient also occurs, with approximately 230 frost-free days in the northwest and 275 in the southeast with mean annual temperatures ranging from 18 to 21°C.

Reports providing anecdotal information on Edwards Plateau vegetation are available from writings of the earliest travelers (see Inglis, 1962). These writings mostly concerned the south and southeastern part of the Edwards Plateau, the area previously bounded by grasslands. Essentially all who wrote about the area mentioned verdant tree-covered hills, including thick stands of juniper and live oak. Thus, the descriptions of early travelers are in agreement: the vegetation of the south and southeastern part of the Edwards Plateau was a juniper-live oak woodland (Fig. 1 A and B).

No information is available concerning the rest of the Plateau, but more open savanna or at least open woodland vegetation intermixed with small prairies may have been characteristic of level areas (Fig. 1 C and D). Many, if not all, of the early travelers in Central Texas mentioned riparian forests. All referred to *Taxodium distichum* (bald cypress) and *Carya illinoinensis* (pecan) along the rivers (Fig. 2 A and B) and oaks in upland communities (Fig. 2 C and D) (see Inglis, 1962). In addition, grassland communities occurred on the upper part of the Plateau and in the larger canyons (Fig. 3 A-D).

Changes have occurred in the plant communities in this region over the past 300 years, apparently caused by increases in grazing and reduction in fire frequency (Smeins, 1980). Changes include thicketization or an increase in density of *Juniperus ashei* (Mexican juniper) and its spread into areas of grassland vegetation (Fig. 1 C). However, evidence is very limited. Certain plant community analyses can suggest stability or lack of stability in a population. In addition, these measurements can sometimes suggest previous community composition and future community changes (Bush and Van Auken, 1987).

Here I report a series of descriptions of the population structure of *J. ashei, Quercus taxana* (Texas red oak), *Q. glaucoides* (Lacy oak) and *T.*

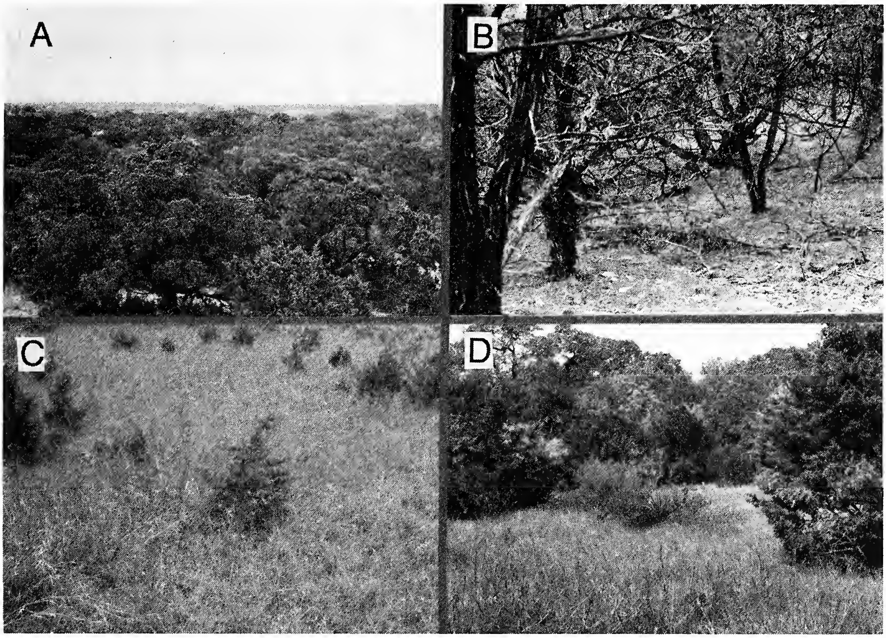

FIGURE 1. Photographs of examples of some of the major Edwards Plateau communities. A. Overview of a mature *Juniperus* - *Quercus* evergreen woodland; B. Interior of a *Juniperus* - *Quercus* evergreen woodland; C. Early establishment of *Juniperus* in unburned prairie; D. Two-phase nature of the evergreen woodland in certain areas, *Quercus fusiformis* mottes or clumps with a high density of *J. ashei* in the understory.

distichum. These are dominant species in the evergreen woodlands, deciduous woodlands and riparian forest communities of the Edwards Plateau Region. Major questions asked concerning the population structure of these species included: (1) Are the populations of these species normally distributed according to size? Woody plant populations measured after fires or harvest demonstrate characteristic stages. These stages are typical of communities during secondary succession and may be found if recruitment occurs over a short period of time. Woody plants of the Edwards Plateau could demonstrate specific stages of population growth after periods of heavy grazing or browsing. (2) Are these populations in the establishment stage, transition stages, or self-thinning stage of community development?

METHODS

Five hilltop evergreen woodland stands on Edwards Limestone were selected for study in Bandera County, Texas (98°36′W and 29°48′N). Stands ranged in development from early successional or newly established *J. ashei* communities to apparently mature *J. ashei* communities. Nine north-slope deciduous woodland communities on Edwards Limestone, but lower in *J. ashei* density, were also studied. In addition, three deciduous forest riparian communities of the Guadalupe River flood plain in nearby Comal and Kendal counties,

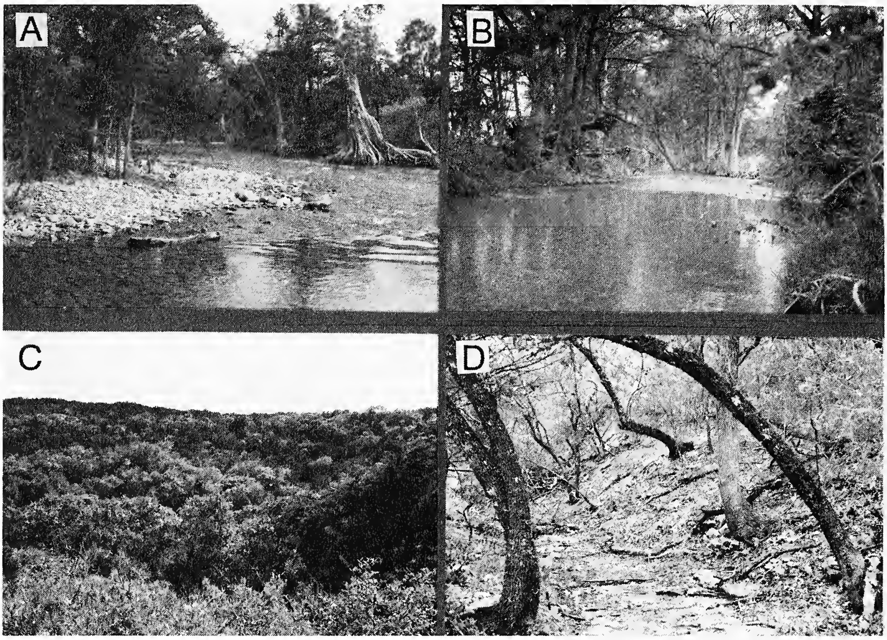

FIGURE 2. Photographs of examples of some of the major Edwards Plateau communities. A. Riparian forest of the Medina River showing *Taxodium distichum* establishment on a bar at the river edge; B. Interior of the riparian forest of the Medina River demonstrating large *T. distichum* trees; C. Overview of a *Quercus texana* - *Q. glaucoides* deciduous woodland with *J. ashei* above and below the deciduous woodland community; D. Interior of the *Q. texana* - *Q. glaucoides* deciduous woodland. Note relatively open understory and lack of *Quercus* seedlings and few *J. ashei* trees, saplings or seedlings.

Texas, were studied. Stands were considered representative of plant communities in the area. All were grazed, but lacked signs of fire, cutting, or other major disturbances.

Upland stands were sampled with the point-centered-quarter method (Cottam and Curtis, 1956). All trees, shrubs and vines greater than one centimeter in basal diameter were measured 10 centimeters above the soil surface. This height, which is below the level of trunk branching, was used to reduce problems associated with the multi-stemmed morphology of many species found in the study area. Only *J. ashei* data were used from each hill-top stand to generate the frequency plots used to infer population change. Because of low density, data for *Q. texana* and *Q. glaucoides* were pooled from all nine deciduous woodlands stands sampled. The riparian stands were sampled with the quadrat procedure (Van Auken and Kaply, 1979). All woody plants greater than one centimeter in diameter were measured at 10 centimeters above the soil surface. Only data for *T. distichum* are presented, pooled over the three stands sampled. Other phytosociological data for these stands may be found in Van Auken et al. (1979, 1980, 1981) and Ford and Van Auken (1982).

The diameters for each woody species were grouped into appropriate size classes by dividing the diameter of the largest individual measured for each species sampled by 12. Thus, 12 contiguous, non-overlapping size classes were used. Frequency distributions were compared with χ^2 analyses (Steel and Torrie, 1980). Species frequency distributions also were compared for skewness (g1, asymmetry) and kurtosis (g2, peakedness) (Sokol and Rohlf, 1981). All analyses were done with the SAS computer system (SAS Institute, 1982).

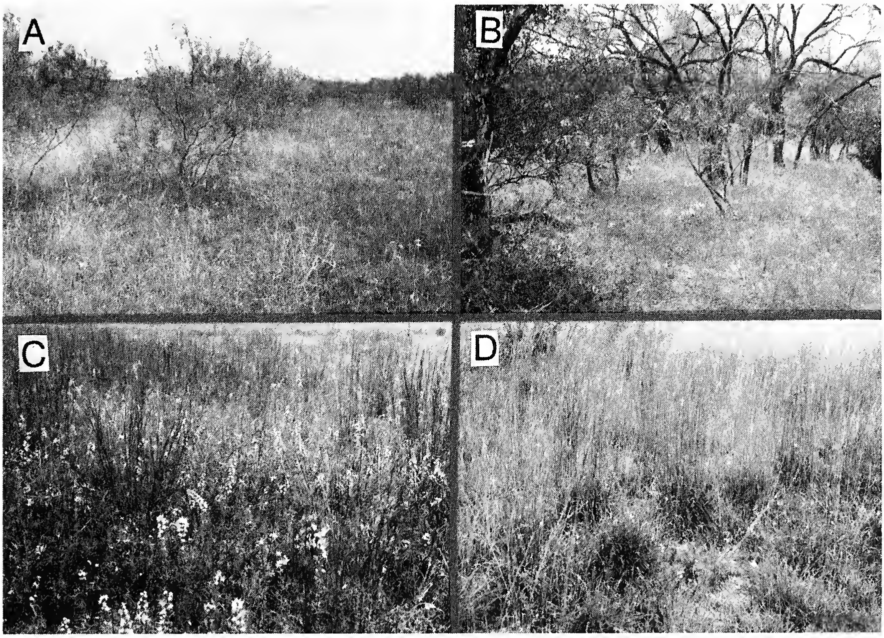

FIGURE 3. Photographs of examples of some of the major open communities of the Edwards Plateau. A. Early colonization of overgrazed prairie by *Prosopis glandulosa* on deeper soils; B. Later stage of an open canopy *P. glandulosa* deciduous woodland; C. Relic midgrass prairie with *Schizachyrium scoparium* as the dominant grass and *Liatris mucronata* in bloom; D. Relic *S. scoparium* stand on deeper soils in the escarpment region.

RESULTS

The frequency distribution of *Juniperus ashei* was non-normal in all stands. In four of the five stands examined, the population appeared to be expanding with an inverted "J" or negative exponential distribution, which has the greatest percent of individuals in the smallest size class (Fig. 4 A-D). The population structure of *J. ashei* would be expected to be non-normal if *J. ashei* were an early successional species establishing after a community disturbance. The non-normalcy of the distribution is also demonstrated by examining skewness and kurtosis (Table 1). The fifth stand is also non-normal and positively skewed, but this stand demonstrates some interesting trends (Fig. 1 E). There were only eight individuals (9% of the population) in the smallest size class compared with 40-65% for the other stands. When the smallest size class of the fifth stand was examined by subdividing it into 12 additional size classes (Fig. 1 F), it was obvious there were no very small individuals entering the population. In addition, qualitative observation during the study did not reveal smaller *J. ashei* individuals in the study areas.

Table 1. Analyses of size-class frequency distributions of some of the major Edwards Plateau upland and riparian forest species. Components presented include sample size (n), distribution (D, normal N or non-normal -), skewness (S), and kurtosis (K). Probability values (*P*) are the probability of making a type I error (* = $P < 0.05$, **=$P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$). *Juniperus ashei* A, B, C, D and E refer to the stands presented in Figure 4.

Species	Stand	n	D	S	K
Juniperus ashei	A	16	-*	1.75**	2.40*
	B	71	-****	0.74**	-0.77
	C	76	-****	1.14***	0.38
	D	79	-***	0.81***	0.81
	E	89	-***	0.50*	-0.26
	F	8	N	0.60	-1.28
Quercus texana		122	-****	0.90***	0.91*
Q. glaucoides		95	N	0.81***	0.43
Taxodium distichum		46	-****	1.03***	2.02***

The trend in total woody plant density, from high in Juniper stand A (Table 2) to low in stand E (Table 2), suggested community self-thinning. The trend in total basal area per hectare was the reverse: lowest in A and highest in E. *Juniperus ashei* basal area followed the same trend. When total woody plant density was regressed on *J. ashei* total basal area, a significant negative regression was found with a high coeffiecient of determination ($r^2 = 0.75$, $P<0.05$), again suggesting self-thinning. All stands presented in Figure 4 had a very high *J. ashei* relative basal area (76 - 98%). In addition, a large percent of the *J. ashei* population was in the smallest size class in stands A-D, however, that trend changed in the fifth and apparently oldest stand examined (Fig. 4 E).

When the size-frequency distributions for the two upland deciduous forest species were examined, other patterns appeared (Fig. 5 A and B). The distribution of *Q. texana* was not normal, but the distribution approached a normal curve. The distribution was significantly skewed and leptokurtic (peaked) (Table 1). The population of *Q. glaucoides* was normally distributed, not skewed and kurtosis was normal (not peaked or flat). The interesting aspect about these two species was a lack of recruitment into the population. *Taxodium distichum*, the only riparian forest species examined, did not have a normal population distribution (Fig. 5 C) and the distribution exhibited significant skewness and kurtosis (Table 1). Casual examination of Figure 5 C suggests some recruitment into the *T. distichum* population. However, *T. distichum* was a much larger tree than the other species, with the largest individual greater than 300 centimeters in diameter. When the smallest size class from these populations was subdivided into 12 equal classes, it was apparent that

TABLE 2. Comparison of total density (plants/ha), total basal area (m^2/ha), and density and basal area for *Juniperus ashei*, in the five woodland communities studied. Letters correspond to stands used in Table 1 and Figure 4.

Community Type Juniper Woodland	Total Density	Total Basal Area	*J. ashei* Density	*J. ashei* Basal Area
A	4053	17.5	649	13.4
B	1165	34.1	689	33.2
C	1166	50.2	874	48.5
D	1424	48.5	1253	48.1
E	763	66.8	679	64.7

very little recruitment was occurring for bald cypress (Fig. 5 D). The smallest individuals found were greater than 15 centimeters in diameter, not seedlings. The frequency of plants present in the seven smallest size classes was zero.

DISCUSSION

Evidence of change in community composition in the Edwards Plateau Region is more hearsay than fact. However, photographic evidence presented in Figure 1 C certainly demonstrates what many people living in and traveling through the Edwards Plateau Region have seen time and time again: a large number of small *J. ashei* seedlings beginning growth in a heavily grazed grassland. In addition, certain analyses can suggest previous and sometimes future community changes. Earlier studies of composite data using means from a series of *J. ashei* communities demonstrated an apparent expanding population with a negative, exponential function (Van Auken et al., 1979, 1980; Van Auken, 1988). Analyses of single stands were not attempted because of high stand-to-stand variability and lack of a perceived pattern. However, population structure analyses using more standard techniques (Mohler et al., 1978) and single stands of *J. ashei* demonstrated several different population patterns rather than just high variability (Fig. 4). Four of the stands suggested an expanding population, while the fifth stand examined suggested the self-thinning stage of a population with a contracting or reduced density. Furthermore, the smallest individuals sampled in the fifth stand were two centimeters in diameter and there were only three individuals. In addition, there were no plants found in the one centimeter size class, the smallest size class examined. The population of this stand appeared to be quite different from all others studied.

It is easy to measure the size of woody plants in a population, and assume that size is equal to age, which is not necessarily true (Harper, 1977). It is probably better to measure size because reproductive behavior appears to be more closely correlated with size (Harper, 1977). In the

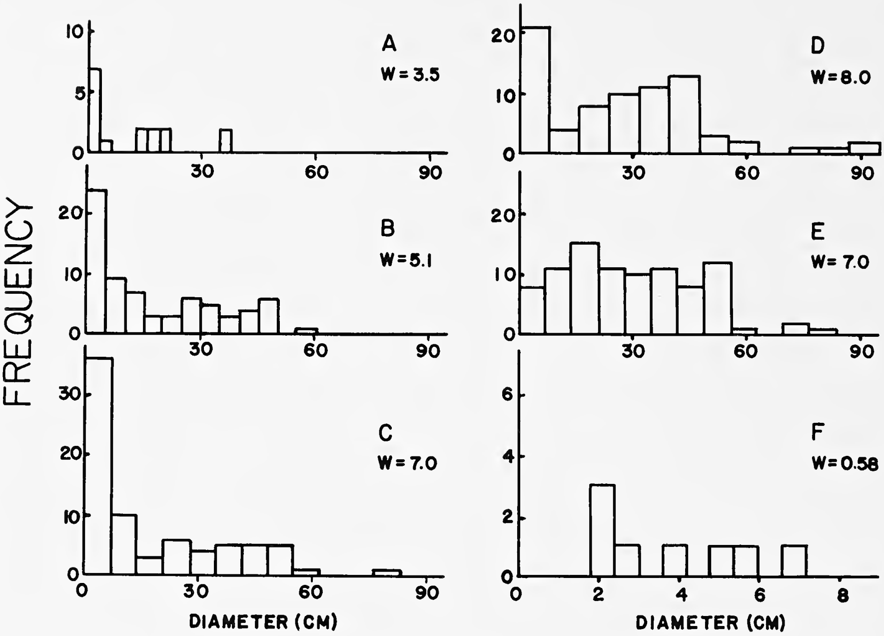

FIGURE 4. Frequency diameter size-class distributions for *Juniperus ashei* in five Edwards Plateau evergreen woodland stands. The population of each stand was apportioned into equal size classes by dividing the diameter of the largest tree by 12. The smallest size class in E was divided by 12 and that information is presented in F. The size class width in cm = w.

present study, population structure was used to estimate current or previous woody plant establishment. Under-representation of *J. ashei*, which appears to be a pioneer species, could certainly be interpreted as future loss of this species from the ecosystem (Whittaker, 1975). This does not seem to be a reasonable conclusion based on the current widespread distribution and high density of *J. ashei* in the Edwards Plateau. Changes appear to be taking place, suggesting reduced density in the future in many stands. Certainly, there are other interpretations of the population structure of *J. ashei*. It is possible that *J. ashei* could have constant age specific mortality resulting in non-normal size distributions. I would argue against this interpretation because of the lack of recruitment in stand E (Fig. 4 F) which appears to be the most mature stand. Perhaps constant age specific mortality occurs until canopy closure, resulting in almost 100 percent seedling mortality. I think that most *J. ashei* stands in the Edwards Plateau region are probably not mature stands because of past cutting, and possibly the presence of fire, but unfortunately almost no evidence is available to support this claim.

Species size- or age-distributions should not be considered separately

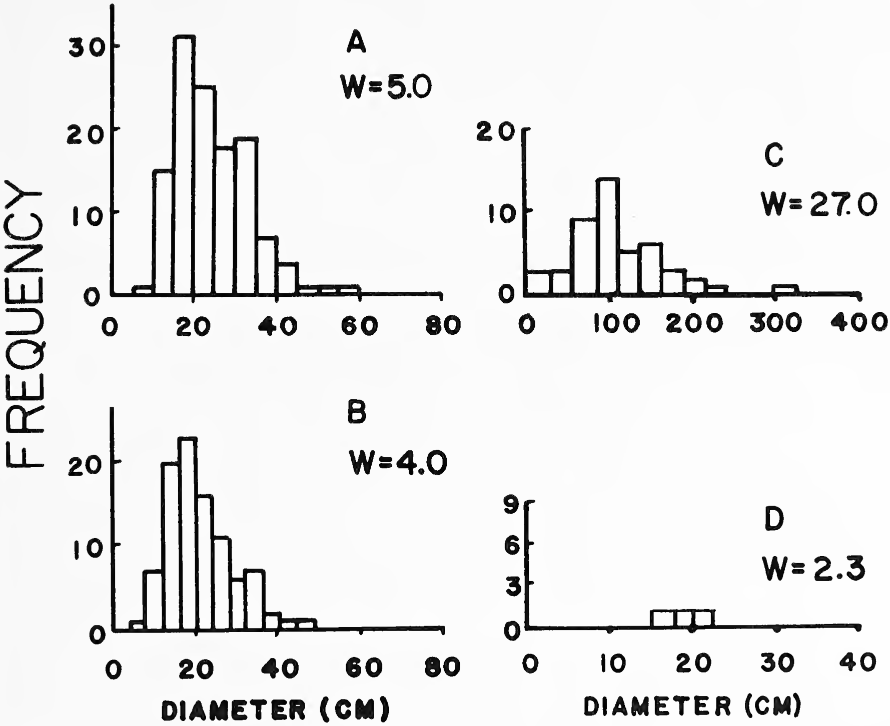

FIGURE 5. Frequency diameter size-class distributions for *Quercus texana* (A), *Q. glaucoides* (B), and *Taxodium distichum* (C, D). The data for *Q. texana* and *Q. glaucoides* from nine deciduous woodland stands were pooled because of low density and stand similarity. Data for three stands of bald cypress were also pooled for the same reasons. Figure 5 D represents the smallest size class from 5 C. Populations were apportioned into equal size classes by dividing the diameter of the largest individual of each species by 12. The size class width in cm = w.

but as part of a time continuum (Mohler et al., 1978). The population distribution for *J. ashei* was, in four of five cases examined, a negative exponential, which suggests a population expanding into a new site such as an overgrazed grassland or a recently cut woodland, but proof using a marked segment of the population is not available. Populations of *J. ashei* may be adjusting to relatively new conditions of low fire frequency caused by fuel removal by excessive overgrazing of the associated grasses, and considerable cutting. Juniper species seem to grow whenever resources are available (Lassoie et al., 1983), so that it is impossible to age from growth rings, and replacement dynamics are unknown. Several Juniper species are old-field invaders, and appear to be well adapted to low nutrient-high light environments (Ormsbee et al., 1976). *Juniperus ashei* probably has very similar requirements and occupies a similar niche. The *J. ashei* stand that showed a lack of recruitment of small individuals may have been disturbance-free for a considerable period of time, as evidenced by the large *J. ashei* basal area. Although most evidence for *J. ashei* suggests a species expanding its population, at least one stand appears to be mature and its' density may be declining.

There does not seem to be any ambiguity about the under-representation of small *Q. glaucoides* and *Q. texana*. The data suggest no recruitment of juveniles of these species into the adult population. The reason for this is not known. Possible reasons include changes in local climate, changes in disturbance regime, increases in herbivore populations, or establishment may be episodic and reflect local environmental conditions (Auclair and Cottam, 1971; Harper, 1977; Harcombe and Marks, 1978). The populations of many other species of the Edwards Plateau may also be adjusting to such changes. Records do not indicate local climate changes. On the other hand, populations of white-tailed deer (*Odocoileus virginianus*) in the Edwards Plateau have increased dramatically in the last 50 years (Doughty, 1983). These large deer populations could well be the cause of lack of recruitment of many deciduous species. Changes in the population of *T. distichum* also seem to be occurring, but the reason may be very different. *Taxodium distichum* populations appear to require disturbances such as large floods for recruitment. The canopy overstory must be open for sufficient light to reach the understory for establishment and seedling growth, and seedlings must have sufficient water (Neufeld, 1983; Titus, 1990). If the bands of *T. distichum* that are presently found along the many creeks and rivers of the Edwards Plateau are to be perpetuated, future disturbances in the way of floods must occur in this ecosystem, or artificial manipulation such as thinning may be required. Similar lack of recruitment for *T. distichum* has been reported for the floodplain forests of the Savannah River (Sharitz et al., 1990).

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INHERENT LEVELS OF SOMATIC CHROMOSOMAL ABERRATIONS AMONG THREE POPULATIONS OF *SIGMODON HISPIDUS* FROM NORTH—CENTRAL TEXAS

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Abstract.—Somatic chromosomal variation in *Sigmodon hispidus* from three closely situated localities in north-central Texas is restricted to uniformly low levels (mean frequency of abnormal cells = 0.064). Inter- and intrapopulational variation was insignificant, and breaks of chromosomes or of individual chromatids account for most of the observed cytogenetic aberrations. Comparisons of this study with other investigations must be made with caution, however, because of the possibility of more widespread geographic variation in the incidence of chromosomal variation. Further caution is also warranted because of variables inherent to the philosophy of individual investigators. *Key words*: chromosomal variation; north-central Texas; *Sigmodon hispidus.*

The hispid cotton rat, *Sigmodon hispidus*, is a subtropical grasslands mammal which ranges from Panama into the United States as far north as Nebraska (Hall, 1981). The species is practically ubiquitous in Texas, and is usually readily obtainable in sufficient numbers for any number of comparative studies. Its ground-dwelling life style and herbivorous feeding habits make the species an ideal candidate for absorbing residual soil contaminants.

The use of rodents as indicators of mutagenesis resulting from exposure to contaminated environments has not been fully explored (McBee and Bickham, 1990). McBee et al. (1987) reported the cytogenetic effects of petrochemical pollutants on natural populations of small mammals. They described a significantly higher incidence of somatic chromosomal abnormalities among the 10 individuals of *S. hispidus* from a petrochemical waste disposal site when compared to 11 animals from a nearby and presumably pristine control site.

A possible criticism, as pointed out by McBee et al. (1987), of studies such as theirs is the lack of knowledge of the inherent genetic (somatic) variability of those species being examined, as well as the extent that such levels of variability may differ geographically. These data for most natural populations, including those for *S. hispidus*, are presently lacking. The purpose of this study was to evaluate inter- and intrapopulational levels of somatic chromosomal variation among three separate populations of the hispid cotton rat from presumably uncontaminated areas. Only by establishing such baseline data for purposes of comparison can we hope to determine the effects of artificially introduced pollutants or contaminants on natural populations.

Methods and Materials

A total of 25 specimens of *Sigmodon hispidus* were live-trapped in natural habitats from three different sites in north-central Texas, using aluminum Sherman live traps baited with rolled oats. Sample sizes and a brief description for each site are presented below.

Collecting localities.—The first site, collected on 3 February 1991 (n=10; 3.0 mi. S, 0.5 mi. W Windthorst, Archer County), is a 24.3 hectare soil bank dominated by mesquite (*Prosopis glandulosa*) and Johnsongrass (*Sorghum halepense*). The second locality was collected on 14 February 1991 (n=10; near Wichita Falls Clinic in Wichita Falls, Wichita County), and is about 40 kilometers northeast of the first site, where broomweed (*Amphiachyris dracunculoides*) and dense stands of mesquite predominate. The third area, collected on 21 February 1991 (n=5; near Lake Wichita in Wichita Falls, Wichita County), is approximately 32 kilometers north of the first site, and about eight kilometers to the southwest of the second locality. Winter wheat fields abut a housing development here, and traps were set along a fencerow dominated by Johnsongrass and various forbs.

Karyotypic analysis.—Animals were transported to the laboratory, where they were maintained in cages. They were yeast-stressed for periods of one to three days and karyotyped following the protocol of Lee and Elder (1980), as modified by Baker and Qumsiyeh (1988). Depending on the mitotic index, five to 10 slides were prepared from the cell suspensions of each individual. These were non-differentially stained with a Giemsa solution for microscopic examination. Voucher specimens, accompanied by standard field data, are deposited in the Collection of Recent Mammals, Midwestern State University.

Only isolated cells with a discernibly complete diploid complement (2N=52, Fig. 1; Zimmerman, 1970) were included in the analyses. Individual cells were judged "abnormal" if one or more chromosomal aberrations were observed in a given spread, without regard to type of abnormal chromosomal configuration or to number of aberrations per cell. Initial scoring for each locality was accomplished immediately upon completion of processing of the last individual from each site, by examining from 100 to 500 cells per individual. Slides representing each of the 25 specimens were then disguised and coded before blind scoring of a total of 20 complete spreads per individual.

Frequencies of occurrence of abnormal cells were noted for each individual and lumped for each locality in both initial and blind studies.

Results

No distinction was made between types of somatic mutations, because detected chromosomal abnormalities were almost entirely breaks of chromosomes or of individual chromatids (Fig. 1). Rarely were spreads interpreted as exhibiting a translocation, acentric chromosome, or dicentric chromosome.

Initial scoring, by locality, of 4000 cells from the 10 Windthorst site animals, 1000 cells from the 10 Clinic site animals, and 500 cells from the five Lake site animals produced respective abnormal cell frequencies of 0.117, 0.055, and 0.080, but results from Student's *t*-tests showed no significant differences between individuals from the same locality.

Blind scoring of 20 cells per slide from each of the 25 individuals (Table 1) statistically analyzed by using Student's *t*-tests revealed no significant differences between the frequency of occurrence of abnormal cells from samples taken at the Windthorst (f=0.065), Clinic (0.065), and Lake (0.060) sites. Individual frequencies of occurrence of abnormal cells

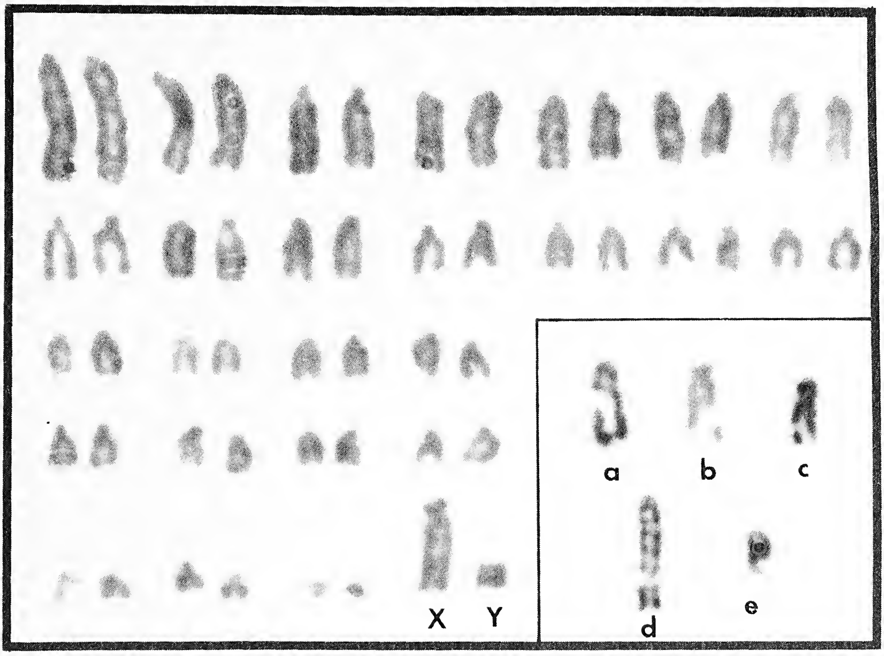

FIGURE 1. Normal non-differentially stained standard karyotype of a male *Sigmodon hispidus* for comparison to observed examples of somatic chromosomal aberrations: a-c, chromatidal breaks; d, chromosomal break; e, translocation.

from the pooled sample (results from the blind study) ranged from 0.000 (n=3) to 0.150 (n=1).

DISCUSSION AND CONCLUSIONS

Of the 550 cells from 11 individuals of *Sigmodon hispidus* examined by McBee et al. (1987) from their study's control site, 15 were judged abnormal (f=0.027), and 13 of these were breaks of chromosomes or individual chromatids. Comparing this study with McBee et al. (1987) permits certain conclusions to be drawn pertaining to somatic variation in the hispid cotton rat and the conduction of similar studies in the future.

Analysis of the large sample sizes from the initial scoring in this study provides evidence that a certain degree of somatic chromosomal variation is inherent to natural populations of the species, that breaks of the chromosomes and chromatids account for most of this variation, and that the frequency of occurrence of abnormal cells is rather uniform within populations.

Given the similarity of frequencies from each of the localities in the blind study (Table 1), the discrepencies of the frequency with which

Table 1. Results of blind scoring of frequency of abnormal cells in 25 individuals of *Sigmodon hispidus* from three collecting localities described in text. Descriptive statistics are sample size (n), mean frequency (f), and standard deviation (SD). Differences between localities are not significant.

Individuals	Cells Normal (abnormal)	Frequency
	Windthorst (n=200, f=0.065, SD=0.034)	
W1	19 (1)	0.050
W2	18 (2)	0.100
W3	19 (1)	0.050
W4	19 (1)	0.050
W5	20 (0)	0.000
W6	18 (2)	0.100
W7	18 (2)	0.100
W8	19 (1)	0.050
W9	18 (3)	0.100
W10	19 (1)	0.050
	Clinic (n=200, f=0.065, SD=0.047)	
C1	17 (3)	0.150
C2	19 (1)	0.050
C3	19 (1)	0.050
C4	20 (0)	0.000
C5	18 (2)	0.100
C6	19 (1)	0.050
C7	18 (2)	0.100
C8	20 (0)	0.000
C9	18 (2)	0.100
C10	19 (1)	0.050
	Lake (n=100, f=0.060, SD=0.022)	
L1	19 (1)	0.050
L2	19 (1)	0.050
L3	19 (1)	0.050
L4	19 (1)	0.050
L5	18 (2)	0.100

abnormal cells were recorded by locality in the initial scoring are attributed to such temporal influences as acquisition of experience and adjustments in scoring methodology and philosophy for each scoring run.

Discrepencies between the mean frequency of abnormal cells from the control site of McBee et al. (1987) in Brazos County of southern Texas (0.027) and the three closely situated sites in Wichita and Archer counties of north-central Texas (0.064) may be partly due to geographic variation in the incidence of such abnormalities. However, the initially scored frequency differences among the three north-central Texas localities indicate that experience is influential. Individual scoring techniques doubtless introduce other variables, for some workers will be more discerning, or perhaps less conservative in the assignment of questionable spreads as "abnormal". The comparisons of results from studies by different workers must therefore be made with caution, and the determination of any widespread geographic variation in somatic chromosomal variability in *Sigmodon hispidus* must await a broader-scoped study by a single investigator.

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DETERMINATION OF AGE GROUPS IN *THOMOMYS UMBRINUS* (RODENTIA: GEOMYIDAE)

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Abstract.—A series of qualitative characters, especially the development of the zygomatics and rostrum, was used to assess four age groups of 288 specimens of *Thomomys umbrinus* from Sierra de Tlaxco, México. Twenty-two cranial measurements were evaluated and a subset of 11 variables was subjected to both a discriminant analysis and a canonical discriminant analysis. All analyses were performed with the sexes separated. In males, the height of the maxillary crest, middle zygomatic breadth and breadth across bullae were the best discriminating characters among age groups. In females, the anterior zygomatic breadth, followed in order of importance by the middle zygomatic breadth, length of braincase and length of nasals were the best discriminators of age. To compare the efficacy of the method proposed here, to the closure of the basioccipital-basisphenoid suture, specimens were rearranged in four age groups using the condition of the suture and the set of 11 variables was subjected to discriminant techinques. Efficacy by the method of the suture was 80.4% for males and 63.1% for females. Although both methods are useful to separate male individuals in extreme age classes (I, IV), the suture-method is less accurate for age groups II and III in either sex.

Age determination is fundamental in systematic and taxonomic studies to assess non-geographic and geographic variation of species. Because most of the morphological systematic or taxonomic studies of pocket gophers are based on randomly trapped, *post mortem* specimens, Thaeler (1967) and Hoffmeister (1969) proposed the degree of fusion of five and two skull sutures, respectively, as criteria for age determination in pocket gophers. Of these seven sutures, the basisphenoid (i.e., basioccipital-basisphenoid) has been the most commonly used since it was recommended by Hoffmeister (1969). However, when we examined this suture to assign specimens of *Thomomys umbrinus* to age groups (during a study on non-geographic variation in the species) we noticed that the criterion was highly influenced by the individual perception of relative terms such as "very" or "slightly" closed or open. Indeed, some authors have considered only three age classes in pocket gophers and have discarded specimens that did not have "closed" or "almost closed" basisphenoid suture (considered "adult" specimens) from their studies of morphological variation (Honeycutt and Schmidly, 1979; Heaney and Timm, 1983; Wilkins, 1985). However, during the examination of more than 800 specimens of *Thomomys umbrinus*, we noticed a number of females with "open" sutures bearing fetuses. Therefore, if the term "adult" is to reflect sexual maturity, these specimens should be included in the analyses.

Patton and his coworkers have studied a population of *T. bottae* in a restricted area for many years and have correlated the closure of cranial sutures, including the basisphenoid, with known-aged individuals (Smith and Patton, 1980; Daly and Patton, 1986; Patton and Brylski, 1987). Although their system allowed them to arrange skulls into six age groups, as well as to distinguish adults from juveniles, most investigators studying morphological variation in other species of pocket gophers by sampling or examining voucher specimens lack conditions in which subjectiveness can be avoided.

As a result of measuring more than 800 museum specimens from the Mexican Transvolcanic Belt, we propose a series of qualitative criteria from the general morphology of the skull of *T. umbrinus* which comprise the: 1) inflation of braincase; 2) proportion between braincase and rostrum; 3) development of zygomatic arches; and 4) presence and conspicuousness of parietal and, especially, maxillary crests.

Here, we present the results of discriminating multivariate techniques which we used to test the efficacy of our criteria in a sample of field-trapped *T. umbrinus* from Sierra de Tlaxco, State of Tlaxcala, México. Among other advantages, these statistics allow the assessment of specific characters whose ranges can be described. We also show the result of comparing such efficacy with that obtained from assessment of the basisphenoid suture.

METHODS

A sample of 288 skulls from several nearby (no more than five kilometers apart) and ecologically similar localities of Sierra de Tlaxco, Tlaxcala, México, which is housed at the Mammal Collection, Universidad Autónoma Metropolitana, Unidad Iztapalapa (UAMI), was selected and all individuals were separated by sex and arranged in one of four age groups as follows (Fig. 1):

Age I. Neither parietal nor maxillary crests present. Braincase highly inflated and much larger than rostrum. The rostrum is concave, fine, and short. Very slender zygomatic arches converging anteriorly.

Age II. Cranial crests starting to appear. Rostrum more developed; braincase less inflated, but still short and slightly concave. Zygomatic arches less slender, but still converging anteriorly.

Age III. Parietal and maxillary crests present. Skull completely developed. Rostrum straight and well developed. Zygomatic arches robust and parallel or tending to diverge anteriorly.

Age IV. Parietal and, especially, maxillary crests well developed and very conspicuous. Skull very ossified and bulky. Zygomatic arches very robust and diverging anteriorly.

To compare this approach with the condition of the basisphenoid suture (Hoffmeister, 1969), specimens were rearranged in four age groups according to the degree of closure. In the first age group (I), the basioccipital and the sphenoid bones are completely separated and a wide portion of cartilage is present between them. In the second age group (II), the bones are still separated and the cartilage is narrower. In the third age group (III), the

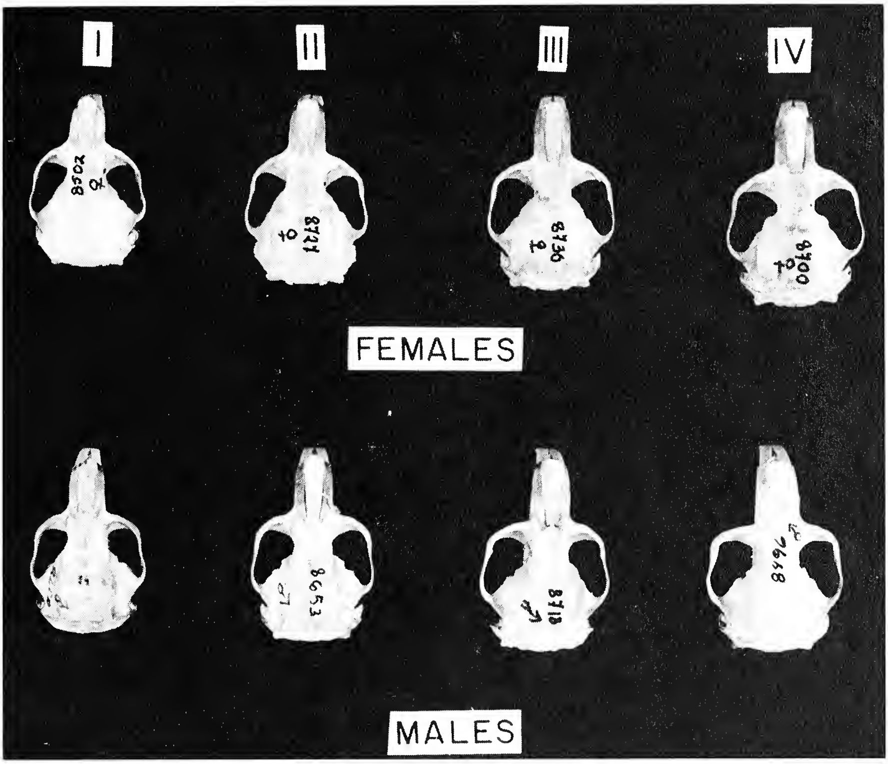

Figure 1. Dorsal view of eight skulls of *Thomomys umbrinus* showing the four (I-IV) age groups considered in this study. Note the progressive development of the rostrum and zygomatics. See text for details.

bones are still separated, but their epiphyses are beginning to touch by their lateral extremes and the disappearing portion of cartilage comprises a thin layer or remains in the middle between the bones. In the fourth age group (IV), both bones are completely fused with a line of suture present or absent and the cartilage is absent.

A total of 22 measurements were taken from the skulls with a dial caliper to the nearest 0.01 millimeter; however, we only examined the 11 characters which separated every age group (Table 1). These mensural characters (Fig. 2) include: total length of skull (TLS); length of nasals (LNA); length of zygomatic arch (LZA); length of braincase (LBC); length of maxillary diastema (LDI); anterior zygomatic breadth (AZB); middle zygomatic breadth (MZB); posterior zygomatic breadth (PZB); breadth across bullae (BAB); height of maxillary crest (HMC); and middle height of braincase (HMB).

Data for each sex were entered and processed separately in a PC, using Statistical Analysis System, versions 85 and 89 (SAS Institute, Inc., 1985). Statistics for determining the accuracy of the characters proposed here were performed in two steps according to the discriminant analysis theory (Anderson, 1958; Press, 1971; Tatsuoka, 1971). The first step included a direct approach with an analysis of variance and multivariate discriminant techniques. The second step included Wilks' lambda test followed by the discriminant statistics (Norusis, 1978).

To determine which of the 22 measurements separated ($P \leq 0.05$) every age group, a simple analysis of variance and Duncan's test for multiple means (PROC GLM) were run

TABLE 1. Mean value ($\bar{x}$), interval (Min-Max) and sample size (N) of 11 mensural characters of the skull which separate age groups (I-IV) within sexes (males, M; females, F) using 288 specimens of *Thomomys umbrinus* from Sierra de Tlaxco, Tlaxcala, Méxíco. Measurements are given in millimeters.

	Males			Females		
Age Groups	$\bar{x}$	Min-Max	N	$\bar{x}$	Min-Max	N
		Total length of skull (TLS)				
I	30.67	28.3-32.3	11	30.91	29.4-32.1	19
II	33.98	31.6-36.5	30	33.27	30.9-35.1	84
III	36.44	34.6-38.2	47	34.67	33.1-37.3	57
IV	37.64	35.5-40.0	22	36.12	34.2-37.6	6
		Length of nasals (LNA)				
I	9.65	8.5-10.6	10	9.66	8.8-10.5	16
II	11.32	9.5-13.1	30	10.84	9.2-12.0	82
III	12.41	11.0-14.2	47	11.65	10.6-13.2	60
IV	13.01	11.6-14.0	22	12.47	11.2-13.7	6
		Length of zygomatic arch (LZA)				
I	14.21	13.4-15.1	11	14.13	13.4-15.2	20
II	15.64	14.4-17.1	31	15.53	14.2-16.9	86
III	16.96	16.0-18.5	49	16.20	15.1-17.2	63
IV	17.38	16.0-18.5	22	17.13	16.1-19.0	6
		Length of braincase (LBC)				
I	20.84	19.7-22.0	11	21.00	20.1-22.3	19
II	22.79	20.9-24.4	30	22.46	20.8-23.7	84
III	24.15	23.2-25.3	47	23.16	22.2-24.8	57
IV	24.63	23.3-25.6	22	24.05	23.5-22.2	6
		Length of the diastema (LDI)				
I	10.36	9.2-11.3	11	10.52	9.1-11.3	20
II	12.48	11.0-14.3	31	12.17	10.6-14.4	86
III	13.98	13.0-15.2	49	12.94	12.2-14.5	63
IV	14.70	13.6-15.8	22	13.80	12.6-15.2	6
		Anterior zygomatic breadth (AZB)				
I	18.75	17.2-20.2	10	19.07	17.5-20.1	19
II	21.93	20.3-23.9	30	20.96	11.8-22.8	78
III	23.87	21.9-25.6	46	22.15	20.6-24.0	61
IV	24.94	23.7-25.8	21	23.75	22.4-25.3	6
		Middle zygomatic breadth (MZB)				
I	18.80	17.9-19.8	8	19.25	18.0-20.0	11
II	22.11	20.5-24.2	28	21.17	22.2-22.9	74
III	24.02	22.3-25.6	44	22.36	21.1-24.2	59
IV	25.24	23.8-26.4	21	23.82	22.7-25.5	6

TABLE 1. Continued.

		Posterior zygomatic breadth (PZB)				
I	20.24	19.2-21.2	8	20.41	18.6-21.6	13
II	23.20	21.4-24.8	28	22.40	21.3-24.0	77
III	25.19	23.6-26.5	45	23.66	22.0-25.5	58
IV	26.44	24.9-27.8	21	24.70	23.1-26.8	6
		Breadth across the bullae (BAB)				
I	17.13	16.1-18.0	11	17.38	16.0-18.9	19
II	18.92	17.3-19.9	30	18.39	16.6-20.0	84
III	19.84	18.9-21.1	47	18.93	17.5-20.4	57
IV	20.40	19.7-21.5	22	19.83	19.0-21.0	6
		Height of maxillary crest (HMC)				
I	9.98	9.1-10.7	11	10.21	9.3-11.0	20
II	11.71	10.6-12.8	31	11.48	10.2-12.3	86
III	12.94	12.2-14.0	49	12.18	11.1-14.2	63
IV	13.50	12.7-14.1	22	12.83	12.0-13.9	6
		Maximum height of skull (MHS)				
I	11.85	10.9-12.7	11	11.92	10.8-13.0	20
II	12.77	11.8-13.4	30	12.57	11.4-13.5	85
III	13.52	12.8-14.7	48	13.05	12.1-14.2	62
IV	13.98	13.2-14.8	22	13.57	12.9-14.4	6

for each variable. Because SAS eliminates all specimens with one or more missing values and, therefore, results in different sample sizes for each variable, these analyses were performed on a subset of 90 females and 80 males of the specimens from Tlaxcala, which had data for all the variables. All other analyses were executed on the total sample (Table 1).

A discriminant analysis (PROC DISCRIM, SAS) was performed to ascertain the percentage of correctly-classified individuals in each of the *a priori* assigned age groups; the degree of overlap between age groups, and the age groups with no overlap (Table 2). The analysis also was used to examine the efficacy (or percentage success) of the characters as a function of the total number of specimens correctly classified, divided by the total number of individuals entered in the analysis.

Discriminant functions necessary (CAN) for separating age groups, and determination of their relative importance for explaining total variation, were assessed with a canonical discriminant analysis (PROC CANDISC, SAS). Canonical coefficients (Table 3) were used to determine which variables were most useful as discriminating criteria for the age groups. Centroids of each age group were calculated, and these, together with all individuals, were plotted in a bidimensional territorial map, using CAN1 and CAN 2 (Fig. 3).

Wilks' lambda analysis (PROC STEPDISC, SAS) was executed to reduce the number of variables employed in the separation of individuals into the age groups, in terms of their computed discriminating relevance. The efficacy of the resulting set of variables was estimated with PROC DISCRIM and PROC CANDISC (Tables 2 and 3).

To compare our characters for discriminating age groups with the basisphenoid suture, all procedures except Wilks' lambda were performed on the reclassified specimens. Percentage success and distributional plots (Tables 2 and 3; Fig. 3) also were obtained.

Specimens examined (288 UAMI).- TLAXCALA: El Final de la Senda, 2700 m, 16; El Final de la Senda, 1750 m, 36; El Final de la Senda, limite Puebla-Tlaxcala, 15 km N

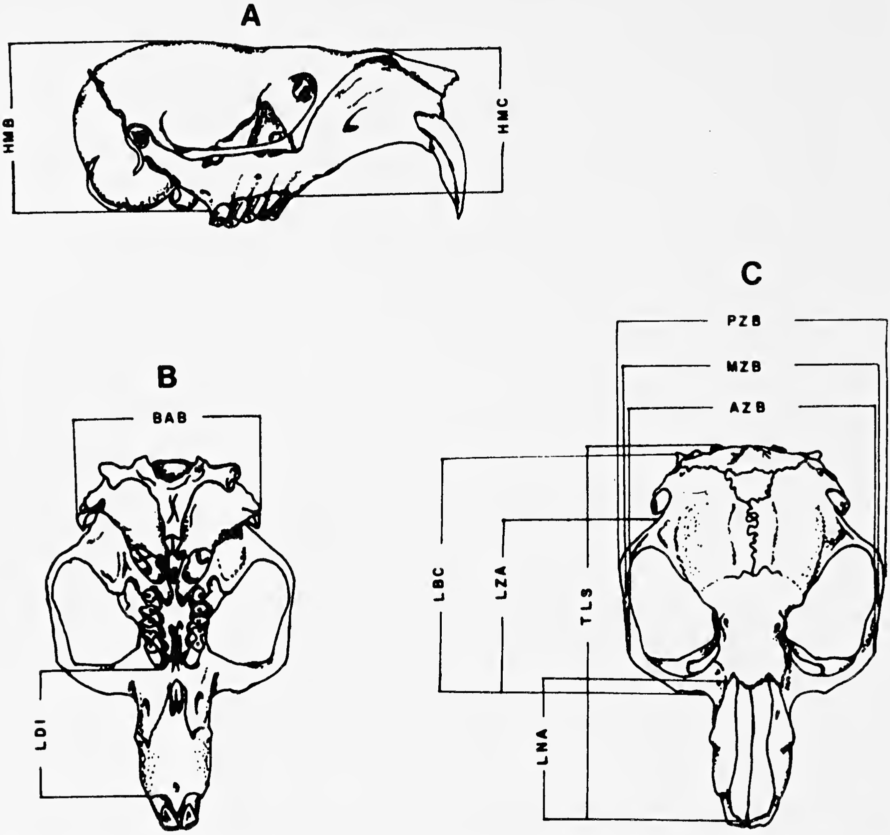

Figure 2. Lateral (A), ventral (B), and dorsal (C) views of *Thomomys umbrinus* illustrating the characters measured. Definitions of measurements are given in Methods. The skull was drawn from a male specimen (6810 UAMI).

Tlaxco, 2856 m, 4; Limite Puebla-Tlaxcala, 15 km N Tlaxco, 2750 m, 11; Limite Puebla-Tlaxcala, 15 km N Tlaxco, 2856 m, 12; 1 km S El Final de la Senda, 2700 m, 2; 15 km N, 3 km E Tlaxco, 2865 m, 1; Paso Ancho, 12.5 km N, 6 km E Tlaxco, 2620 m, 5; 8 km N Tlaxco, 2820 m, 1; 6 km N, 2 km E Tlaxco, 2770 m, 4; 5 km N, 3 km E Tlaxco, 2960 m, 3; 5 km N, 3 km E Tlaxco, 2920 m, 2; 5 km N, 3 km E Tlaxco, 2600 m, 2; 3 km N, 1 km E Tlaxco, 2820 m, 140; 3 km N, 1 km E Tlaxco, 2640 m, 6; 2 km N, 1 km E Tlaxco, 2880 m, 7; Acopinalco del Peñón, 2730 m, 5; Acopinalco del Peñón, 2800 m, 1.

RESULTS

Method Using the General Morphology of Skull

Table 1 shows the standard statistics of the 11 mensural characters examined. Of these, nine separated ($p = 0.0001$) all age groups in male gophers (79 df): TLS ($F = 62.25$); LNA ($F = 39.55$); AZB ($F = 94.95$); MZB ($F = 88.16$); PZB ($F = 91.06$); LDI ($F = 74.94$); BAB ($F=53.9$); HMC ($F = 88.46$); HMB ($F = 47.17$). In the females (89 df), five of the seven variables, which separated ($p = 0.0001$) the age groups, coincided

TABLE 2. Numbers and percentages of individuals of *Thomomys umbrinus* correctly classified in four age groups (I-IV) as corroborated by discriminant analysis and Wilks' lambda test. Specimens were assigned *a priori* into the age categories according to a series of qualitative characters from the general morphology of skull (A) and by the basisphenoid suture (B).

A. General Morphology of Skull

11 Variables

		Males = 79.6%					Females = 76.5%			
	n	I	II	III	IV	n	I	II	III	IV
I	8	8	0	0	0	9	9	0	0	0
		100.00	0	0	0		100.00	0	0	0
II	27	1	23	3	0	70	8	48	14	0
		3.70	85.19	11.11	0		11.43	68.57	20.00	0
III	42	0	11	30	1	51	0	6	42	3
		0	26.19	71.43	2.38		0	11.76	82.35	5.88
IV	21	0	0	4	17	6	0	0	1	5
		0	0	19.05	80.95		0	0	16.67	83.33

5 Variables

	Males = 75.5%				Females = 74.6%			
	I	II	III	IV	I	II	III	IV
I	8	0	0	0	9	0	0	0
	100.00	0	0	0	100.00	0	0	0
II	2	21	4	0	9	43	17	1
	7.41	77.78	14.81	0	12.86	61.43	24.29	1.43
III	0	2	29	11	0	6	41	4
	0	4.76	69.05	26.19	0	11.76	80.39	7.84
IV	0	0	5	16	0	0	2	4
	0	0	23.81	76.19	0	0	33.33	66.67

B. Basisphenoid Suture

11 Variables

		Males = 80.6%					Females = 63.1%			
	n	I	II	III	IV	n	I	II	III	IV
I	6	6	0	0	0	4	3	1	0	0
		100.00	0	0	0		75.00	25.00	0	0
II	7	2	4	0	1	13	1	9	2	1
		28.57	57.14	0	14.29		7.69	69.23	15.38	7.69
III	32	1	2	25	4	64	0	8	35	21
		3.12	6.25	78.12	12.50		0	12.50	54.69	32.81
IV	52	0	0	9	43	56	0	3	13	40
		0	0	17.31	82.69		0	5.36	23.21	71.43

TABLE 3. Classifying criteria (VAR) used in the separation of 234 skulls of *Thomomys umbrinus* from Sierra de Tlaxco, Tlaxcala, México, in four age groups based on the general morphology of skull (A) and the closure of the basioccipital-basisphenoid suture (B). The five variables in A were selected by Wilks' lambda test. Only the coefficients of the canonical functions which were significant (p = 0.0001), correlated (R ≥ 0.70) and most important for explaining the variation are shown (11 variables=a; 5 variables=b).

VAR	MALES			FEMALES	
	A. General Morphology of Skull				
	CAN1a	CAN1b	CAN2b	CAN1a	CAN1b
LTC	0.1405			0.3628	
LNA	-0.2989			0.2868	0.5389
LAC	-0.0829	0.0416	-1.5514	0.1765	
LBC	-0.0022			0.2421	0.5651
ACA	0.4793			1.2380	0.8581
ACM	0.6978	1.1250	3.9863	-0.6082	
ACP	0.0564	0.0710	-3.0903	-0.2297	-0.3712
LDI	0.4651			0.0512	
AAB	0.6035	0.5162	1.1450	0.0457	
HBR	0.8269	0.8307	-0.5614	0.2810	
HMC	-0.2832			0.1503	0.3926
	B. Basioccipital-Basisphenoid Suture				
	CAN1a			CAN1a	
LTC	-0.2708			-0.4813	
LNA	0.3237			0.1750	
LAC	-0.5416			0.3775	
LBC	0.2366			0.3536	
ACA	0.9945			-0.1924	
ACM	-0.2340			0.4394	
ACP	0.2272			0.1002	
LDI	-0.1574			0.7740	
AAB	0.5486			-0.0391	
HBR	1.1153			0.2296	
HMC	-0.3927			-0.1868	

with those of the males: TLS (F = 35.05); LNA (F = 26.56); AZB (F = 17.29); LDI (F = 25.87); HMC (F = 30.18). The remaining two measurements were LZA (F = 24.89) and LBC (F = 29.22).

In the discriminant analysis with 11 variables, 79.6% of the 98 male individuals were correctly classified in the *a priori* assigned age categories (Table 2, Fig. 3-A). After the Wilks' lambda test, only five variables were left (LZA, AZB, PZB, BAB, and HMC), but these resulted in the correct discrimination of 74.6% of the 98 males (Table 2). In both analyses, CAN1 is highly significant (p = 0.0001), highly correlated with the variables (R = 0.92 for both), and explains most of the variation (95.01% and 96.3%, respectively). The discriminant function, CAN2, is significant

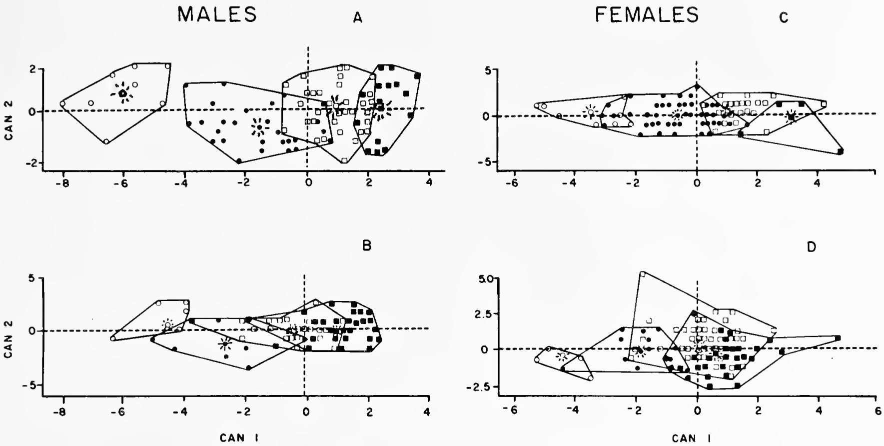

FIGURE 3. Efficacy of two methods for classifying specimens of *Thomomys umbrinus* in four age groups (I-IV) as shown by the distributional maps of 234 individuals in the first two canonical functions from a discriminant analysis. A and C illustrate results using the method proposed here. B and D correspond to the basisphenoid suture method. Open circles = age group I; solid circles = age group II; open squares = age group III; solid squares = age group IV. Marked symbols indicate age group centroids.

($p = 0.02$) in the analysis with five variables, though less correlated with the variables ($R = 0.37$), and together with CAN1 explains 99.1% of the total variation.

Canonical coefficients (Table 3) of the variables indicate that the height of the maxillary crest (HMC), the middle zygomatic breadth (MZB) and the breadth across the bullae (BAB) are the most important criteria among the 11 variables for discriminating the age groups. After the Wilks' test, these mensural characters are still the best, but in a different order (Table 3).

Similar results were obtained for the 136 females where the Wilks' lambda also reduced the number of variables to five (LNA, LBC, AZB, PZB, and HMB). In this case, the analysis with 11 characters discriminated 76.5% (Table 2, Fig. 3-C) of the females and the analysis with five, 74.6% (Table 2). In either analysis, only CAN1 was highly significant ($p = 0.0001$), highly correlated with the variables ($R = 0.82$ and 0.81), and explained almost all the variation by itself (93.02% and 95.85%).

Within females the most important characters for discriminating among the age groups differed from those for the males, and all but one (AZB) changed from one analysis to the other (Table 3). In fact, AZB was the best criterion in both analyses. MZB with half the value of AZB, was the second-best criterion in the analysis with 11 variables, whereas LBC and LNA were second best in the other analysis (Table 3).

Method Using the Basisphenoid Suture

In general, results with this approach are less accurate and become quite different for the sexes (Table 2). In males the percentage success or efficacy (80.4%) is almost equal to that in our method (79.6%), but in females it is 13.37% lower (63.1% vs 76.47%).

In spite of the similarity between the two methods, male specimens of ages II and III are poorly discriminated with the suture-method (Table 2, Fig. 3-A, B). Males considered in age group II overlap with those of age group I and, most noticably, with age group IV, but not with age group III. Also, specimens assigned to age class III overlap with every other group except with age group IV. The remaining specimens in age group I and IV behave much the same as in the other method.

There is only one discriminating canonical function (CAN1, p = 0.0001) for males with this method. However, it is less correlated with the variables (R = 0.84) and explains only 88.6% of the variation in the analysis. As in our method, the best discriminating characters among age groups (Table 3) are HMC, BAB, and, instead of MZB, AZB. In this analysis, LZA also is important.

The lower efficacy obtained by this method for females results in an impoverished discrimination in all age categories (Table 2, Fig. 3-C, D). In contrast to the results of our method, a specimen previously assigned to age group I is classified in category II; specimens assigned to age groups II and IV overlap with every other category; and a third of the specimens assigned to age group III are placed in the next age class. Also, the only resulting discriminant function (CAN1, p = 0.0001) is less correlated (R = 0.72) and explains 10.63% less of the total variation (82.39% vs 93.02%). Except for MZB, none of the mensural characters most important for discriminating among age groups coincide in both methods (Table 3).

DISCUSSION

In general, all statistical analyses support the validity of the qualitative characters employed here to classify specimens of *T. umbrinus* into age groups. The 11 variables obtained in the analysis of variance and Duncan's test (Table 1) are closely related to such characters, especially with regard to the development of the zygomatic arches, the rostrum, and the maxillary crests (Figs. 1 and 3).

Indeed, in the Wilks' test and all canonical discriminant analyses (Tables 2 and 3), the most important variables have to do with the expansion (AZB, MZB, PZB) and enlargement (LZA) of the zygomatic arches, the appearance and development of the maxillary crest (HMC), and the enlargement of the face (LDI, LNA). And, discriminant analyses show that more than three-fourths of the total specimens of *T. umbrinus* of either sex are correctly classified using this set of characters (Table 2).

Results of Wilks' method emphasize that even though the classifying efficacy in both sexes remains almost the same with 11 as with five variables (Table 2), the accuracy in the discrimination is better with more than with fewer variables because there is more overlap between age categories with five variables.

Conversely, while the qualitative characters are useful for both females and males, the mensural characters are distinctively important both in number and nature between the sexes (Table 3). In males, the main discriminating measurements are related to the maxillary crest, the middle zygomatic breadth and the breadth across the bullae in all discriminating analyses, but in females the anterior zygomatic breadth is the only consistent measurement. Other measurements seemingly important in females are the length of the nasals and the length of the braincase.

The fact that mensural characters for females and males of *T. umbrinus* are divergent, reflects characteristic differential allometric rates of development, which in turn, result in sexual dimorphism in the species. Whereas the widening of the skull with the development of the maxillary crest is characteristic for males, the enlargement of the skull is peculiar to the females. Thus, the data in this study have implications for understanding differential patterns in the development of the sexes. The means and ranges (Table 1) of the variables investigated imply a starting point for an *a priori* assignment of specimens to age groups in each sex.

The comparison between this and the basisphenoid suture approach shows that either method is useful when dealing with very young and old male specimens (Table 2, Fig. 3A, B) of *T. umbrinus*. This results from the ease with which a wide open suture is distinguished, and from the readiness with which one notices the poor development of the rostrum and the convergence of the zygomatics (Fig. 1). However, the method proposed here is more accurate with regard to intermediate age categories in males of *T. umbrinus* because the overlap of specimens is less extensive in either number or categories (Table 2, Fig. 3A, B).

The situation is even more critical in females of *T. umbrinus*, where the use of the basisphenoid suture is much more subjective and results in an extensive overlap in all age categories (Table 1, Fig. 3C, D). Here, the evidence that a set of characters is more useful than a single criterion is supported. Moreover, the fusion of the basisphenoid suture appears to be independent of sexual maturity. This possibly indicates that the energy necessary for the deposition of calcium in the female skull is secondary to the maternal role which, in turn, implies more energy input into gestation and nursing activities, especially in intermediate age classes, as in other rodent species (Eisenberg, 1981). This may also be the reason why female skulls are not as readily separated into age groups as male skulls of *T.*

umbrinus. Unlike males, females divert substantial energy in maternity roles, hence, calcium deposition in their skull is perhaps of less adaptive value, thus, the skull morphology remains almost the same during their most actively reproductive ages (i.e., intermediate age groups). The presence of very old females whose skulls resemble those of males in their highly developed maxillary crests, as well as expanded and bulky zygomatics, reinforces this idea because those females may be no longer reproductively active and, consequently, experience deposition of calcium in their skulls. Ossification of the skull in males by the deposition of calcium, on the other hand, might be sexually adaptive for their role in territorial and mating behaviour.

Although the continuous growth of cheekteeth in geomyids prevents use of degree of wear of the occlusal surface (Hoffmeister, 1951), several methods have been proposed for determining age classes. Some authors sought a relationship between age and size or weight, but Hansen (1960 and references therein) has thoroughly discussed and discarded such an approach. More recently, Patton and Brylski (1987) have shown that, besides development, several intrinsic and extrinsic factors affect both size and weight. Therefore, the most suitable methods for determining age categories in field-trapped geomyids have been those based on the closure of the cranial sutures (Thaeler, 1967; Hoffmeister, 1969), especially of the basisphenoid suture. Nevertheless, in the light of our results, we think that the method proposed here represents a better option because of reduced subjectiveness due to the consideration of more than one character to determine age class, and what we think are more reliable characters than closure of cranial sutures.

This approach, as any method based on the aspect of one or more characters, results in a discontinuous view of the growth and development of a species and has to be used with appropriate caution. Construction of growth curves by means of regression analysis or determination of age groups using principal components analysis are among the strategies recently implemented in *Geomys* by systematic researchers with the intent of avoiding this fragmented panorama (M. Smolen, pers. comm.). These methods will certainly allow a better understanding of age development and growth patterns in pocket gophers, but they imply access to a known population and are not necessarily related to analyses of intra- and interpopulation variation.

Patton and his colleagues (Daly and Patton, 1986; Patton and Brylski, 1987) used the basioccipital-basisphenoid and the exoccipital-supraoccipital sutures to distinguish three age classes in *T. bottae*. These authors considered midpoints between classes, thus reducing the discontinuous appreciation of growth and development, and ended with a total of six age categories or scores. Also, they had the advantage of being able to establish the relationship between cranial scores and chronological age from known-age individuals. This highly recommendable approach involves (as with growth curves) a long-term study in a known population.

Until studies *sensu* Daly and Patton (1986) of growth curves are made for *T. umbrinus* and other species of pocket gophers, the method presented here offers a valid option for randomly-trapped or museum specimens. We believe that the authors' experience and knowledge of the species let them understand their results of age variation, in spite of the discontinous pattern inherent to the method. Furthermore, the statistical techniques used here provide a robust option to test any qualitative characters used in the determination of age groups in geomyids.

DEDICATION

This paper is dedicated to the memory of Dr. J. Knox Jones, Jr., a man who became a legend by his way of being but, especially, by his labor among mammalogists. Dr. Jones knew how to incite our minds and our smiles at the same time with a roguish flash in his eyes. While his behavior harmonized with his free spirit, his advice, comments, and works let us know how he cherished any genuine intent to contribute to mammalogy, both among his colleagues and his students.

ACKNOWLEDGMENTS

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REVISION OF AGES OF THE FUSSELMAN, WRISTEN, AND THIRTYONE FORMATIONS (LATE ORDOVICIAN-EARLY DEVONIAN) IN THE SUBSURFACE OF WEST TEXAS BASED ON CONODONTS AND GRAPTOLITES

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ABSTRACT.—Conodonts obtained from the Socony Mobil Pegasus Unit 3 #7-20 core, Midland County, Texas, permit more reliable dating of Ordovician-Devonian West Texas subsurface units. The Fusselman Formation consists of two major lithostratigraphic units, a thin basal, Late Ordovician (Hirnantian) oolite that is overlain unconformably by a thicker Llandoverian (Silurian) complex of carbonates. The Wink Member of the Wristen Formation is Wenlockian (Silurian) in age. Overlying dark shales questionably placed in the Frame Member extend into the Early Devonian. Restudy of graptolite collections of Decker (1942, 1952) from nearby wells in Crane County, Texas, indicates that dark shales (Frame Member) previously assigned to the Silurian, range from the Ludlovian (Silurian) into the Pragian (Early Devonian). *Key words:* West Texas; conodonts; graptolites; Ordovician; Silurian; Devonian.

Regional correlation of subsurface units of the "Siluro-Devonian" of the Permian Basin region of West Texas and southeastern New Mexico has been hindered by a lack of published data on biostratigraphically useful fossils. Although "Siluro-Devonian" strata have been extensively explored for hydrocarbons, most of the information available consists of cuttings and geophysical logs, supplemented by a smaller number of cores. This body of data has been important in determining the spatial relations of the major lithologic units, and more recently, in permitting detailed reconstructions of the environments of deposition of "Siluro-Devonian" strata. However, the paleontological control required to ascertain chronostratigraphic relations among the depositional sequences is lacking, and detailed reconstruction of the geological history for this interval of the Paleozoic has not been possible.

Herein we provide new information on the chronostratigraphy of the "Siluro-Devonian" succession in the subsurface of West Texas based on conodonts from a core from the Pegasus field in Midland County, Texas, and a reevaluation of graptolites originally described by Decker (1942, 1952) from wells in adjoining Crane County.

STRATIGRAPHY AND PREVIOUS WORK

Most workers recognize three major stratigraphic subdivisions of the subsurface Silurian and Lower Devonian in West Texas (Fig. 1), in

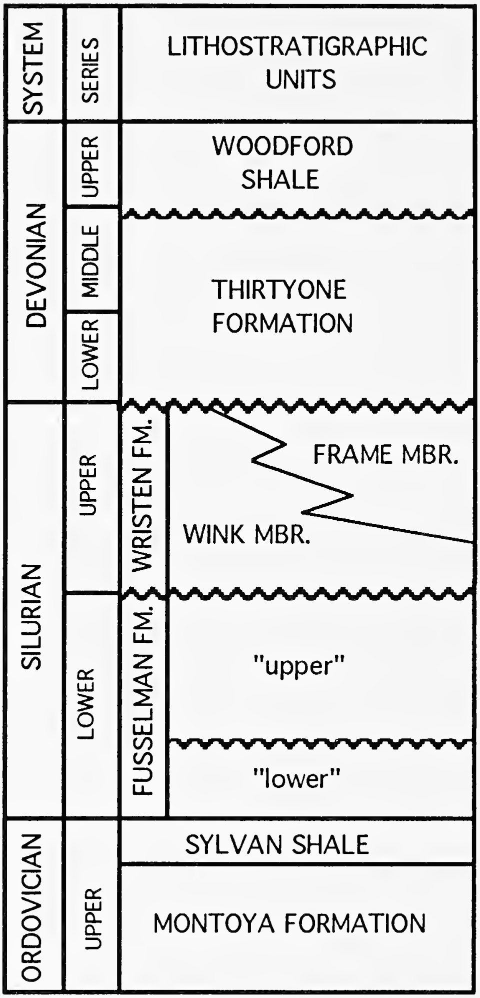

Figure 1. Summary of lithostratigraphic nomenclature of Upper Ordovician through Devonian units in West Texas. Age assignments shown for the units are a composite of correlations previously published, not all of which are in agreement. The most important sources are Wilson and Majewske (1960), Hills and Hoenig (1979), and Wilde (1990).

ascending order: (1) Fusselman Formation, (2) Wristen Formation - the "upper Silurian shale" of older works, and (3) Thirtyone Formation - the "Devonian cherty limestone" of older works. McGlasson (1967) and Hills and Hoenig (1979) have summarized the general lithostratigraphic distribution of Silurian and Lower Devonian strata in West Texas, and Geesaman and Scott (1989), Garfield and Longman (1989), and Mazzullo et al. (1989) provide a modern understanding of facies relationships and depositional sequences. The most thorough discussion of biostratigraphic information and chronostratigraphic relationships was given thirty years ago by Wilson and Majewske (1960).

In the subsurface of West Texas, the Fusselman Formation comprises a complex series of carbonate facies, including light-colored ooid grainstones, green glauconitic and pink pelmatozoan grainstones and packstones, and sparse skeletal wackestones with minor shaly intercalations. Geesaman and Scott (1989) and Garfield and Longman (1989) divided the Fusselman into two informal units in the subsurface of the central Midland Basin, a lower Fusselman and an upper Fusselman, each of which represents a separate depositional sequence. The lower Fusselman consists of a thin (<20 feet thick) unit of oolitic grainstone in the center of the basin that becomes dominantly dolomitic mudstone, of inferred peritidal origin, in the eastern part of the basin. According to these authors, the base of the lower Fusselman is intimately associated with the underlying Upper Ordovician Sylvan Shale. Contrary to previous work (e.g., Hills and Kottlowski, 1983), Garfield and Longman (1989) concluded that no unconformity exists between the upper Sylvan and lower Fusselman, and therefore, either the upper Sylvan must be Early Silurian in age or the lower Fusselman is Late Ordovician in age. Diagenetic textures suggest that the top of the lower Fusselman was exposed to subaerial conditions before deposition of the upper Fusselman (Geesaman and Scott, 1989; Garfield and Longman, 1989).

The upper Fusselman is dominated by widespread thick, crinoidal grainstones, and lesser amounts of dolomitic wackestone to skeletal packstone. These three lithofacies are interbedded such that they reflect minor differences in paleotopographic setting and degree of relative subsidence during deposition (Canfield, 1985; Geesaman and Scott, 1989). All available information indicates that the upper Fusselman in the Midland Basin was deposited in a spectrum of shallow-water, high-energy open marine to peritidal environments. The top of the upper Fusselman in a number of wells is characterized by diagenetic textures indicative of karstification and soil formation, both of which suggest a prolonged period of subaerial erosion prior to deposition of the overlying Wristen Formation (Garfield and Longman, 1989; Mazzullo et al., 1989).

The age of the subsurface Fusselman is poorly known due to a paucity of fossil material from only limited core studies. Wilson and Majewske (1960) concluded that insufficient macrofossil material (largely brachiopods and trilobites) existed to date the subsurface Fusselman any better than it possibly being Early Silurian in age (Fig. 1).

In the West Texas subsurface, the overlying Wristen Formation as defined by Hills and Hoenig (1979) includes strata often referred to as the "upper Silurian shale" (Fig. 1). From Andrews County, Texas, southward, the Wristen consists of two major lithofacies that Hills and

Hoenig (1979) placed into separate members. The lower member, the Wink Member (15-130 feet thick), consists of argillaceous carbonates that grade upward and laterally into silty shales of the Frame Member (0-200 feet thick). A thin green shale or shaly mudstone, termed the "Lower Wristen Marker" by Garfield and Longman (1989), occurs at the base of the Wristen in Midland County. Elsewhere, dark greenish, nodular, peloidal ostracode mudstones and wackestones of the Wink Member of the lower Wristen rest directly on the Fusselman. The Wink Member is relatively more uniform in lithology and thickness than the underlying Fusselman, and is interpreted to represent a new transgressive phase of sufficient magnitude to establish relatively uniform environmental conditions over the low-relief Fusselman erosional surface (Garfield and Longman, 1989, p. 200 and figure 17).

The Frame Member of the Wristen Formation is restricted to the area extending southward from Andrews County, Texas. It consists of dark gray to gray-green shales that grade northward into thicker sections of carbonate-dominated undifferentiated Wristen Formation (700 feet thick). Hills and Hoenig (1979, p. 1518) included the thin dark shale unit that Jones (1953) placed at the base of the Devonian in the Midland Basin as a local facies of the uppermost Frame Member.

Wilson and Majewske (1960) recovered a shelly fauna from undifferentiated Wristen carbonates in the northern part of the Midland Basin that Berry and Boucot (1970) interpreted to be pre-Ludlovian (late Llandoverian-Wenlockian?) in age. Decker (1942, 1952) reported Ludlovian (Late Silurian) graptolites from the Frame Member from wells in Crane County, Texas. This sparse faunal information suggested that the Wristen Formation in the West Texas subsurface might be late Llandoverian to Ludlovian in age.

Jones (1953) and Wilson and Majewske (1960) recognized four subdivisions of the "cherty Lower Devonian" in the subsurface of the Midland Basin, in ascending order: (1) dark shale with conodonts and spores (0-45 feet thick); (2) dark chert and cherty limestone (100-300 feet thick); (3) fossiliferous calcarenitic limestone (450 feet thick); and (4) light-colored chert and limestone (200 feet thick). Hills and Hoenig (1979) combined the upper three units into the Thirtyone Formation (Fig. 1), and included the basal dark shale unit in the Frame Member of the underlying Silurian Wristen Formation. In the Midland Basin the Thirtyone Formation includes a variety of marine litho- and biofacies that suggest deepening conditions going from north to south. The proportion of siliceous strata in the Thirtyone Formation varies geographically as well, with cherts and tripolitic beds dominating in the south and limestones becoming more prevalent in the north (McGlasson, 1967; McWilliams, 1985; Speer, 1989).

Abundant shelly macrofossils were reported from the limestones of the upper two units by Wilson and Majewske (1960), who indicated a late Early Devonian age (Deerparkian to Onesquethawian). The lower two units of dark shale, chert, and cherty limestone did not yield diagnostic fossils, but were provisionally placed in the earliest Devonian (Helderbergian) by Wilson and Majewske (1960). Stainbrook (in Jones, 1953, p. 14) and Wilson and Majewske (1960) reported lowermost Devonian (Helderbergian) shelly macrofossils from unspecified beds near the base of the Thirtyone Formation in Andrews County.

From Andrews County northward, the Fusselman and Wristen Formations become extensively dolomitized and can not be reliably distinguished. In these areas the more general terms "Silurian" or "Siluro-Devonian" have been applied to the carbonate interval extending from the top of the Sylvan Shale to the base of the Woodford Shale.

CONODONT BIOSTRATIGRAPHY OF THE PEGASUS CORE

The most complete information on the conodont biostratigraphy and biofacies of the Fusselman and Wristen Formations was obtained from a core from the Socony Mobil Pegasus Unit 3 #7-20 well in Midland County, Texas (Fig. 2; sec. 30, Blk. 40, T-4-S, T&P RR Survey). The nearly complete core extends from the top of the Upper Ordovician Montoya Group into the Devonian Thirtyone Formation (Fig. 3). The stratigraphic sequence and lithofacies present in the core were described by Canfield (1985).

Montoya Group and Sylvan Shale

The upper part of the Montoya Group in the Pegasus core is brownish-gray cherty limestone (Fig. 3). Samples from the top of the Montoya yielded a typical Late Ordovician conodont fauna that is dominated by elements of *Plectodina tenuis* and *P. florida*. *Pseudobelodina dispansa, Ps. kirki*, and elements of *Aphelognathus* and *Panderodus* species are present. The fauna is relatively undiagnostic, and may range in age from late Edenian into the Richmondian. The *Plectodina*-dominated biofacies association is indicative of open marine shelf conditions of moderate depth (Sweet and Bergström, 1984). The overlying Sylvan Shale comprises four feet of greenish-gray shale that did not yield any conodonts.

Fusselman Formation

The lower Fusselman in the Pegasus well consists of eight feet of light-gray oolitic grainstone that rests with an abrupt contact on the Sylvan Shale. The grainstone is composed of about 80 percent ooids nucleated on a variety of bioclasts that include crinozoans, bryozoans, trilobites

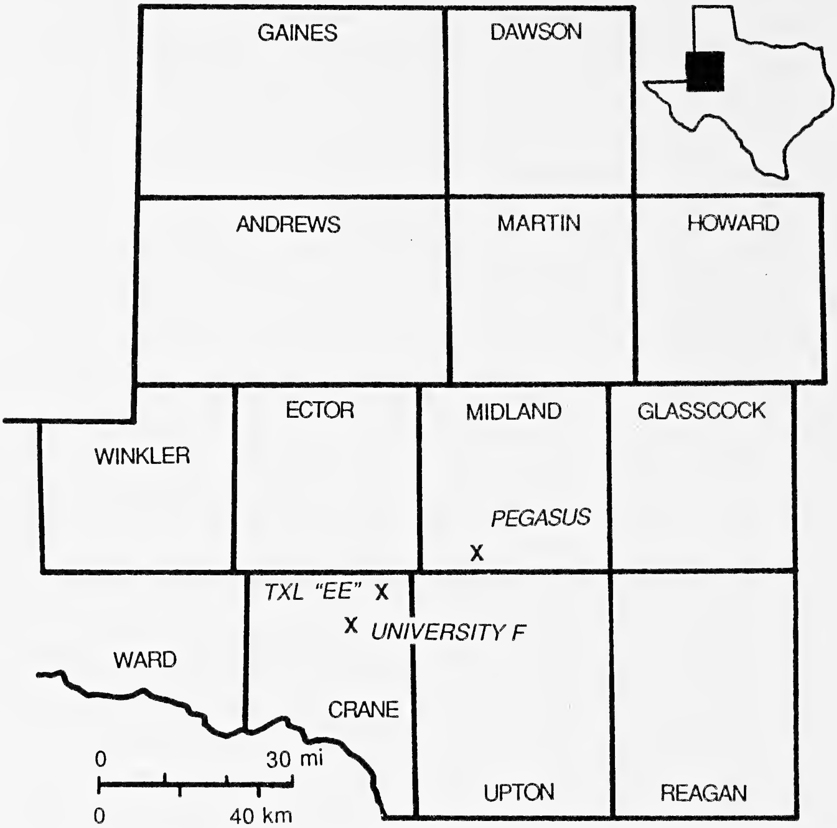

FIGURE 2. Locations of wells from which conodont faunas and graptolite collections were obtained. Pegasus = Socony Mobil Pegasus Unit 3 #7-20 well; University F = Gulf University No. 1 F well; TXL "EE" = Gulf TXL No. 1 "EE" well. Well locations are given in the text.

and ostracodes. At some levels peloids and grapestone textures occur. A small, but important, conodont fauna was obtained from the lower Fusselman. Several elements of *Noixodontus girardeauensis* were recovered in addition to a few specimens of *Panderodus* and *Decoriconus*. In the southern cratonic region of North America, *N. girardeauensis* is restricted to strata that contain a latest Ordovician, Hirnantian, brachiopod fauna (Amsden and Barrick, 1986).

The upper Fusselman in the Pegasus core comprises 93 feet of limestone. The contact between the lower Fusselman and upper Fusselman was missing from the core. The lower 75 feet of the upper Fusselman is dominated by pelmatozoan grainstones containing abundant bryozoans, trilobites, brachiopods, ostracodes, and mollusks (Canfield, 1985). The color of the grainstones varies irregularly from pink to white to gray, and a few glauconitic horizons occur. The upper 16 feet are

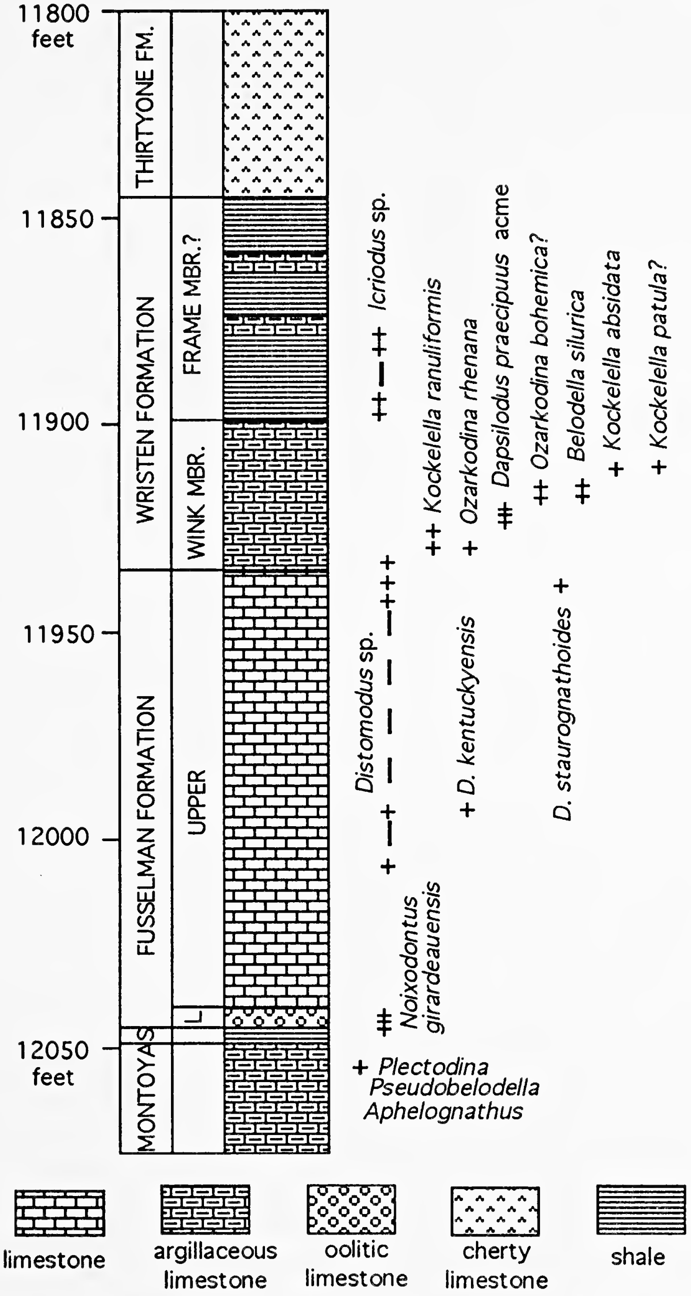

FIGURE 3. Lithologic column of the Socony Mobil Pegasus Unit 3 #7-20 core, showing distribution of the most significant conodont species. Only the upper part of the Montoya Formation and the lower part of the Thirtyone Formation are shown. S = Sylvan Shale; L = lower Fusselman.

characterized by light gray and tan wackestones and packstones with a similar fauna.

The lower grainstone unit of the upper Fusselman yielded only a sparse conodont fauna, averaging just 15 elements per kilogram of sample. The coniform taxa *Panderodus unicostatus* (67%) and *Walliserodus curvatus* (31%) constitute the vast majority of elements. This *Panderodus/ Walliserodus* faunal association is characteristic of shallow water marine carbonate environments from the Llandoverian into the early Wenlockian (Silurian). The only diagnostic species recovered was a single Pa element of *Distomodus kentuckyensis* at 11,992 feet. It ranges from the uppermost Rhuddanian into the middle of the Aeronian Stage of the Llandoverian Series (Aldridge, 1975; Armstrong, 1990). Also, *Walliserodus curvatus* has not been reported from strata younger than the Aeronian.

The top of the grainstone interval and the overlying wackestones and packstones at the top of upper Fusselman contain a slightly more diverse and abundant conodont fauna (55 elements/kg). *Panderodus unicostatus* (39%) and a species of *Walliserodus* (39%) still strongly dominate the fauna. A few elements of a species of the *Panderodus recurvatus* group are present, *Aspelundia* and *Oulodus* species appear, and in the highest samples, *Dapsilodus* and *Distomodus* elements occur. The most diagnostic species is *Distomodus staurognathoides,* which ranges from the upper part of the Aeronian Stage into the base of the Wenlockian Series (Aldridge, 1975; Kleffner, 1989).

Wristen Formation

The Wristen Formation in the Pegasus core can be divided into two lithologic units. A lower unit of gray shale, limestone, and dolostone is assigned to the Wink Member. The overlying unit of black shale and carbonate is questionably assigned to the Frame Member.

Wink Member. - The base of the Wink Member consists of four feet of greenish-gray dolomitic shale that contains silt-sized quartz and minor amounts of glauconite(?) and pyrite. The remainder of the Wink is carbonate, grading from limestone near the base to dolostones at the top. The lower four feet of the carbonate unit is light gray, silty, dolomitic biopackstone and biowackestone. A diverse shelly fauna is recognizable in thin sections: brachiopods, crinozoans, trilobites, ostracodes, bryozoans, and mollusks. The Wink grades upward into darker gray biowackestones that bear only sparse remains of ostracodes, trilobites, brachiopods, and bryozoans. Dark gray, silty calcitic dolostones characterize the upper part of the Wink Member (11,910-11,900 feet), where skeletal remains are obscured by dolomitization.

The basal shale of the Wink member yielded only a few conodont elements, largely a result of our inability to completely disaggregate the shale. Among the few elements extracted from the shale were ramiform elements of a *Distomodus* species.

In contrast, the biowackestone and biopackstone in the lower four feet of the Wristen carbonate unit produced abundant conodonts, averaging 4750 elements per kilogram. The fauna is overwhelmingly dominated by elements of the coniform species *Dapsilodus obliquicostatus* (88%). Elements of *Pseudooneotodus bicornis* (7%), *Panderodus unicostatus* (2.5%), and *Decoriconus fragilis* (2%), all coniform taxa, constitute nearly all the remainder of the fauna. Other taxa present include *Walliserodus sancticlairi, Dapsilodus sparsus, D. praecipuus, Ozarkodina excavata excavata,* other *Ozarkodina* species, and *Kockelella* species. Microfossil residues are also characterized by abundant acrotretid brachiopods, the most common of which is *Artiotreta parva.*

In the overlying biowackestones conodont abundance falls to about 1200 elements per kilogram. *Dapsilodus* elements continue to dominate the faunas (73%), but in the interval 11,922-11,919 feet, *D. praecipuus* increases sharply in numbers to become nearly as abundant as *D. obliquicostatus.* Other conodont taxa become relatively more abundant with the decline in *Dapsilodus* elements: *Panderodus unicostatus* averages 11%, and *Decoriconus fragilis* averages 5.5% of the elements. At 11,917 feet, *Belodella silurica* appears in the Wristen, contributing about 3% of elements. No conodont elements were recovered from 11,910 to 11,900 feet. Although dissolution of the dolostones was incomplete, sufficient rock was dissolved to obtain conodont elements, even if they had been present in low numbers.

Despite the great abundance of conodont elements, few age-diagnostic species were obtained from carbonates of the Wink Member. The presence of *Kockelella ranuliformis* (11,930-11,927 feet) and *Ozarkodina rhenana* (11,930 feet) at the base of the carbonate section, above the last occurrence of *Distomodus* in the underlying shale at the base of the Wink Member, indicates the *ranuliformis* Zone for the lower Wink carbonates (Sheinwoodian Stage; Wenlockian Series; Barrick and Klapper, 1976; Kleffner, 1989).

Although the range of *Dapsilodus praecipuus* remains undetermined, faunas from the mid-Wenlockian *amsdeni* Zone of Barrick and Klapper (1976) in the Midcontinent region possess acmes in the abundance of this species like those found in the interval 11,922-11,919 feet in the Pegasus core (Amsden et al., 1980). *Belodella silurica*, which first occurs at 11,917 feet, consistently appears in the upper *amsdeni* Zone in the southern Midcontinent, above the acme in *D. praecipuus* (Barrick, 1977, 1983). Samples 11,917 and 11,913 feet contain small Pa elements probably best assigned to *Ozarkodina bohemica*, another species that appears in the upper *amsdeni* Zone (Barrick and Klapper, 1976) and which is indicative of the Homerian Stage of the upper Wenlockian (Aldridge, 1975).

Pa elements of *Kockelella absidata* and *K. patula*? occur in the highest sample of the Wink Member that yielded conodont elements, 11,910 feet. *Kockelella absidata* appears in the *amsdeni* Zone and ranges into the Ludlovian Series (Barrick and Klapper, 1976). The appearance of *K. patula* high in the Wenlockian, above the first occurrences of the taxa listed above, appears to be anomalous. The Pb element associated with the Pa element of *K. patula*? in this sample, however, more strongly resembles the Pb element called "*Ozarkodina*" *crassa*, a species used to indicate the base of the Ludlovian, than typical Pb elements associated with *K. patula* from lower in the Wenlockian (Barrick and Klapper, 1976). Because *K. patula* is the probable ancestor of both *"O." crassa* and the related species, *Ancoradella ploeckensis*, (Barrick and Klapper, 1976; Fordham, 1990), this association of a *K. patula* Pa element with a "*O.*" *crassa*-like Pb element should be expected to occur in the upper part of the Wenlockian.

Frame Member?—The sequence of black siliceous shale and carbonate that extends from about 11,900 to 11,870 feet is questionably assigned to the Frame Member of the Wristen Formation. The limestones are silty, dolomitic biowackestones with sparse, poorly preserved calcitic and phosphatic bioclasts. The contact between the dark gray dolostones at the top of the Wink Member and the beds at the base of the Frame? is indistinct, and is placed where the first definite black strata and shaly layers appear in the core.

The limestones and shales of the Frame? could not be readily processed for conodonts. Typically less than 25 percent of the sample could be disaggregated, using a succession of treatments of formic acid, bleach and Stoddard's solvent. Alternation of bleaching and Stoddard's solvents was the most effective in breaking down the rock, but the sparse conodont elements were badly broken as a result of such processing. Three samples, though, did yield fragments of Pa elements of *Icriodus* (Fig. 3). In the best sample, 11,877 feet, two complete spindles of Pa elements were preserved. These specimens clearly possess a middle denticle row, excluding the oldest species of the genus, *I. woschmidti*. The specimens, however, could belong to any of several other Early Devonian species of *Icriodus*.

Thirtyone Formation

The base of the Thirtyone Formation is placed where the first chert beds occur in the core at 11,840 feet. Strata of the Thirtyone Formation are too well silicified to permit processing for conodonts, and the age of this unit in the Pegasus core could not be determined.

GRAPTOLITE FAUNAS

Decker (1942, 1952) described Silurian graptolites from dark shales from two wells on the Central Basin Platform in West Texas. The dark shales bearing the graptolites are assigned to the Frame Member of the Wristen Formation, based on their position above the Fusselman Formation and the limestones of the Wink Member of the Wristen Formation, and below the cherty limestones of the Thirtyone Formation (Decker, 1952). At the time of Decker's work, however, graptolites were considered to range no higher than the Silurian. For that reason alone, Decker could not interpret a younger age for the graptolite-bearing intervals in the black shale. In the early 1960's, studies of highest Silurian and lowest Devonian strata in Belgium, Podolia, and Czechoslovakia lead to the realization that graptoloid graptolites ranged well into the Early Devonian (see Berry, 1968, for discussion and bibliography). In addition, the 1960's and 1970's were a time in which considerable new light was shed on graptolite morphology as a result of the discovery and description of very well preserved specimens. Graptolite taxonomy was significantly revised and many new late Silurian and early Devonian species were described. In light of these facts, the three segments of cores studied by Decker were borrowed from the University of Oklahoma and re-examined in order to determine correct identifications and age interpretations.

Core segment OU 699 was obtained from the Gulf University No. 1 F well (Fig. 2; sec. 22, University Land Block, 31, Crane County). The graptolites occur in a dense, black shaly limestone at 9,340 feet. Decker (1942) described *Monograptus (Monoclimacis) vomerinus* from this segment, but most specimens are too poorly preserved or are oriented in such a way that distinctive morphological features cannot be seen. The features that are preserved indicated a generic assignment of *Pristiograptus,* which suggests a Late Silurian, probably no older than Ludlovian, age.

Core segments OU 1423 and OU 1424 originated from the Gulf TXL No. 1 "EE" well (Fig. 2; sec. 19, Block 43, T & P RR Survey, Crane County). The graptolites occur in a black shale in two zones at depths of 10,941-10,942 feet (OU 1423) and 10,927-10,928 feet (OU 1424). None of the species reported by Decker (1952) could be recognized in the core segments.

Core segment OU 1423 contains species indicative of latest Silurian to earliest Devonian age; the graptolite-bearing sample is, no doubt, at or close to the Silurian-Devonian boundary. Species recognized upon re-examination include *Monograptus* sp. cf. *M. uniformis, Saetograptus* sp., and *Pristiograptus* sp. Core segment OU 1424, which originated 14 feet higher in the well, contains a definitely younger fauna than present in OU 1423. A specimen of *Monograptus* sp. cf. *M. thomasi* was discovered;

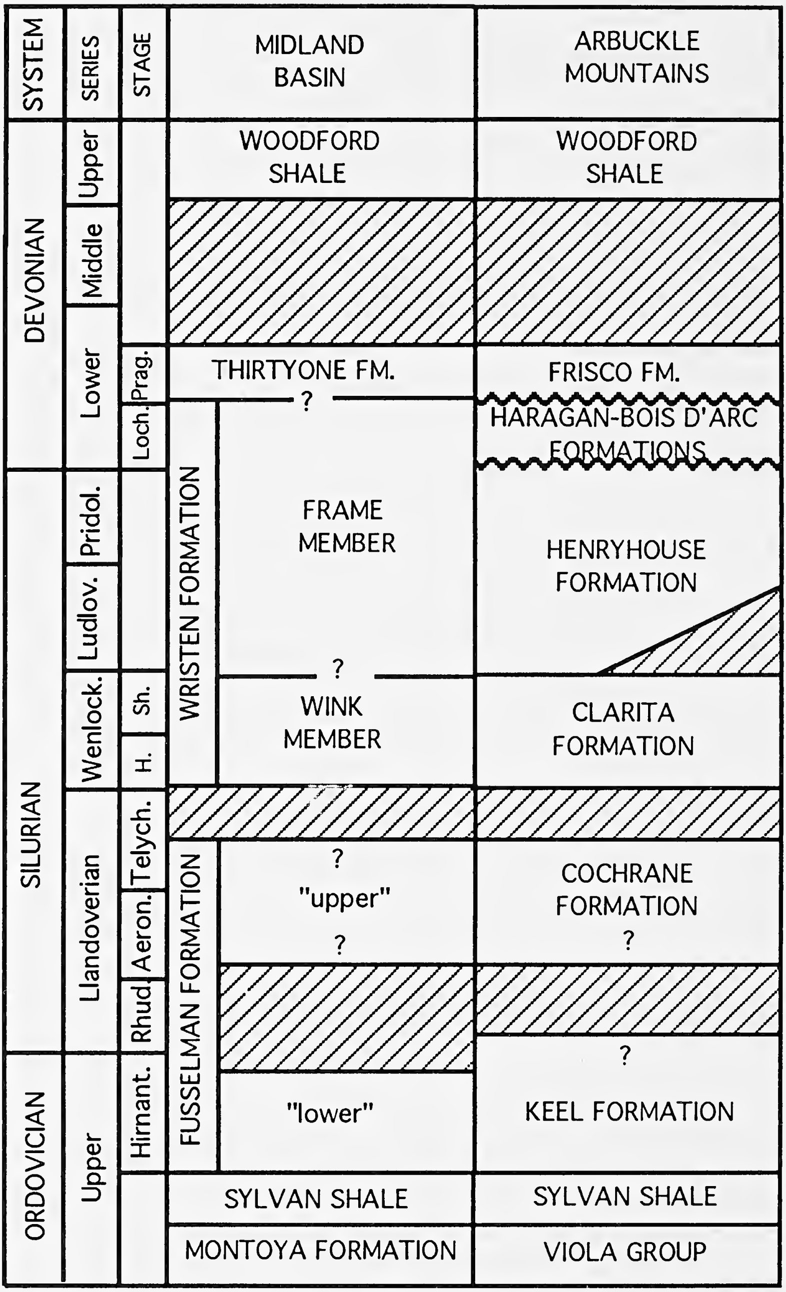

Figure 4. Interpretation of age relations of Upper Ordovician through Devonian strata in the Permian Basin area of West Texas based on conodonts obtained from the Mobil Pegasus core, and restudy of Decker's (1942, 1952) graptolite collections. Correlation with the sequence in the Arbuckle Mountains in southern Oklahoma utilizes conodont data summarized by Amsden and Barrick (1988) and Barrick et al. (1990). H. = Homerian; Sh. = Sheinwoodian.

most other specimens are too poorly preserved to be identified or are preserved in such an orientation that diagnostic features are not visible. This specimen of *Monograptus* is one of the youngest species of graptoloid graptolites known. Its presence indicates that the core segment is correlative with the Pragian Series (Lower Devonian), and thus to a horizon substantially above the Silurian-Devonian boundary.

Discussion

The Hirnantian (uppermost Ordovician) oolitic limestone of the lower Fusselman Formation of the West Texas subsurface correlates directly with the Keel and Petit Oolites of Oklahoma (Fig. 4), the Cason Shale oolite of Arkansas, and the Noix Formation and related units in the Mississippi Valley region. Collectively, these units form a thin, discontinuous sheet of extremely shallow water carbonates of Hirnantian age that stretches across the southern part of the North American craton (Amsden and Barrick, 1986). The presence or absence of an unconformity at the base of these carbonates is difficult to demonstrate, but in the Oklahoma subsurface, as well as the Texas subsurface, it is possible that deposition was continuous from the underlying Sylvan Shale. Regionally, an unconformity separates Hirnantian strata from overlying Silurian carbonates. This unconformity corresponds to the eustatic fall in sea level associated with the terminal Ashgillian event (Berry and Boucot, 1973). Physical evidence of exposure at the top of the lower Fusselman is the result of this fall in sea level.

Shallow water carbonates like those found in the upper Fusselman Formation of the West Texas subsurface occur in Oklahoma (Cochrane and Blackgum Formations), the Mississippi Valley (Sexton Creek Formation), and across the remainder of the southern craton (Amsden and Barrick, 1988). Lowermost Llandoverian (Rhuddanian) strata appear to be absent at most sections on the southern craton, as is the case with the base of the upper Fusselman. Based on community studies of shelly fossils, Johnson (1987) has inferred that four major eustatic highstands of sea level produced transgressive sequences on the North American craton, as well as on other parts of the globe during the Llandoverian (Johnson et al., 1991): a late Rhuddanian-early Aeronian event, a late Aeronian event, an early Telychian event, and a late Telychian event.

Based on our sparse data, the upper Fusselman appears to range in age from the Aeronian into the Telychian. It should represent at least the middle two transgressive events of Johnson (1987), and may also include the oldest one. However, no one has demonstrated any regional transgressive or regressive events in the upper Fusselman. The extensive exposure surface at the top of the upper Fusselman corresponds to the major low stand in sea level that occurred near the middle Telychian that left an unconformity at the top of Llandoverian deposits across North American (Johnson, 1987).

Strata of the lower part of the Wink Member of the Wristen Formation are typical of Wenlockian strata that extend across the southern craton. A thin basal shale rests on the unconformable surface in West Texas. Oklahoma (Prices Falls Shale Member, Clarita Member), as well as in the Mississippi Valley region (Seventy-Six Shale Member, Bainbridge Formation) (Amsden and Barrick, 1988). This shale and the overlying thin sequence of offshore carbonates represent a regional flooding event on the North American craton that corresponds to a eustatic rise in sea level at the end of the Llandoverian (Jeppsson, 1987; Johnson, 1987; Johnson et al., 1991). The appearance of *Dapsilodus*-dominated conodont faunas, in association with abundant acrotretid brachiopods, forms an obvious ecostratigraphic marker for the lower Wenlockian in southern North America (Barrick and Biggers, 1985).

It is more difficult to interpret the topmost beds of the Wink Member and the Frame Member in terms of sea level events. The regional pattern, as exemplified by the Henryhouse-Haragan sequence in Oklahoma, suggests more or less continuous carbonate deposition on the southern craton. Sequences elsewhere on the craton show a gradual shallowing event starting as early as the late Wenlockian and continuing into the Pridolian. A brief break in deposition separates uppermost Silurian from lowermost Devonian (Lochkovian) deposits in most areas (Amsden and Barrick, 1988; Barrick and Klapper, 1992).

Because no diagnostic conodonts were obtained from the top of the Wink and the lower part of the Frame?, the presence or absence of Ludlovian and Pridolian strata can not be demonstrated in the Pegasus core. Based on our restudy of Decker's material, some graptolites from the Frame Member in Crane County (Gulf University No. 1 F well), may be as old as the Ludlovian. Both conodonts from the Frame? Member in the Pegasus core and graptolites from the Frame in the Gulf TXL No. 1 "EE" well in Crane County clearly indicate that the base of the Devonian lies within the black shales and limestones near the top of the Frame Member. If deposition was more or less continuous from the Ludlovian into the Lochkovian in the southern part of West Texas, then this period of time must be represented by the thin sequence of black shale and carbonate in the Pegasus core and in Crane County. Facies relationships (Ruppel, 1991), and the presence of graptolites in some of the black shales suggest deposition in deep water environments, where slow rates of deposition, punctuated by nondepositional hiatuses are likely to occur. To the north, in Andrews County, Texas, strata interpreted to be equivalent to the upper Wristen formed a thick carbonate platform on which a series of carbonate build-ups and related shallow water carbonates accumulated and prograded into deeper water environments at the margin (Ruppel, 1991).

Because Pragian (Early Devonian) graptolites occur in the underlying black shales in the Gulf TXL No. 1 "EE" well in Crane County, the Thirtyone Formation is inferred to be Pragian or younger in age. Preliminary study of conodonts from other wells suggests that the Thirtyone may be equivalent in age to the Frisco Formation of Oklahoma, which is interpreted to be Pragian in age (Barrick et al., 1990). In their analysis of North American Devonian transgressive-regressive cycles, Johnson and Klapper (1992) show the Frisco as part of the late Pragian cycle Ia. The Thirtyone Formation may be part of the same transgressive-regressive cycle.

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A WATER BUDGET FOR THE STATE OF TEXAS WITH CLIMATOLOGICAL FORCING

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Abstract.—The dependence of the Texas water budget upon climatological parameters was examined by a simple annual accounting in which runoff, lake evaporation, municipal-and-industrial water use, power generation and forced evaporation were expressed as specific functions of temperature and precipitation, and the remaining water budget components related proportionately. The state water budget was closed for present conditions, defined to be 1980 water uses in combination with 1951-80 climatological norms, then the water budget was scaled to two different climatological scenarios: the 1950-56 drought conditions and a "greenhouse-warming" condition. The water budget varies markedly across the state with regional hydrometeorology. Dependency on temperature and precipitation is nonlinear, reinforcing, and cumulative, with even modest departures from normal implying large responses of runoff and diversion. Under drought conditions, flow to the coast is reduced to one-third of normal. Under normal conditions with greenhouse-warming alterations, flow to the coast decreases by 35%. Under combined drought and greenhouse-warming, the coastal flows are reduced to less than one-fifth of normal. *Key words:* climate change; water supply; hydrology; streamflow; runoff; estuaries.

Water supply is the keystone of the Texas economy, and over the years the state has evolved a complex system of impoundments and conveyances to meet its increasing water requirements. The vagaries of Texas climate continue to stress the system and challenge its design and operation. This design is founded on an assumption of long-term stability of climate, i.e., that mean and extreme hydrological events may be quantified by examining the historical record. Climate does change, however. Moreover, there is increasing concern regarding the consequences of anthropogenic climate alterations, especially those resulting from the accumulation of so-called greenhouse gases. Therefore, it is appropriate to inquire how changes in basic meteorological parameters will affect the components of the Texas water budget.

This study is restricted to the state of Texas, but the results have implications for adjacent states. Because of its location on the continent, Texas spans a convergence of several climate types, and the behavior of its water budget has implications for water management in much larger regions of the south and central United States.

Water Budget Formulation

To close a water budget for the state requires identifying the various transfers for water, and compiling data on their magnitudes, aggregated in space and averaged over time. For this study the basic unit of time is a year. Most of the data compilation has been done by the Texas Water

Development Board (TWDB) or its predecessor agency the Texas Department of Water Resources (TDWR) as part of its function as the state water-planning agency. For specificity, I use the data on 1980 annual water uses compiled in TDWR (1984). Meteorological data for the 1951-80 climatological normal are employed, because this period is consistent with the period of hydrological data compilations of TDWR (1984). This combination of 1951-80 normal climatology and 1980 water uses is referred to hereafter as "present" conditions.

Spatial aggregation is more problematic. The natural spatial unit for surface water budgeting is the river basin, for water-use the county, and for climate analysis, the climatic zone (a region of relatively homogeneous climate). For this analysis, four broad regions of the state (Fig. 1) were defined to minimize arithmetic complexity and better depict the broad nature of the state water budget. The northern and western boundaries of the South and East regions, respectively, conform to basin boundaries, and the eastern boundary of the High Plains region follows the upper zone (county) boundaries of TDWR (1984), thereby facilitating the use of the TWDB data compilations. While there is clearly a wide range of climate within each of these regions, they are sufficiently distinct among themselves to characterize the major classes of hydroclimate in the state. And they closely resemble the climatic regions delineated by Larkin and Bomar (1983).

The conceptual water budget model for the state is diagrammed in Figure 2, with aggregate values for the state under "present" conditions (as defined above). For simplicity, some elements of water use are combined: ranching is combined with irrigation into "agriculture", municipal, industrial and mining uses are combined, and releases for the purpose of hydroelectric generation (as distinct from ancillary generation from releases for other purposes) are included in "spills". "Downstream" transfer refers to flow in a river channel below all points of diversion or impoundment within the region, and may enter another region, leave the boundaries of the state, or flow to the Texas coastal zone. Agricultural return flow is dominated by rice irrigation in the coastal reaches of rivers, and re-enters the surface-water system in this "downstream" reach.

Precipitation and air temperature were averaged over each region based upon the isopleths of normal values presented in Larkin and Bomar (1983). Runoff was taken from the basin computations of TDWR (1984) and groundwater recharge estimates are taken from Muller and Price (1979); both were cumulated by region. As evident in Figure 2, the surface is subdivided into the terrestrial watershed ("land") and the impoundments ("lakes"). Data on the surface area and conservation volume of the major reservoirs of Texas, provided by the TWDB, were cumulated by region and precipitation then apportioned by surface area.

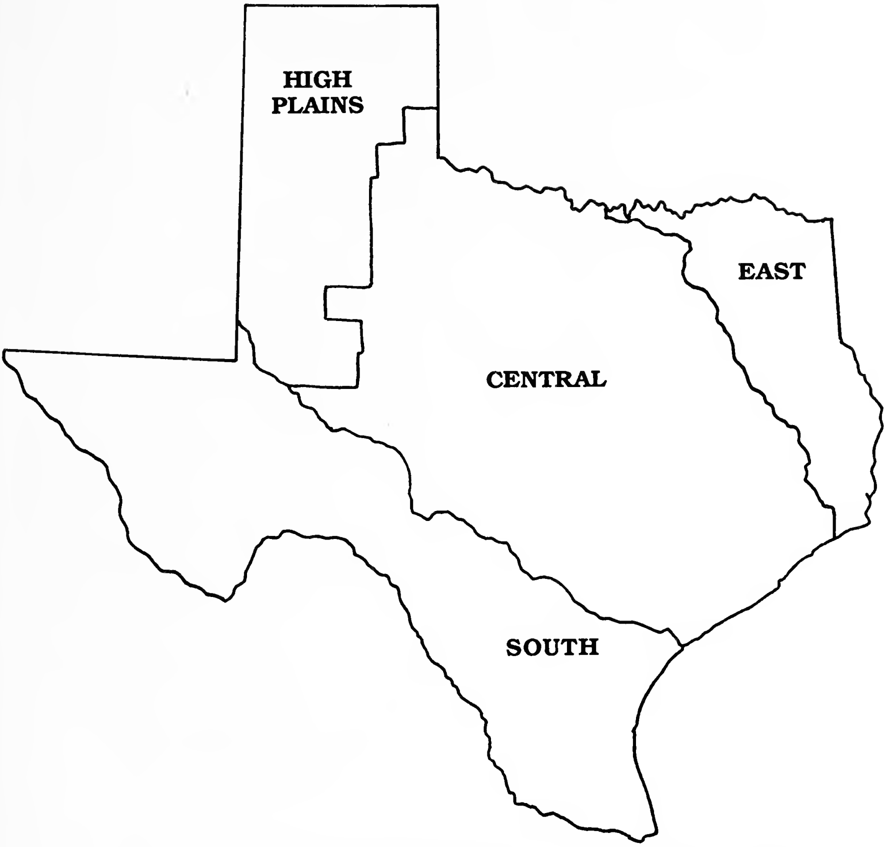

FIGURE 1. Hydroclimatological regions of Texas used in water budget analysis.

For the land compartment, evapotranspiration was computed as the residual from the other transfers. Lake surface evaporation was determined by the method described below, evaluated for the annual-mean normal temperature for the region, which proved to compare favorably with the isoplethed data of Larkin and Bomar (1983). Spills and uncaptured flows were then computed as the residual from the other transfers. When ground-water recharge exceeds withdrawals, the excess is assumed to appear in the surface budget as uncaptured flows, through interflow and springflow "leakage". When there is a deficit of recharge to withdrawals, this is flagged as an overdraft (negative), but does not affect the surface-water budget. It should be noted that this is an accounting of transfers, and assumes constancy of storage in each compartment, an adequate approximation for the large-scale, long-term water budgeting addressed here.

Much of interest concerning the sources and disposition of water within Texas can be inferred from Figure 2. It can also be misleading.

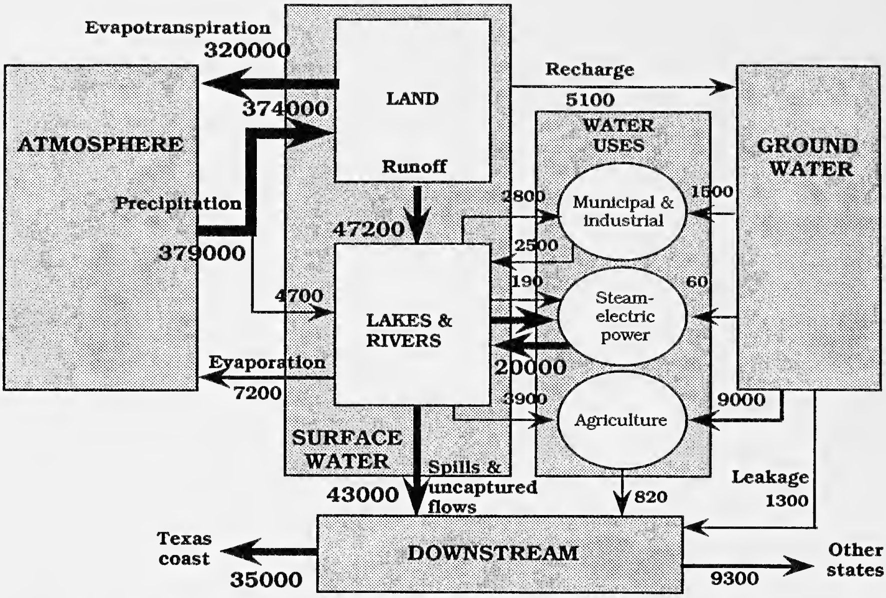

FIGURE 2. Schematic of Texas water budget, showing transfers under normal conditions (thousands of acre-feet per year).

For example, one might infer that Texas is a ground-water state, since that is the predominant source of water, and that runoff is ample to meet the present surface-water demands. Both inferences would be wrong, because both fail to account for the regional variation in the water budget. Table 1 presents the transfers of Figure 2 for each of the four regions of Figure 1.

Special note should be made of steam-electric power generation in Figure 2. The steam-generation cycle employs cooling water to re-condense high-pressure steam that spins the turbines. Data provided by the Public Utilities Commission show that steam-electric generation presently (1990) accounts for 95% of the state's generating capacity. Further, based upon aggregating these data by cooling water source, 65% of this capacity is situated on reservoirs. (About one-fourth of the state's reservoirs serve as cooling water sources for steam-electric generation.) The cooling water volume, estimated by the equation given below, represents the largest diversion of water in the state, nearly twice the agricultural diversion. However, the actual consumption of water by steam-electric generation is minor. The cooling water diversion is, in fact, returned to the surface-water resource, albeit heated (which accounts for the consumption, due to increased evaporation). The difference between cooling-water circulation and consumption is emphasized in Figure 2 by showing these as separate transfers. Steam-electric consumption might be included in lake evaporation, but I prefer to separate it.

TABLE 1. Regional water budgets for Texas, normal conditions (see text). Units 1000 acre-feet per year, except where indicated otherwise.

	EAST	CENTRAL	SOUTH	HIGH PLAINS	TEXAS
Population (1000s)	1513	9831	1887	1000	14231
Mean temp (°F)	65	66	68	59	64
Area (sq. mi.)	27250	116700	78300	42300	264500
Stm-elec cap (MW)	9910	25900	2410	2760 *	41000
Precipitation	68300	193000	79400	38400	379000
Land	66100	191000	79000	38300	374000
Lakes	2180	2110	346	39	4680
Evapotranspiration	49800	167000	75400	36900	329000
Land	47500	163000	74200	36800	322000
Lakes	2280	3540	1203	148	7170
Runoff	17505	24800	3715	1180	47200
Recharge	1090	2600	1090	343	5130
Surface water use	1130	3480	2100	150	6850
M & I	615	1800	274	110	2790
Agr	452	1580	1810	22	3860
Electric	61	101	10	15	188
Ground water use	246	2100	1100	7190	10600
M & I	215	995	178	154	1540
Agr	24	1080	905	7030	9040
Electric	7	27	14	8	56
Return flows	624	2390	210	89	3310
M & I	468	1780	154	89	2490
Agr	156	606	56	0	818
Stm-elec circuln	5120	13500	1290	0	19900
Upstream inflow:	Central 2550 Louisiana 1520	High Plains 912		New Mexico 0	NM & LA 1520
Spills/uncaptured	21000	23200	973	1010	42700
Groundwater leakage/ overdraft	848	501	-9	-6850	-5510
Downstream flow to:					
other regions/states	8380	2550		912	9330
Texas coast	12600	21100	973		34700

* towers only

CLIMATE DEPENDENCIES

The meteorological parameters air temperature and precipitation are taken to specify the "climate" of a region, consonant with the purpose of defining large-scale qualitative behavior of the water budget. Runoff is conceived as the surface-water surfeit above the infiltration rate, therefore capable of movement by hydraulic forces into the organized drainageways of a watershed (Chow, 1964; Eagleson, 1970). It is dependent upon terrain, surface character, and soils, as well as the rate of precipitation delivery. Runoff production is affected by the interval between storm events and the associated desiccation of the watershed, but for Texas the details of the runoff process have received little study. Especially on a long-term average basis, the rate of runoff production (per unit rainfall) is not constant but increases with rainfall. Runoff production was quantified by examining the relation of annual runoff production as a function of annual rainfall, ratio r of runoff to rainfall R, based upon data from the North Bosque River at Hico (U.S. Geological Survey Gauge No. 08094800) because this watershed is largely unimpounded (except for a scattering of small Soil Conservation Service flood-control reservoirs) and is near the center of the state. For present purposes, a dependence $r \propto R^5$ was adopted, because this best depicts the distribution of the data for rainfall rates below normal and can be conveniently implemented mathematically as a function of precipitation ratios. This dependence of runoff production on rainfall was assumed to be exhibited statewide. There is probably a dependence upon other variables as well, e.g. temperature, but quantification would require intensive analysis to extract.

The rate of evaporation from a free-water surface is taken to be governed by a version of Dalton's law, $E \propto (e_s - e)$ where e_s = saturation vapor pressure at the water surface, and e = vapor pressure of the overlying atmosphere. For long-term climatological purposes, air temperature (T) is a good estimator of water temperature. Assuming this, the Clausius-Clayperon equation for e_s implies $E \propto \exp\{T\}$, approximately. National Weather Service (NWS) monthly pan evaporation data were examined from each of the regions for 1989 and 1990 (except the High Plains, where there is no current NWS pan) to determine a temperature dependence of the form $\log E = mT + b$.

A high degree of linear correlation was found, i.e., explained variances on the order of 80% or better, and m for each region was determined from the associated linear regression. Pan data must be reduced to be applicable to a lake surface (Brutsaert, 1982), therefore pan-to-lake coefficients were assigned to each region. The pan-to-lake coefficients, and the value of b in the above regression are used only to establish the evaporation rates for the normal-condition water budget. Once established, evaporation is scaled with air temperature simply by $\exp\{m\Delta T\}$.

As shown by Table 1, water uses comprise a relatively small part of the state water budget. They are important to the activities of man, however, so climate dependencies were examined, particularly for municipal use and power generation. The basic assumption is that this dependence is demonstrated by the seasonal dependence upon meteorology. For municipal usages, the analyses of Maidment and Parzen (1984) and

Maidment (1987) for Texas cities were used. The former separated the "seasonal" variation from records of monthly usage for six Texas cities (*viz.*, Canyon, Littlefield, Andrews, Henderson, Huntsville and Conroe) and the latter performed the same analysis for five cities in the Lower Colorado basin (Austin, Bastrop, Burnet, La Grange and Bay City). Seasonal variation was expressed as a dimensionless normalized multiplier. These data were correlated against the climatological normal data for the respective localities. I found that 80-90 percent of the seasonal variance in the Maidment-Parzen data is explained by a linear dependence upon temperature, so it was feasible to regress the seasonal mulitplier versus mean temperature. The drier, more interior cities exhibited a higher range of seasonal variation in water usage, more than could be accounted for by the higher range of variation in air temperature, probably due to the additional evaporative stress arising from the more continental air.

The cities selected by Maidment and Parzen (1984) are not all situated to be representative of the climatological regions of Figure 1. Canyon and Huntsville are each satisfactory indicators of the High Plains and East Texas regions, respectively. Andrews (with climate data from Odessa) was used for South Texas. For the Central Texas region, average indices for Huntsville and Andrews (from Maidment and Parzen, 1984) regressed versus Dallas-Fort Worth temperatures were averaged with the mean Colorado indices (from Maidment, 1987) regressed versus Austin. Clearly, this analysis could be improved in many ways. Cities more representative of the regions should be used, and the monthly data for municipal usage and temperature should be used directly, not a fitted index and long-term averaged temperatures. Nor does a correlation imply a causal connection, which I in effect assume in associating the seasonal variation in water usage with temperature variation. But, this is an expedient means of estimating how temperature may drive municipal usage, and is at least based upon real utilization records in Texas cities.

This protocol determines the municipal water demand as a function of climate without regard for whether the water source is surface or ground water. In the water budget, a constant proportion of surface-to-ground is assumed for each region. For simplicity the same temperature dependence is applied to the industrial component as well (hence their combination in the water budget). Return flows were taken to be in fixed proportion to withdrawals for each region. Agricultural use varies widely depending upon both precipitation and temperature, but more significantly upon market economics and technology. No attempt was made to scale this usage with climate.

Steam-electric cooling water returned to the surface water resource entails an additional consumption due to the increased evaporation at higher water temperatures, the "forced evaporation", i.e. the incremental evaporation above that which would have occurred naturally. Ward (1986) includes a method for computing this forced evaporation. It can be simplified to $Ep = (0.007\ T + c)G$ where Ep = forced evaporation in ac-ft/yr, T = mean air temperature (°F), c is a function of local climate, principally wind speed (Ward, 1986), and G = annual-mean generation rate (megawatts), itself a product of generating capacity and capacity factor. The annual cycle of monthly capacity factor for the entire Electrical Reliability Council of Texas system (ERCOT, 1988) correlated well with state-mean monthly temperature ($r = 0.81$), as would be expected considering the role of the air-conditioning load in power demand. This was used to specify a temperature dependence of per-capita generation. Finally, 1980 generating capacity for each region was compiled from power-plant data from the PUC. The circulating flow Q_e in ac-ft/yr necessary for heat rejection is estimated by $Q_e = 600\ G$, which assumes a temperature rise of 15°F and an annual-mean capacity factor of 50%.

The remaining elements of the water budget are taken to be in fixed proportions to other (climate-dependent) components, with the proportion established for each region from the present-conditions water budget of Table 1. Recharge is assumed to be in fixed ratio to runoff, presuming the same hydraulic conditions which force runoff are also effective for recharge. Flows to other regions or states are similarly taken to be a fixed proportion of the total spills and uncaptured flows. Return flows for each of the human water demands within each region are taken to be a fixed proportion of diversions.

With these relationships, the water budget of Figure 2 can be recast as a function of precipitation and temperature. Because of the logical connections between the transfers and the simple arithmetic involved, the water budget is particularly amenable to implementation in spreadsheet software. A version for LOTUS 123$^{\text{TM}}$ has been prepared (a copy of which will be provided upon request to the author with a formatted diskette), in which the temperature/precipitation dependencies are expressed relative to normal values: temperature as an increment above normal and precipitation as a fraction of normal. Several of the water uses, viz. municipal-and-industrial and steam-electric, are assumed to be proportional to population, so are similarly scaled as a ratio to 1980 population (for each region of Figure 1). This formulation proves to be especially useful for examination of various scenarios of climate change and population growth.

DROUGHT CONDITIONS

The water budget was developed for normal conditions. Critical water supply conditions are associated with drought, however, and the "drought of record" is the basis for water supply allocation in Texas. In the present context, I hypothesize that the water budget under drought conditions is driven by the climatological parameters temperature and precipitation. A drought condition, therefore, presents a test case, albiet extreme, for the water budget.

I examine the period 1950-56, which in most areas of the state encompasses the infamous 1950's drought. No convenient accounting of all the necessary data is available (and may not exist), and a data compilation *ab initio* would require a major effort. I therefore relied upon selected meteorological stations in each region to determine the departure from the 1951-80 normal of the 1950-56 mean of temperature and precipitation, upon the U.S. Study Commission (1962) for water use data, and upon Lowry (1958) for river flow data. Population data for the state for 1957 (Lowry, 1958) were taken to be distributed in the four regions in the same proportions as 1980. Those major reservoirs impounding prior to 1955 were tabulated for each of the four regions and cumulated to characterize the reservoir area for 1950-56. The resulting climatological/water-resource scenario is summarized in Table 2A, relative to 1980 conditions. In this statewide summary, several key elements of the water budget are listed, both in volume per year, and as a proportion of the 1980 normal scenario. The reduction of flow to the coast, as well as the considerably reduced reservoir development, relative to the present should be especially noted.

The projected 1950-56 municipal and industrial usages, based upon population and temperature, compare acceptably with the USSC (1962) data. The USSC (1962) water-use data applies to 1958, technically after the drought had terminated. Nonetheless, municipal and industrial uses are probably adequate approximations of the 1950-56 period. For irrigation, in contrast, we have no means for projecting usage as a function of climate. Therefore, the USSC 1958 data for irrigation were used directly in the 1950-56 water budget, which indubitably is an overestimate, in that irrigation from surface supplies was seriously curtailed during the drought.

The key test, of course, is how well the downstream flows compare with actual data. Lowry (1958) compiled average data (which he labeled "runoff") for the river basins of Texas for several key historical periods including 1950-56. In Table 3 are compared his mean values, aggregated into the four hydroclimatological regions, with those projected by the methodology described herein. Considering the rather crude approximations involved in the water budget, and the intrinsic sponginess of the hydrological data, the two agree well. The most significant discrepancy is the South Region flow to coast, reported as 1350 x 10^3 ac-ft/yr by Lowry (1958), but projected by this method to be 0. The source of this discrepancy is the 1954 flood on the Rio Grande, which produced significant downstream flow, and then was averaged by Lowry (1958)

Table 2. Water budget projections for various climate scenarios.

	SCENARIO SPECIFICATION					*STATE SUMMARY*	
Region	*Pop rel to 1980*	*Temp incr over norm (°F)*	*Precip rel to norm*	*Reservoir area rel to 1980*		*1000 ac-ft/yr*	*rel to norm*
			A. 1950-56 drought and water demands				
					Land evaptr	290000	0.90
East	0.641	1.7	0.81	0.097	Lake evap	2400	0.33
Central	0.641	1.0	0.87	0.423	Runoff	16600	0.35
South	0.641	1.2	0.76	0.486	Net consumption	2320	0.66
Plains	0.641	0.8	0.75	0.1	Spills/uncap	17000	0.40
					Flows to coast	14500	0.42
			B. Present demands with 1950-56 drought conditions				
					Land evaptr	290000	0.90
East	1	1.7	0.81	1	Lake evap	7430	1.04
Central	1	1.0	0.87	1	Runoff	16600	0.35
South	1	1.2	0.76	1	Net consumption	3700	1.05
Plains	1	0.8	0.75	1	Spills/uncap	10610	0.25
					Flows to coast	10270	0.30
			C. Present demands with greenhouse-altered normal conditions				
					Land evaptr	317000	0.98
East	1	4	0.95	1	Lake evap	8060	1.12
Central	1	4	0.95	1	Runoff	34700	0.74
South	1	4	0.95	1	Net consumption	4110	1.16
Plains	1	4	0.95	1	Spills/uncap	28400	0.67
					Flows to coast	22300	0.64
			D. Present demands with greenhouse-altered drought conditions				
					Land evaptr	28000	0.87
East	1	5.7	0.77	1	Lake evap	8360	1.17
Central	1	5.0	0.83	1	Runoff	12400	0.26
South	1	5.2	0.72	1	Net consumption	4280	1.21
Plains	1	5.8	0.71	1	Spills/uncap	4660	0.11
					Flows to coast	5700	0.16

over the 1950-56 year period. In contrast, my water budget methodology averages runoff over the entire 1950-56 period first, so that the flood event is averaged down to a value that does not exceed the averaged surface water losses in the region. This is an excellent illustration of the potential importance of interannual variability in some of the water budget elements, which is suppressed by the annual-averaging methodology used here.

It is logical to inquire how the water budget would be altered under a drought condition but with present reservoir development and water demands. This is summarized in Table 2B. It should be emphasized that agricultural usage is left unchanged from normal (1980 use), an unlikely prospect during a drought.

TABLE 3. Comparison of projected downstream flows for 1950's drought to data of Lowry (1958).

Downstream flow (*10^3* ac-ft/yr)	*projected*	*1950-56 means*
East, to other states	3110	5100
East, to Texas coast	3950	5530
Central, to Texas coast	9090	8780
South, to Texas coast	0	1350
High Plains, to other states	16	190
Total to Texas coast	12000	15660

CLIMATE-CHANGE EFFECTS ON WATER BUDGET

In recent years, there have been increasing efforts to develop models capable of long-range (many decades) prediction of climate, motivated by the issue of greenhouse warming. These global climate models (GCM's) are very much developmental, and their forecasts must be regarded as tentative, at best. Yet these are our best available means for quantitative estimates of potential future climates. Details of formulations vary, and some of the GCM teams have several models operational, varying in the details of formulation of physical processes. For example, Cess et al. (1990) compared the results of no less than 19 different GCM's. A discussion and comparison of these various models are inappropriate here. Three observations suffice: (1) temperature and, even more so, precipitation are the end result of a concatenation of physical-process calculations, and therefore suffer from a compounding of uncertainty; (2) even if the GCM formulations were precise, the spatial resolution of GCM's is extremely coarse, with a single grid point representing an area at least the size of Texas; (3) there is little unanimity among model predictions for a given scenario, especially for precipitation.

For this study, a consensus prediction was sought for the doubled CO_2 scenario, i.e. the 50-year "nominal" scenario of Wuebbles et al. (1984) and the standard equilibrium scenario of Houghton et al. (1990), using results presented in Grotch (1988), Kellogg and Zhao (1988) and Houghton et al. (1990). Generally, an increase of about 4°C is indicated for the entire U.S. midwestern region, with reduced precipitation and drying soil conditions for the Texas area. This scenario is consistent with reasoning from the predicted change in temperature using historical or prehistorical associations between precipitation and temperature (Kellogg, 1982; Webb and Wigley, 1985). These are equilibrium results. After 50 years (the standard planning horizon for water supply), only a portion of this equilibrium response would be realized. Transient response was judged, based on Hoffert and Flannery (1985) and Houghton et al. (1990), to be approximately one-half of the total warming effect. The "consensus" climate-change scenario appropriate for a 50-year horizon therefore becomes: Temperature: +4° F, Precipitation: -5%. We emphasize that this is a judgement drawn from predictions with a considerable spread, and is used here only to provide a quasi-realistic test case.

The results of the water budget model with these altered meteorological parameters are summarized in Table 2C and 2D, for both normal and drought conditions. "Net consumption" in this table refers to surface uses only. The corresponding regional water budgets for the changed-climate normal condition are given in Table 4. No population change or reservoir expansion is prescribed, so these calculations indicate how the *present* state water budget would change with altered meteorology on the order of that anticipated due to greenhouse warming.

Discussion and Conclusions

The purpose of this study was to demonstrate the dependence of various elements of the water budget of major regions of Texas on climatic controls, by a quantitative formulation with explicit meteorology dependencies. Climatology was approximated by annual-mean air temperature and precipitation. Other parameters, such as humidity, surface radiation, and wind, can be hydrologically important, but were not considered. Water demands and hydrology were evaluated on an annual-mean basis, despite the considerable intra-annual variability in Texas. Existing data were used when possible, aggregated and averaged as necessary, and when data did not exist, representative relations were derived from a combination of theory, specific data sets, or assumption. Nonetheless, the final result is considered to be qualitatively correct, and illustrates several important features of the Texas water budget and its climatological controls:

1. The water budget varies markedly across the state according to regional hydrology and meteorology. The High Plains is, for practical purposes, hydrologically isolated, with a considerable annual overdraft of the ground-water supply. East Texas is the most prolific source of runoff, of which 97% is uncaptured, 40% of which in turn flows out of state.
2. Surface water is central to Texas water supply. The substantive ground-water withdrawal is dominated primarily by irrigation on the High Plains (from the Ogallala aquifer) and secondarily by irrigation and municipal water supply in the South and Central Texas regions (from the Edwards aquifer). Surface water is the predominant source in all other regions and for all other uses.
3. The consumption of water by man's activities is generally a minor portion of the state water budget. Agriculture is the dominant use. Steam-electric power generation is the greatest diverter of water, but is only a minor consumer. However, a substantial volume of water must be available for recirculation as cooling water. This factor is usually

Table 4. Regional water budgets for Texas, greenhouse-altered normal conditions. Units 1000 acre-feet per year, except where indicated otherwise.

	EAST	CENTRAL	SOUTH	HIGH PLAINS	TEXAS
Population (1000s)	1513	9831	1887	1000	14231
Mean temp (°F)	69	70	72	63	68
Area (sq. mi.)	27250	116700	78300	42300	264500
Stm-elec cap (MW)	9910	25900	2410	2760 *	41000
Precipitation	64900	183400	75400	36400	360000
Land	62800	181300	75000	36400	356000
Lakes	2070	2000	329	37	4440
Evapotranspiration	51700	165000	72900	35400	325000
Land	49100	161000	71500	35300	317000
Lakes	2530	3990	1370	164	8060
Runoff	12900	18200	2730	868	34700
Recharge	804	1910	800	252	3770
Surface water use	1290	3970	2160	156	7580
M & I	635	1920	308	119	2980
Agr	452	1580	1810	22	3870
Electric	202	471	45	16	734
Ground water use	253	2170	1120	7200	10700
M & I	222	1060	201	166	1650
Agr	24	1080	905	7030	9040
Electric	7	27	14	8	56
Return flows	639	2510	230	96	3470
M & I	483	1900	174	96	2650
Agr	156	606	56	0	818
Stm-elec circuln		13500	1290	0	19900
Upstream inflow:	Central	High Plains		NM	NM & LA
	1690	613		0	1450
	Louisiana				
	1450				
Spills/uncaptured	14900	15400	-248	681	28400
Groundwater leakage/ overdraft	551	-256	-319	-6950	-6950
Downstream flow					29000
other regions/states	6990	1690		613	6380
Texas coast	8900	13700	0		22600

*towers only

overlooked in drought planning. Reduction of reservoir volumes below the operating levels of power-plant intakes would jeopardize the state's generating capacity. This warrants study, but lies beyond the present scope.

4. Dependency of elements of the water budget on temperature and precipitation is nonlinear, reinforcing, and cumulative. Even modest

departures from normal imply large responses of runoff and diversion. Under drought conditions, the reduction in flows to the coast is even more dramatic, reducing to one-third of normal. The flow to the coast is projected to decrease by 35-55 percent due to greenhouse-warming alterations of climate, which in combination with drought conditions implies a reduction to less than one-fifth of normal.

5. Relative to the main transfers of the water budget, human uses are typically an order of magnitude smaller under normal conditions. However, the elements of the water budget involved in human use are sensitive to both rainfall and temperature. Uses increase by about 20 percent with greenhouse-warming, from 7.5 percent of runoff to 12 percent of runoff under normal conditions, and from 22 to 34 percent of runoff under drought conditions (assuming constancy of the agricultural component). Therefore, under climate stress, the human component becomes increasingly important in the overall water budget. Of the non-agricultural uses, steam-electric comprises 12 percent under normal conditions, but increases to 29 percent with the temperature increment of the greenhouse-warming scenario.

6. This water budget, considering only transfers, does not yield information directly related to adequacy of water supply. From the cumulated conservation capacity of present reservoirs, however, the human and evaporative losses computed above imply about a three-year supply, which decreases about 10 percent with greenhouse warming. One implication of this water budget analysis is that climate change is potentially significant to Texas water supply and should be accommodated in the planning process.

This water budget would be greatly improved by utilizing a monthly, rather than annual, time frame. Significant problems in water supply may occur during specific seasons (notably summer) that are not resolved on an annual basis. Furthermore, many of the climate-dependent processes and uses vary significantly on a month-to-month basis, and impose an average water transfer that is lost in using only annual-mean parameters to drive the water budget. The water budget could also be improved by a finer spatial resolution, on at least a basin unit. This is the approach used by Schmandt and Ward (1990), to examine long-term water supply problems in the Trinity, Colorado and Rio Grande basins. Because the purpose here is to examine the effect of climatological drivers, greater detail in space and time resolution of the water budget would not compensate for the coarseness of climate "forecasts".

Finally, the three-significant-digit reporting of the results of Table 1 *et seq.* is meretricious: the water budget is accurate to no better than two significant digits and is probably not that good. Moreover, it should be noted that our knowledge of a hydrological transfer is inversely proportional to its importance in the water budget. In particular, the driving processes of evapotranspiration and runoff are poorly quantified for Texas, and their meteorological dependencies even more imperfectly known. Of the human water uses, the largest, agriculture (which is also central to the state economy), is the least well-quantified. Research is very much needed on all of these aspects.

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The work of the Texas Water Development Board on Texas hydrology and water use was crucial to this study. I thank the Board's staff, especially Dr. Bill Longley of the Bays and Estuaries Program for their assistance and generosity. Ms. Joan Flowers of the Institute for Applied Environmental Research, Tarleton State University, assisted in the runoff production computations. Mr. Joe Castleberry of the Public Utilities Commission kindly provided data on power plants in Texas.

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DIURNAL DISTRIBUTION OF HOURLY RAINFALL EVENTS DURING JANUARY BY SYNOPTIC WEATHER TYPES AT LAKE CHARLES, LOUISIANA

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Abstract.—The occurrence and amounts of hourly precipitation recorded from 1951 to 1990 at the city of Lake Charles, Louisiana during the month of January are analyzed on a diurnal basis by synoptic weather type. The effects of each weather type on the temporal distribution of diurnal precipitation is discussed. Frontal Overrunning (FOR) has the greatest effect on the overall diurnal precipitation pattern. The merit of identifying the underlying processes which create distinct diurnal patterns is examined. *Key words*: precipitation; diurnal rainfall patterns; synoptic weather types; Lake Charles.

Lake Charles is located in the southwestern corner of Louisiana, just inland from the Gulf of Mexico. Over 1,360 millimeters of precipitation per year fall on average at this site. There are two notable wet periods at Lake Charles, one in the late summer and fall and another in December and January. The late summer and fall rainfall results from frequent convective storms combined with occasional cyclonic systems of tropical origin. The winter maximum primarily results from frequent frontal passages and cyclogenesis in the western Gulf of Mexico (Saucier, 1949).

Throughout most of the year, the diurnal pattern of precipitation at Lake Charles is centered in the mid to late afternoon. The afternoon maximum is most noted in the April through September period (Faiers, 1983) and results from afternoon instability combined with abundantly available atmospheric moisture. In December and January, however, the occurrence of measurable precipitation at Lake Charles peaks in the mid-morning hours. The diurnal pattern during January is depicted in Figure 1. Such a diurnal pattern is not easily explained but this pattern does persist in January across much of southwestern Louisiana and southeastern Texas (Faiers, 1986). Typically, the weather conditions which create such diurnal patterns are alluded to, but not examined in detail (Schwartz and Bosart, 1979; Conner, 1981; Giles and Flocas, 1990). The purpose of this study is to use synoptic climatology to understand the processes which produce this diurnal rainfall pattern.

Materials and Methods

Each measurable hourly precipitation event during January (1951 - 1990) at Lake Charles has been recorded by year, day, time, and amount. The weather occurring at the time of observation has been identified using Muller's synoptic weather type classification for Louisiana (Muller, 1977; Muller and Willis, 1983). Such an application was useful in explaining the frequency and intensity of January hourly rainfall at Lake Charles (Faiers, 1988; Faiers, 1991). National Oceanographic and Atmospheric Administration (NOAA)

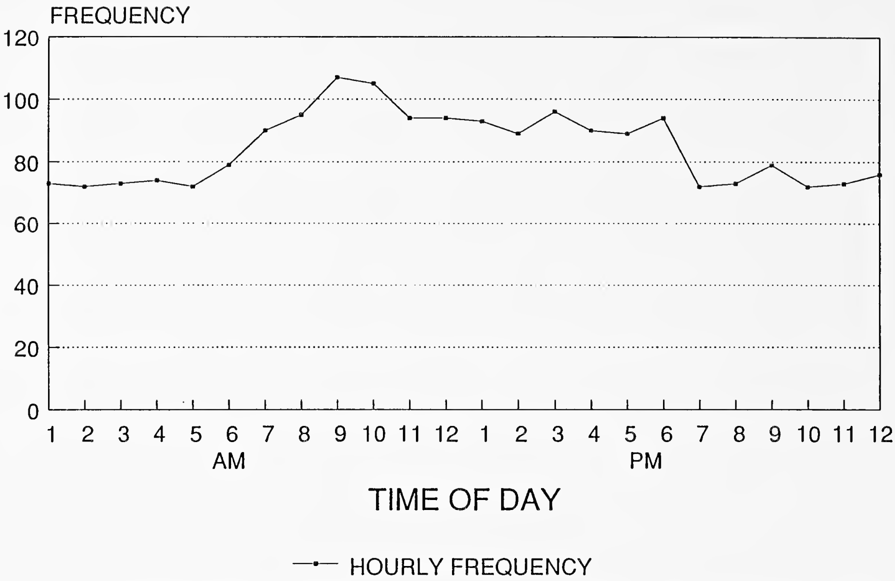

FIGURE 1. Diurnal distribution of hourly precipitation events at Lake Charles during January (1951-1990).

publications *Local Climatological Data* and *Daily Weather Maps* were utilized to identify the synoptic weather type at the time of each observation.

Muller and Willis (1983) identified eight distinct weather types for Louisiana (Fig. 2). Pacific High develops when a deep low pressure system over the Central U.S.A. allows a strong westerly wind to pull air of a Pacific origin into Louisiana. This type is also characterized by clear to partly cloudy skies and relatively mild temperatures. It is primarily a winter-spring weather type. Continental High weather is another fair-weather type but is colder with north or northwest winds across the state. This type can occur during any month.

Frontal Overrunning produces extensive cloudiness and quite often is associated with steady light to moderate rainfall (or sometimes snowfall) as a surface front becomes stationary in the Gulf of Mexico. This type can develop ahead of a warm front advancing northward out of the Gulf of Mexico. Northeast to east winds prevail at the surface under these conditions. Warm air is forced aloft over the cooler surface air and the clouds and precipitation result from this lifting. This type occurs year-round, but is most persistent during the winter.

Coastal Return conditions develop as a high pressure area drifts eastward off the Atlantic Coast and the airflow becomes more easterly across the region. This is usually a fair-weather type, but during the summer especially, it can be associated with showers as heat and humidity combine to produce the necessary convection for rainfall. Coastal Return often is a transitional type between Continental High and Gulf Return. Gulf Return weather develops as a high pressure area is offshore in the Atlantic Ocean and a southerly flow of warm and humid air flows into the state. This weather type is characterized by fair to partly cloudy skies, but occasionally surface or upper-air conditions are conducive to showers or thunderstorms.

Frontal Gulf Return weather develops as a cold front approaches the state and the warm south to southwesterly winds converge upon the frontal boundary. Partly cloudy to cloudy

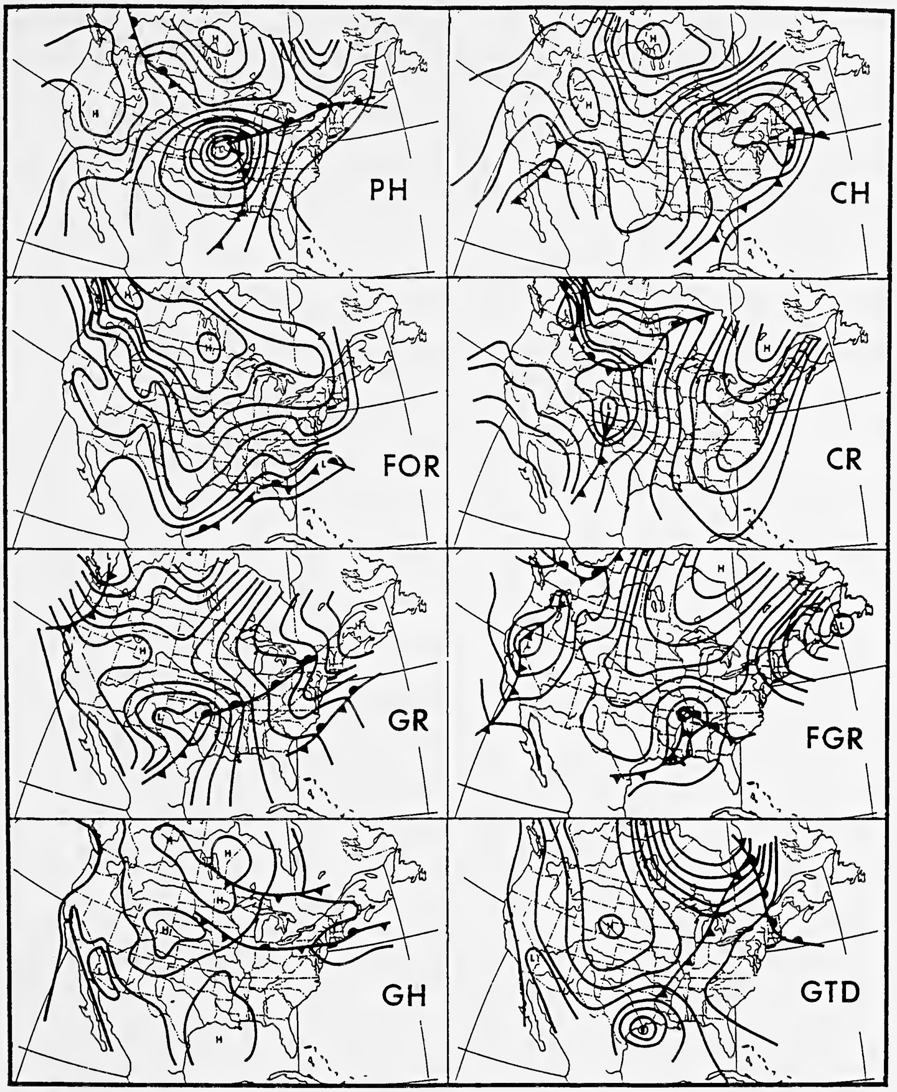

FIGURE 2. Eight synoptic weather types for Louisiana (after Muller and Willis, 1983). PH = Pacific High, CH = Continental High, FOR = Frontal Overrunning, CR = Coastal Return, GR = Gulf Return, FGR = Frontal Gulf Return, GH = Gulf High, GTD = Gulf Tropical Disturbance.

COLD FRONT

WARM FRONT

STATIONARY FRONT

OCCLUDED FRONT

H = HIGH PRESSURE

L = LOW PRESSURE

TABLE 1. Frequency and Intensity of Hourly Precipitation by Synoptic Weather Type. FOR = Frontal Overrunning, FGR = Frontal Gulf Return, GR = Gulf Return, CR = Coastal Return.

Synoptic Type	N	Intensity
FOR	1510	1.79 mm
FGR	448	3.08 mm
GR	58	2.56 mm
CR	18	1.28 mm
TOTAL	2034	2.05 mm

skies and showers and thunderstorms are characteristic of this type. Most of the severe thunderstorms and associated tornadoes are associated with Frontal Gulf Return weather.

Another fair-weather type is Gulf High. Gulf High conditions develop when high pressure forms over the Gulf of Mexico. The subsidence produces clear to partly cloudy skies and light winds. Gulf High is most common in the summer and produces some of the most uncomfortable conditions in the region as a result of excessive heat and humidity combined with little or no movement in the surface air.

Gulf Tropical Disturbance weather occurs when tropical disturbances ranging from easterly waves to hurricanes affect the state. These conditions are primarily confined to summer and fall and can be associated with some of the heaviest rainfall and most destructive weather-related events in the state.

RESULTS

Over the course of the forty Januaries, 2,034 measurable hourly rainfall observations were made at Lake Charles (Table 1). Of these, 1,510 (74%) occurred during Frontal Overrunning weather. The average hourly intensity of precipitation during Frontal Overrunning weather in January was only 1.8 millimeters (mm) due to the gentle lifting over the shallow frontal boundary and the lack of surface heating.

Frontal Gulf Return weather accounted for 448 (22%) of the hourly events. These events were usually more short-lived than Frontal Overrunning events, but also more intense (3.08 mm per hour) due to the instability and rapid lifting associated with cold frontal passages.

Non-frontal rainfall events were less common during the winter than in the summer months in Loiusiana (Muller and Willis, 1983). The non-frontal types, i.e. Gulf Return and Coastal Return, produced 58 (3%) and 18 (1%) hours of rainfall, respectively, during these Januaries. Due to the lack of surface heating at this time of year, there were relatively few events in these categories. However, when there was some upper air support, some events did take place, with an average intensity of 2.56 mm per hour in Gulf Return weather and only 1.28 mm per hour during Coastal Return conditions.

Figure 1 displays the diurnal pattern of precipitation at Lake Charles during January (1951-1990). As illustrated, the majority of the rainfall occurs during the daylight hours, but with a pronounced maximum

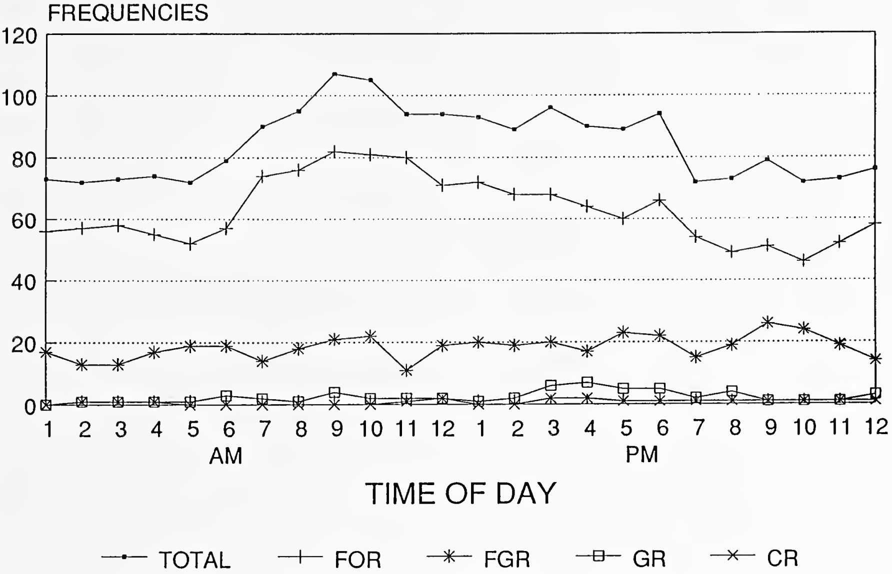

FIGURE 3. Diurnal distribution of hourly precipitation events at Lake Charles during January by synoptic weather type (1951-1990).

centered around 0900. During these Januaries, 107 hourly events were observed at 0900 and 105 measured observations occurred at 1000. No other hours surpassed 100 observations. The lowest hourly total was 72, observed at four times (0200, 0500, 1900 and 2300).

When the diurnal pattern is examined by synoptic weather type (Fig. 3), it is revealed that the diurnal pattern of Frontal Overrunning is responsible for the overall diurnal trend at Lake Charles in January. Frontal Overrunning events are at a minimum overnight until around 0400, when a noticeable increase in frequency begins and peaks at 0800, and then falls steadily throughout the remainder of the day. Frontal Gulf Return has no discernable diurnal pattern, while the non-frontal types of Gulf Return and Coastal Return tend to produce more events during the afternoon, in response to surface heating. It is clear, therefore, that the overall diurnal pattern of rainfall at Lake Charles during January is primarily the result of processes associated with Frontal Overrunning weather.

As stated previously, the morning peak in diurnal precipitation is common along the Texas Gulf Coast as well. It is not surprising that there is such a diurnal pattern to Frontal Overrunning weather in this region at this time of year. January is the peak month for cyclogenesis in the western Gulf of Mexico (Saucier, 1949), and under these conditions, Frontal Overrunning weather spreads across much of Texas and southwestern Louisiana. Cyclogenesis in this region during the winter is enhanced nocturnally by the temperature gradient which exists between the colder land mass and the warm waters of the Gulf of Mexico. This gradient is steepest in the early morning hours and the cyclogenesis is enhanced at this time of day. Upper level steering currents direct developing systems in a northeast direction, especially during this time of year (Elliott, 1949), bringing precipitation into the Lake Charles area around dawn or shortly thereafter. Other research has supported the nocturnal enhancement of Frontal Overrunning precipitation (Hewson, 1937).

Conclusion

Frontal Overrunning weather accounts for the greatest number of hours of rainfall at Lake Charles during January, and it also controls the diurnal pattern of hourly precipitation. The occurrence and diurnal pattern associated with Frontal Overrunning weather during January at Lake Charles is primarily associated with cyclogenesis in the western Gulf of Mexico. It is anticipated that similar results can be expected for sites extending southwestward along the Texas Gulf Coast. This research illustrates the utility of stratifying hourly precipitation events into associated synoptic weather types to achieve a better understanding of the mechanisms creating diurnal patterns.

Acknowledgments

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GENERAL NOTES

FIRST RECORD OF *NOCTILIO ALBIVENTRIS* (CHIROPTERA, NOCTILIONIDAE) IN EL SALVADOR

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On the evening of 23 June 1989, Owen set two 60-foot mist nets over shallow water in an estuary at Barra de Santiago, 2 m, Departamento de Ahuachapán, El Salvador (13° 41′ N, 90° 01′ W, tropical dry forest). Nets were erected about 1.5 kilometers from the Pacific Ocean. The estuary is surrounded by dense mangrove stands (*Mangifera mangle*), but inland from the intertidal zone vegetation is dominated by scattered tall standing trees, and patches of corn and pasture.

Among bats captured were two specimens (one male, one female, TTU 62403-04) of *Noctilio albiventris.* These are the first records of this species from El Salvador and bring the total bat fauna known historically from this country to 59 (Owen et al., 1991). Specimens are preserved in fluid and they, along with chromosome preparations and frozen tissues, are deposited in the mammal collection of The Museum of Texas Tech University, Lubbock, Texas.

The subspecies from Central America is *N. a. minor* according to Davis (1976), who cited its geographical distribution as extending from the Atlantic versant of Honduras, near San Pedro Sula, southward through Central America and thence into South America. Davis' (1976) distribution map shows the lesser bulldog bat present on the Pacific versant of Central America from near Rivas, Nicaragua southward.

Dolan and Carter (1979) extended the known range of *Noctilio albiventris* to southeastern Guatemala, Departamento de Santa Rosa. This range extension was confirmed by six additional specimens collected in the Pacific lowlands of Santa Rosa, Guatemala, by Dickerman et al. (1981). Polaco (1987) reported the first record of the lesser noctilio from México, near Escuintla, Chiapas. Polaco's (1987) specimens extended the known range approximately 240 kilometers (Dickerman et al., 1981), and represent the northernmost record for this species.

Dolan and Carter (1979) opined that the lesser bulldog bat is not continuously distributed along the Pacific coast from his Guatemala localities to Rivas. Their opinion would now seem less probable in light of this report from El Salvador, and that of Polaco (1987) from México. Hood and Pitocchelli (1983) state that *Noctilio albiventris* primarily inhabits mesic tropical forest habitats, foraging over rivers, streams, and marshes. This habitat type probably occurs extensively along the Pacific versant of Central America. Owen has observed abundant mangrove swamps and estuaries along the coast of El Salvador and around the Gulf of Fonseca in Honduras. It would now seem plausible that, in suitable habitat, *Noctilio albiventris* occurs along the Pacific versant of Central America northward to at least Chiapas, México.

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DISCOVERY OF *ZAPUS HUDSONIUS* IN NORTHEASTERN OKLAHOMA, WITH COMMENTS ON ITS ECOLOGICAL STATUS

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The meadow jumping mouse, *Zapus hudsonius*, is a boreal species which ranges from Alaska across Canada to the Atlantic coast southward throughout the eastern United States, west to the central Great Plains (Hall, 1981), with one subspecies restricted to lowland montane habitats in eastern Arizona and central New Mexico (Hafner et al., 1981; Morrison, 1992). The species inhabits mesic environments with dense herbaceous ground cover, such as streamsides, grassy meadows, forest edges, and abandoned fields (Whitaker, 1972; Bee et al., 1981; Jones et al., 1985; Morrison, 1990; 1992). In Oklahoma, two specimens of *Z. hudsonius* were collected from Tulsa County in 1936 (Blair, 1938), and since that time, the species has not been documented in the state (Caire et al., 1989). Sealander and Heidt (1990:251) made a reference (in the section concerning species of unverified occurrence in Arkansas) that "Bryan P. Glass collected this species from Adair County, Oklahoma," however, this report is erroneous (B. P. Glass, pers. comm. to Husby).

On 11 July 1992, two female *Z. hudsonius* were collected 8.5 mi. N, 1.5 mi. W Welch, Craig County, Oklahoma (T29N, R20E, Sec. 21), which documents the occurrence of the species in the state. Records for the species are known from the tallgrass prairie in the eastern two-thirds of Kansas, the nearest being an old record approximately 80 kilometers north in Neosho County (Bee et al., 1981). No specimens are reported from Arkansas (Sealander and Heidt, 1990), although the state's northwestern corner is only 82 kilometers southeast of the Craig County locality. Specimens have been taken sporadically from southwestern Missouri (Schwartz and Schwartz, 1981).

Fossils of *Z. hudsonius*, outside the present range, are included in three deposits from Meade County, Kansas. These fossils date from the late Illinoian glacial (Mt. Scott local fauna) to the late Sangamon interglacial (Jinglebob local fauna) periods (Klingener, 1963) and into the latest Pleistocene (radiocarbon dated at 11,110 YBP) of the Robert local fauna

(Davis, 1987). The only fossil deposit in Oklahoma containing *Z. hudsonius* is from the Illinoian glacial of the Doby Springs local fauna from Harper County (Klingener, 1963), approximately 418 kilometers west of the Craig County site. Fossils identified as *Z. hudsonius* (Hafner, 1993) are included in the late Pleistocene deposits from Schulze Cave on the Edwards Plateau of Texas (Dalquest et al., 1969), the southernmost locality for the species.

During the Pleistocene to about 11,000 years ago, *Z. hudsonius* occurred south and west of its current range. The climate at that time was more equable, with cooler, moister conditions allowing for more effective moisture (Davis, 1987; Kasper, 1992), which would provide more optimal habitat for a boreal species such as *Z. hudsonius*. Since the last meadow jumping mice were collected in Oklahoma by Blair in 1936, the climate associated with the eastern tallgrass prairie has become significantly cooler and moister as indicated by a decrease in mean annual temperatures and an increase in total annual precipitation (Frey, 1992). These changes in temperature and precipitation stimulated the expansion of habitats suitable for *Z. hudsonius*, and as a consequence, vegetation was modified along the edge of the species' range. When marginal habitats become more optimal for a species, population density will increase and the species will disperse by utilizing newly created marginal habitat (Frey, 1992). Therefore, *Z. hudsonius* is presumably expanding its range southward into Oklahoma through changes in habitat structure caused by overall cooler, moister conditions. A similar response by *Z. hudsonius* has been indicated in Kansas, where the species has expanded its range westward and southward (Choate et al., 1991; Frey, 1992).

Whether the meadow jumping mouse has recently dispersed into Oklahoma or merely avoided detection, the utilization of man-made mesic habitats (roadsides and irrigation/ drainage ditches) would serve as both corridors of dispersal (Choate et al., 1991) and persistent suitable habitat amid agricultural fragmentation (Morrison, 1992). The occurrence of *Z. hudsonius* in northeastern Oklahoma probably results by diffusion via rank vegetation along roadsides and water courses. Similarities in the vegetative composition are reported between natural riparian habitat of *Z. hudsonius* and along man-made waterways (Morrison, 1990), implying that food and cover requirements of meadow jumping mice may be met along man-made mesic habitats (Morrison, 1992).

The two Craig County specimens were collected in dense grasses along the edges of revegetated spoil piles of an old coal strip mine. Prominent grass species were big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and Johnsongrass (*Sorghum halepense*). Associated woodland vegetation included oak (*Quercus* sp.), elm (*Ulmus* sp.), cottonwood (*Populus* sp.), sumac (*Rhus* sp.), poison ivy (*R. radicans*), and greenbrier (*Smilax* sp.).

A collection effort of approximately 1,790 trap-nights on 10-12 July was required to catch the two *Z. hudsonius*. Earlier trapping at the same locality on 18 March did not reveal the species' presence, however, *Z. hudsonius* hibernates from six to seven months from late September or October to April (Bee et al., 1981; Jones et al., 1985; Muchlinski, 1988). Other small mammals which were collected from the area (from greatest to least abundant) included *Peromyscus leucopus*, *Neotoma floridana*, *Sigmodon hispidus*, *P. maniculatus,* and *Blarina hylophaga*. In addition *Sylvilagus floridanus*, *Microtus pinetorum*, and the distinctive signs of *Scalopus aquaticus* were observed.

One of the specimens (TTU 62982) collected from Craig County was lactating and carried five embryos (2R x 3L), with crown rump measurements of 17 mm; the other (TTU 62983) was lactating and had three visible placental scars. Each specimen's diploid karyotype ($2N = 72$) was consistent with the reported karyotype for the species (Whitaker, 1972). The two specimens were assigned to the subspecies *Z. h. pallidus* based on geographic distribution (Hall, 1981). Measurements in mm for each specimen (TTU 62982, 62983, respectively) are as follows: total length, 230, 203; tail length, 121, 118; hind foot length, 26, 26; ear length, 12, 12; weight in grams, 19.5, 16.0. Study skins and skeletons are deposited in the mammal collection at The Museum of Texas Tech University. Embryos, tissues, and cells (OK 2001, 2002) are housed in the frozen tissue collection of Oklahoma State University.

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DIFFERENTIAL RATES OF DEVELOPMENT BETWEEN TWO LITTERS OF THE FOX SQUIRREL, *SCIURUS NIGER*

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Details for many aspects of the growth and development of the fox squirrel (*Sciurus niger*) are sketchy and anecdotal, which is surprising for such a common, economically important and widely distributed mammal. Accounts on the subject (Asdell, 1946; Davis, 1974; Jones et al., 1983; Lowery, 1974; Moore, 1957, Schmidly, 1983) are rather consistent, inferring a uniform rate of growth and development for the species. A representative synopsis of these works suggests that two litters per year are usually produced, that newborn fox squirrels are naked, blind, and weigh about 14 grams, grow slowly, and that eyes are opened after 32-35 days. The only suggestion of differential rates of development was the statement by Moore (1957:45) that a young fox squirrel taken at an early age "did not grow so well under the artificial conditions imposed".

Two litters of fox squirrels were recovered by students from nests which had accidently become dislodged by storms during the early fall seasons of 1986 and 1992 on the campus of Midwestern State University, Wichita Falls, Texas. Sibling littermates were practically indistinguishable from one another in size and stages of development. However, while members of the two litters were comparable in size, each litter represented markedly different stages of development.

The first litter, from 13 August 1986, comprised two healthy females, which were both prepared as study skins with skulls (MWSU nos. 13594, 13595). Respective standard measurements (in millimeters) were: total length, 237, 238; tail length, 98, 97; hind foot length, 42, 42; and height of ear pinna, 16, 15. The eyes were still closed, and the emergent dorsal pelage was quite short, although venters were nearly naked. Skulls were not well-ossified, and the frontals and parietals separated during the cleaning process. Respective selected cranial measurements (in millimeters) were: greatest length, 41.3, 41.0; zygomatic breadth, 23.5, 23.6; least interorbital breadth, 12.4, 12.5; and length of auditory bulla, 9.2, 9.4. The upper P4 crowns had fully formed, but had not yet emerged. Molars deep in their alveoli were still in the process of forming.

The second litter, from 1 September 1992, comprised three individuals. One died in the fall and was discarded by the discoverer. Of the two specimens which survived, the female was kept by the student as a pet, and the male (MWSU 18783) was prepared as a study skin with skull. In body size (same measurements as above: 225, 98, 40, 14) and cranial measurements (same measurements as above: 41.3, 23.2, 12.2, 9.7), the male closely approximated the two specimens from the other litter, and was, in fact, slightly smaller by most measures. However, development was comparatively advanced in most respects. The pelage was complete and plush, and the eyes were opened (Fig. 1). The skull was more completely ossified, to include the tightly articulated skull roof complex, although dental development was comparable to the more altricial specimens of the first litter.

FIGURE 1. Representatives from two fall litters of the fox squirrel (*Sciurus niger*). Note the precocial state of specimen below (MWSU 18783), with eyes opened and plush pelage, when compared with the other (MWSU 13594).

The differential patterns of development cannot be easily explained at this time. Geographic or seasonal variation would not seem to be factors, and to attribute these observations to any proximate (e.g. prevailing climatic conditions, nutritional status or age of mother) or genetic variables would be preliminary, pending a series of controlled studies. Given the lack of specific and detailed information on the early growth and development of *Sciurus niger*, it is also impossible to determine which of the two litters would best typify the species, unless the observations reported herein represent a normal range of variation. It is clear that accounts relating to early life stages in the fox squirrel (and also probably for many other species) are oversimplified, and published characterizations of growth and development which are based on few examples must be viewed with caution.

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DISSEMINATED MYCOTIC DERMATITIS IN A WILD-CAUGHT TIMBER RATTLESNAKE, *CROTALUS HORRIDUS* (SERPENTES: VIPERIDAE), FROM ARKANSAS

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Mycotic infections in the skin of reptiles are well documented (Jacobson, 1980; Autstwick and Keymer, 1981; Migaki et al., 1984; Frye, 1991). However, these reports primarily concern captive animals and there is little information available on the occurrence of fungal infections in wild reptiles. The purpose of this note is to describe a case of mycotic dermatitis in a wild-caught timber rattlesnake, *Crotalus horridus* Linnaeus.

The infected *C. horridus* [adult female, 1,230 millimeters (mm) snout-vent length (SVL), Arkansas State University Museum of Zoology (ASUMZ) 18621] was one of three collected on 17 October 1992 at Crater of Diamonds State Park, 3.2 kilometers SE Murfreesboro off State Highway 301, Pike County, Arkansas.

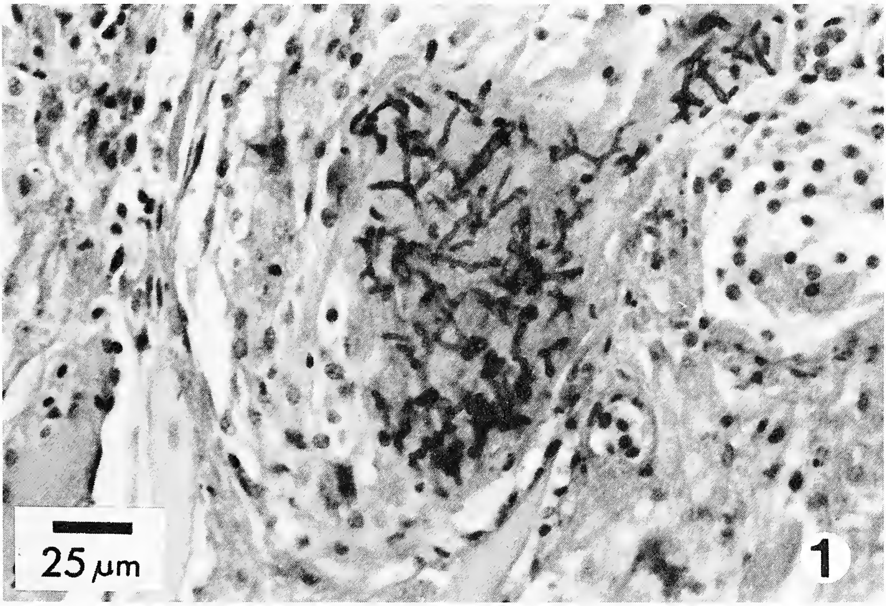

Figure 1. Fungal hyphae in dermal granuloma of timber rattlesnake, *Crotalus horridus* from Arkansas. PAS.

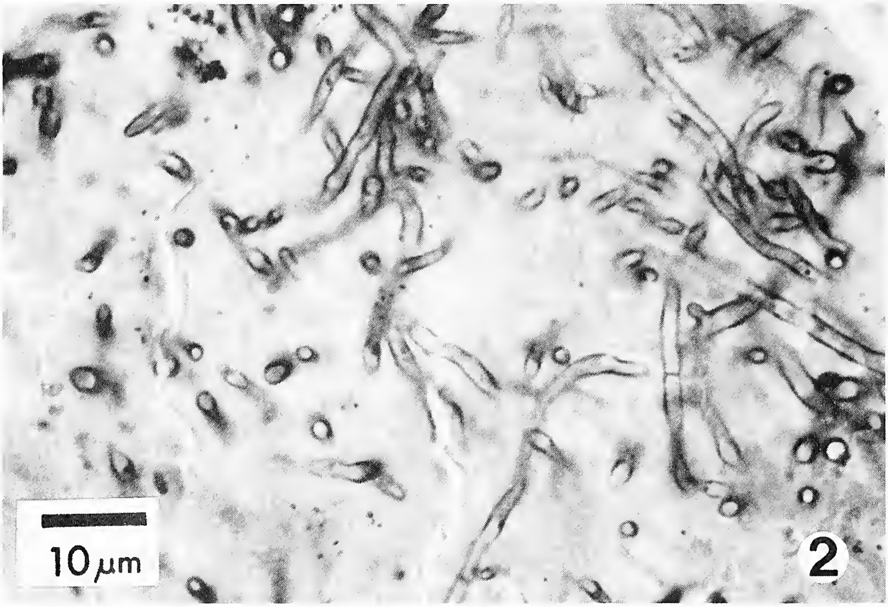

FIGURE 2. Oil immersion of hyphae showing rather uniform morphology with septation and irregular branching. PAS.

The snake was noticeably emaciated and lethargic and did not rattle when disturbed. Some fecal material was present in the rectum, but the stomach and intestines were empty. The dorsal and ventral skin surfaces from the snout to the vent (including some of the tail) were covered by innumerable raised nodules, the largest of which was 15 x 20 mm. The other two *C. horridus* (adult female 1,158 mm SVL, ASUMZ 18616, juvenile female 544 mm SVL, uncatalogued) appeared healthy, rattled, and attempted to strike, and lacked the skin nodules that characterized the infected snake. The snake was returned to the laboratory within 48 hours and killed with an overdose of sodium pentobarbital. Selected fixed tissues were embedded in paraffin, sectioned at 5 micrometers and stained with hematoxylin and eosin, Price's Giemsa or PAS.

The gross lesions appeared as partially ulcerated nodules raised above the skin surface and fixed to the underlying musculature. Histological examination revealed severe multifocal to confluent necrotizing, granulomatous inflammation involving the epidermis and dermis. The remaining epidermis showed evidence of exocytosis and inflammatory crusts as well as ballooning degeneration of portions of the residual epithelium. The dermal reaction was poorly organized, but had nodular foci of fibrinoid eosinophilic material surrounded by macrophages and some fibroblasts. PAS stain revealed numerous tangles of fungal hyphae, both in the necrotic areas (Fig. 1) as well as on the skin surface and in the serocellular crusts. The hyphae were somewhat irregular with slender forms that had spherical buds at right angles (Fig. 2). The morphology is suggestive of Ascomycetes, but fresh cultures, which, unfortunately were not collected, would be necessary for definitive identification. Based on the severity of the infection and the emaciated condition of the snake, it is doubtful it would have survived overwintering. The factors that made the infected *C. horridus* susceptible to mycotic infections are not known, but lymphoid tissues were not scrutinized.

The significance of our case finding is that it involves a wild-caught reptile rather than one that had been held in captivity. While there is information on prevalence of helminth infections (Goldberg and Bursey, 1990), and their resultant pathology in natural reptile populations (Goldberg and Bursey, 1988, 1989), the prevalence and effects of mycotic infections in natural reptile populations has received little attention and warrants further investigation.

We thank Tom Stolarz, Park Interpreter, Crater of Diamonds State Park, for showing us the collecting locale, John Balch, Nashville News, for photographic assistance in the field, and Patrick Daniel and Richard Smith for help with collecting. We also thank the Arkansas Game and Fish Commission for Scientific Collecting Permits Nos. 775 and 831 to CTM and SET, respectively.

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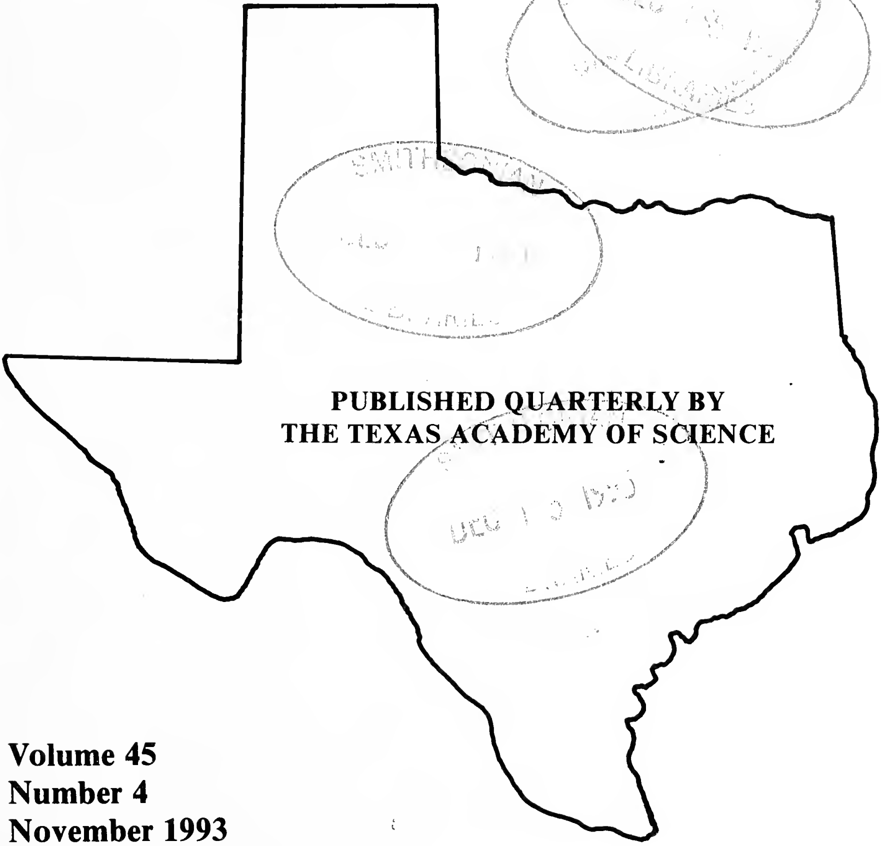

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SURFICIAL MANIFESTATIONS OF PERMIAN SALT BED DISSOLUTION NEAR LOCO HILLS, NEW MEXICO

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Abstract.—Thick and laterally extensive Permian aged evaporite sequences cover much of southeastern New Mexico. The Salado Formation, or main salt, consists of thick halite intervals interbedded with anhydrite, polyhalite, and siltstone. The overlying Rustler Formation consists of approximately 50 percent halite with anhydrite, dolomite and clastics comprising the remainder of the formation. The formation of sinks, depressions and karst topography in southeastern New Mexico is attributed either to the dissolution of the Salado followed by differential collapse of the overlying Rustler or by differential dissolution of the Rustler followed by collapse of the overlying Dewey Lake Redbeds. Subsurface mapping of the Salado and Rustler formations in the Cedar Lake Draw area near Loco Hills, New Mexico indicates extensive dissolution of halite in the Salado and Rustler formations has occurred. However, it is differential dissolution of the Rustler Formation and subsequent collapse of the overlying Dewey Lake Redbeds which created Cedar Lake Draw. *Key words*: dissolution; karst; collapse features; sinkholes; New Mexico.

Cedar Lake lies on the Mescalero Plain of the Pecos section of the Great Plains Physiographic Province (Fig. 1). The Mescalero Plain extends from Fort Sumner, New Mexico to Loving County, Texas, sloping westward at about 5.7 meters per kilometer from the base of the Llano Estacado (Mescalero Ridge) to the Pecos River (Fenneman, 1931). Topographically the Mescalero Plain is flat and covered with areas of coppice dunes and thin aeolian sheets. Sporadic depressional areas (San Simon Swale, Clayton Basin, Williams Sink, Laguna Plata), often enclosing large alkaline playas, exist throughout the area.

Cedar Lake, a relatively small playa in Cedar Lake Draw, is located about 48 kilometers north of Carlsbad, New Mexico and approximately 5.6 kilometers east of Loco Hills, New Mexico. Cedar Lake Draw, which is about 4.8 kilometers long and up to 1.6 kilometers wide, trends northeast to southwest across U.S. Highway 82. Relief surrounding the Cedar Lake depression is approximately 24 meters in an area where normal topographic relief, due mainly to dune sands, ranges from three to six meters.

Dissolution of Permian salt beds has apparently occurred since late Permain time in southeastern New Mexico (Adams, 1944). In fact, Adams (1944) identified three major dissolution episodes which occurred during the Permian, Triassic and Tertiary periods. Adams (1944), Hendrickson and Jones (1953), Maley and Huffington (1963), Vine (1963) and Gard (1968) described dissolution processes along the Salado-Rustler contact. Vine (1963) and Gard (1968) discussed dissolution within the more soluble beds of the Rustler. Hendrickson

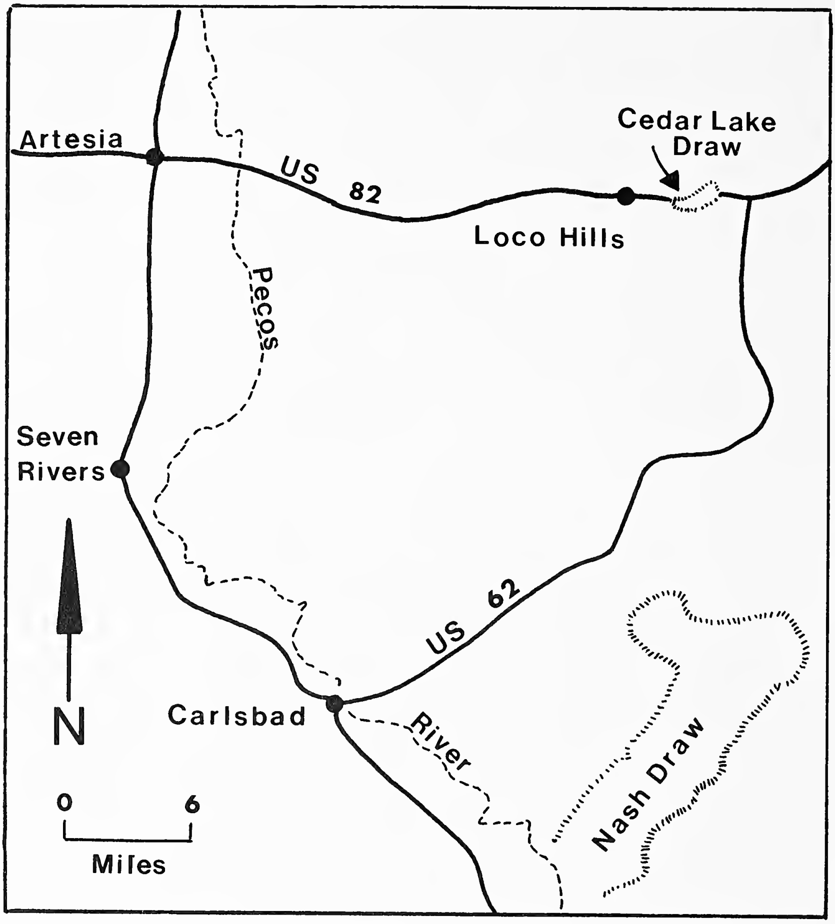

FIGURE 1. Index map showing a part of southeastern New Mexico.

and Jones (1953) and Maley and Huffington (1963) noted the relationship between thinning in the Salado Formation and development of sinks in southeastern New Mexico. Gard (1968) concurred, adding that solution of the Salado Formation, followed by lowering of the land surface and differential collapse of the Rustler Formation, created sinks and karst topography. However, Vine (1963) thought solution in the Salado Formation resulted in a relative uniform lowering of the land surface with differential solution in the Rustler causing the formation of sinks and karst topography.

METHODS

Cedar Lake basin was chosen for study because the overall topography of the basin is suggestive of Permian salt bed dissolution. Secondly, numerous oil well tests in the area insured sufficient subsurface control would be available to allow mapping of the Permian evaporite sequences.

Structural and isopach maps of the various evaporite sequences, along with appropriate cross sections, were constructed using 50 geophysical logs. Cross sections were used to correlate the Permian formations and to measure amounts of dissolution. Well log correlations of the Rustler and Salado formations are based upon their geophysical profiles as identified in geophysical well logs from the Waste Isolation Pilot Project (Chaturvedi and Channell, 1985).

Results

Stratigraphy of Cedar Lake Draw

The Salado Formation, or main salt, consists of thick halite intervals with interbedded anhydrite, siltstone and polyhalite. The upper Salado is characterized by unconsolidated, reddish-gray to brown silt and clay with interbedded brecciated gray or red gypsum, which is thought to represent the insoluble residues of dissolved halite (Vine, 1963). This leached zone is significant because it often forms locally important brine aquifers (Hendrickson and Jones, 1953; Vine, 1963). The thickness of the Salado Formation is variable and the upper contact is irregular due to dissolution. The thickness ranges from 215 to 276 meters in the Cedar Lake area.

The late Permian Rustler Formation conformably overlies the Salado Formation. Vine (1963) divided the Rustler into five members; the lower unnamed member and the overlying Culebra, Tamarisk, Magenta and Forty-niner members. Borehole data from the Waste Isolation Pilot Project (WIPP) near Carlsbad, New Mexico indicates the Rustler consists of approximately 50 percent halite where it attains maximum thickness. At WIPP, three thick halite beds were identified in the Rustler: the upper halite, 9.75 meters thick, located above the Magenta member; the middle halite, 32 meters thick, located between the Magenta and Culebra members; and the lower halite, 36.6 meters thick, located below the Culebra member (Chaturvedi and Channell, 1985). The remainder of the Rustler is comprised of anhydrite and dolomite with interbedded siltstone. Chaturvedi and Channell (1985, p. 26) characterized an intact section of the Rustler "as mainly a salt formation with anhydrite, dolomite and clastics". The thickness of the Rustler observed at WIPP ranges from approximately 140 meters at maximum to about 80 meters where complete dissolution of halite has occurred. At Cedar Lake the Rustler ranges in thickness from approximately 34 to 87 meters.

The Dewey Lake Redbeds conformably overlie the Rustler. The Dewey Lake Redbeds are pale-reddish brown siltstones, polka-dotted with green reduction spots and irregularly veined with secondary selenite fillings (Vine, 1963).

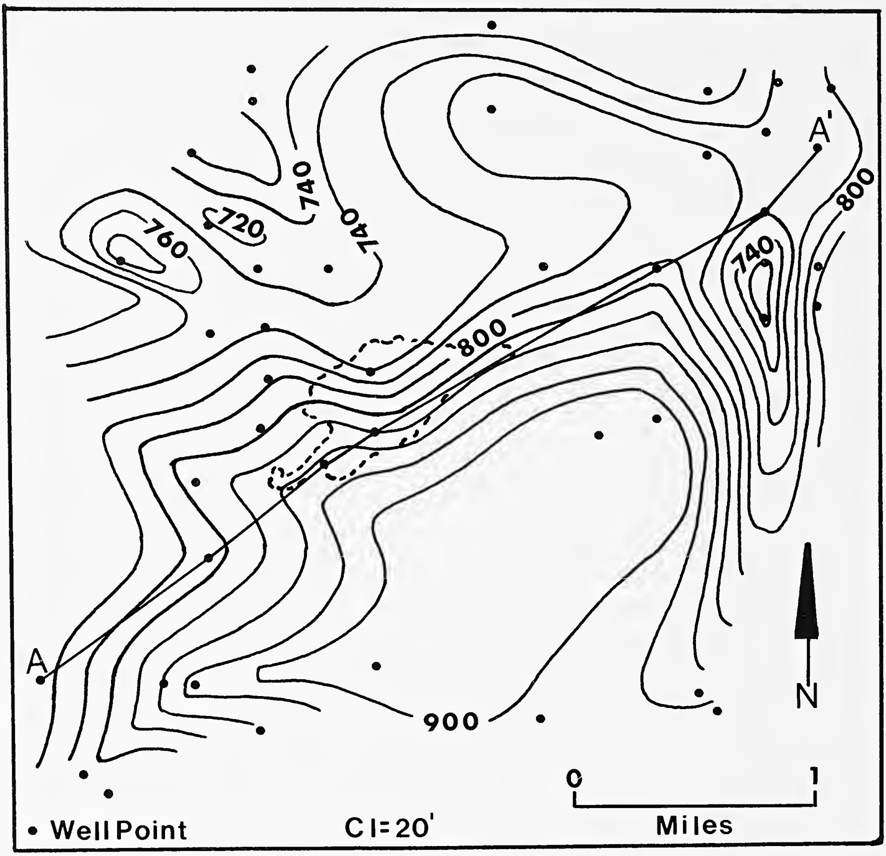

FIGURE 2. Isopach map of Salado Formation. Dashed area represents the location of Cedar Lake Playa.

The Gatuna Formation unconformably overlies the Dewey Lake Redbeds. The Gatuna consists of pale-red to moderate brown fine grained sandstone with locally important gypsum, shale and claystone (Vine, 1963). The Gatuna is typically found as deposits in sinks or as resistant domal karst features (Gard, 1968).

Recent-aged sediments are thought to be derived from the Gatuna Formation or the Pliocene Ogallala Formation which once covered the area. The Recent deposits, which form the pediments, playa deposits and dunes that mantle the area, are typically unconsolidated, moderate-brown, fine to medium grained quartz sands (Vine, 1963).

Dissolution of the Salado Formation

The isopach map of the Salado Formation (Fig. 2) shows the thickness of Salado salt ranges from 285 meters (935 feet) at CL-21 to

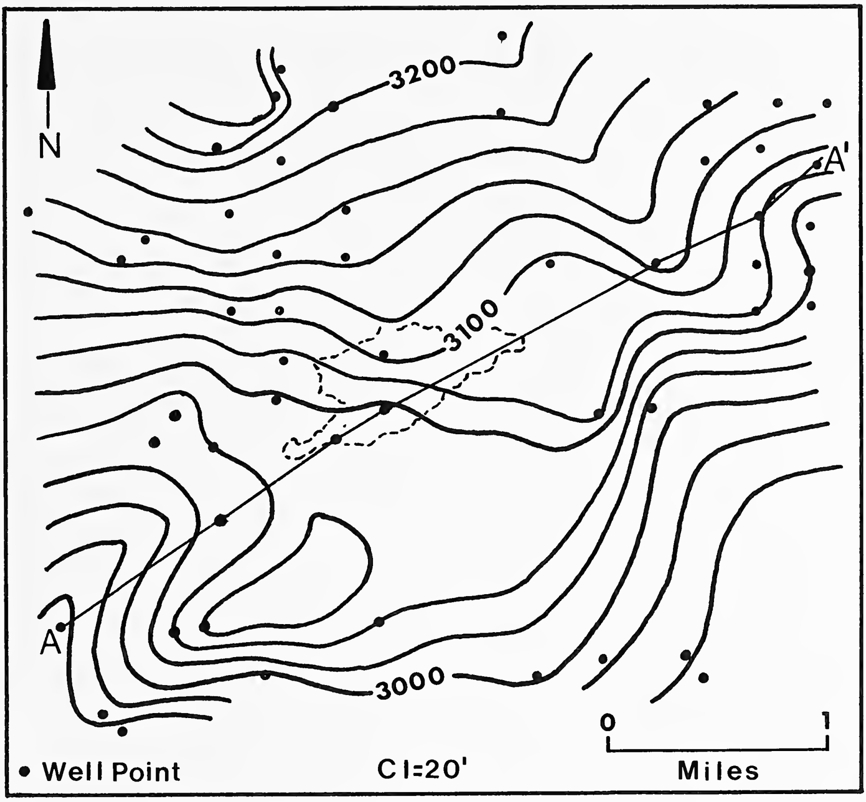

FIGURE 3. Structure map showing elevation, in feet above sea level, of the top of the Salado Formation. Dashed area represents the location of Cedar Lake Playa.

215 meters (705 feet) at CL-32. In general, the formation thickens to the south, with irregular thinning occurring beneath the Cedar Lake depression. The structure map of the Salado Formation (Fig. 3) indicates a generally southerly dip and irregular surface. Although up to 95 meters of relief exists on top of the Salado, no closed depressions or troughs are observed beneath the Cedar Lake area.

A comparison of the structure map on the Salado Formation (Fig. 3) with the topographic map of the Cedar Lake area (Fig. 4) shows no relationship between Salado structure and surface features. This assertion is further substantiated by cross-section A-A' (Fig. 5) which shows no sagging of the overlying Rustler Formation on the Salado Formation beneath Cedar Lake Draw (Howard, 1985).

Dissolution of the Rustler Formation

As shown by the Rustler Isopach Map (Fig. 6) the thickness of the Rustler Formation ranges from 87 meters (285 feet) at CL-34 to 33.5

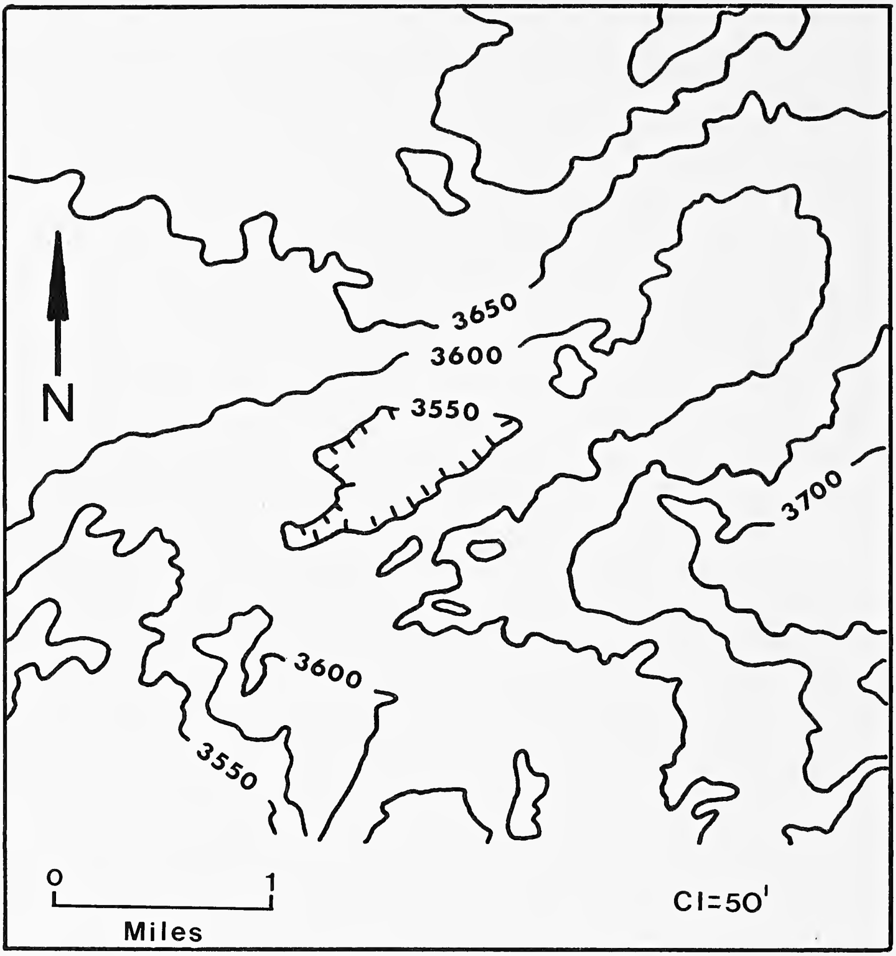

FIGURE 4. Topographic map of Cedar Lake Draw area.

meters (110 feet) at wells CL-10 and CL-30. The principal area of thinning, trending northeast-southwest, is located below Cedar Lake Draw. Although a smaller area of thinning is located to the southwest of the Cedar Lake Playa, it is not manifested at the surface. This is likely due to the fact the size of the collapse feature is dependent upon the size of the subsurface cavity and the thickness of the strata between the cavern and land surface (Gustavson et al., 1981). Thus, if the voids are small the collapse debris will fill the cavity and the void will not be propagated to the surface (Gustavson et al., 1981; Ege, 1984).

The Rustler structure map (Fig. 7) shows that a small enclosed depression, surrounded by a much larger northeast-southwest trending trough, is located beneath Cedar Lake Draw. A comparison of the

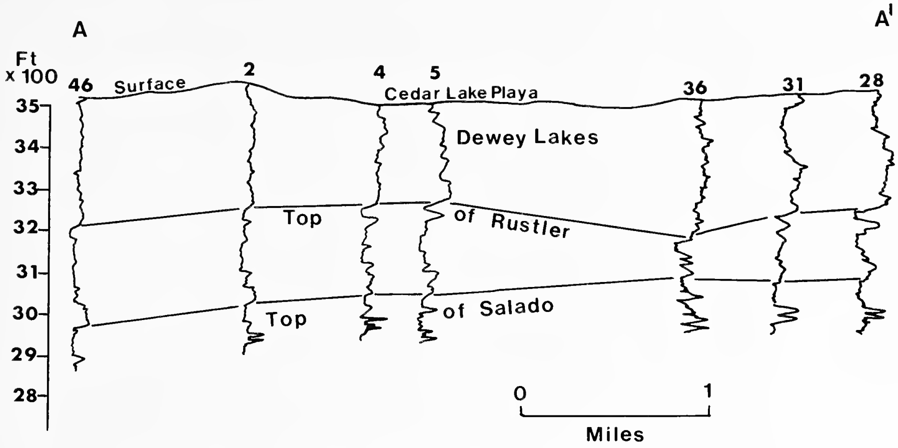

FIGURE 5. Cross section A - A' drawn southwest to northeast along length of Cedar Lake Draw.

Rustler isopach, structure and topographic maps shows a strong relationship between thinning, structure and topography. The Rustler isopach map shows a northeast to southwest trending area of thinning located northeast of Cedar Lake Playa. The Rustler structure map indicates a northeast to southwest trending trough is coincident with thinning. As demonstrated by the topographic map, Cedar Lake Draw is manifested on the surface as a northeast to southwest trending surface depression coincident with Rustler thinning and structure (Howard, 1985). Cross-section A-A' illustrates the basinward thinning of the Rustler Formation along the length of Cedar Lake Draw.

DISCUSSION

Comparison of Salado and Rustler isopach (Figs. 2, 5) and structure maps (Figs. 3, 7) show differing dissolution patterns between the two formations. For example, Figure 5 reveals a dissolution area in the Rustler Formation located below the surficial location of Cedar Lake Draw, but a corresponding dissolution area is not indicated in the underlying Salado Formation. This dissimilarity, coupled with the lack of sagging of the Rustler Formation over the Salado Formation, and the thickening of the Salado Formation beneath the Cedar Lake Draw area indicates there is no correlation between thinning in the Salado Formation and formation of Cedar Lake Draw (Howard, 1985).

As indicated by the geophysical well log response of P-8 from WIPP, the Rustler is approximately 140 meters thick at maximum and consists of approximately 50 percent halite (Chaturvedi and Channell, 1985). The remainder of the formation is comprised of anhydrite,

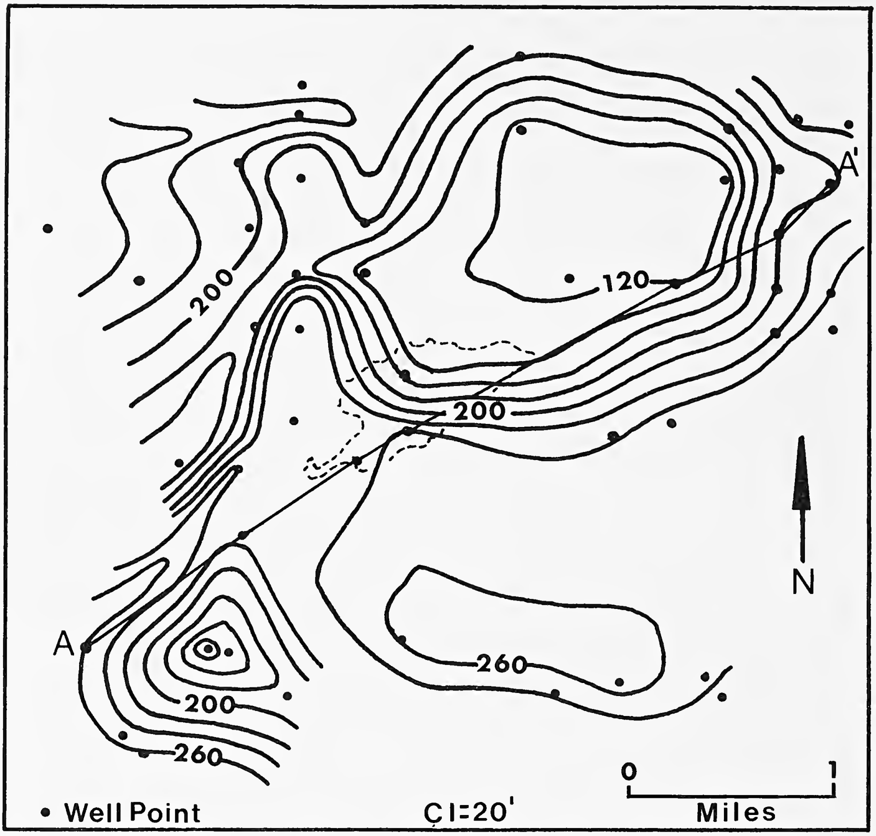

FIGURE 6. Isopach map of Rustler Formation. Dashed area represents the location of Cedar Lake Playa.

dolomite and clastics. Figure 8 is a comparison of the geophysical log from CL-46 and the geophysical logs from wells P-6 and P-18 at WIPP. P-8 represents a section of Rustler showing maximum thickness and P-16 is representative of the Rustler from which the halite is completely dissolved (Chaturvedi and Channell, 1985). CL-46 is typical of the geophysical responses from the Cedar Lake Draw area. The similar formation thickness of the Rustler between CL-46 and WIPP P-16 indicates complete dissolution of halite has also occurred from the Rustler at the CL-46 location and throughout the Cedar Lake Draw area. For example, the total thickness of the Rustler below the Culebra member at P-18; where the Rustler shows maximum thickness, is approximately 49 meters. The same section at CL-46 is approximately 24 meters thick. Thinning is also noted at CL-46 between the Magenta and Culebra members. At P-18 the total thickness

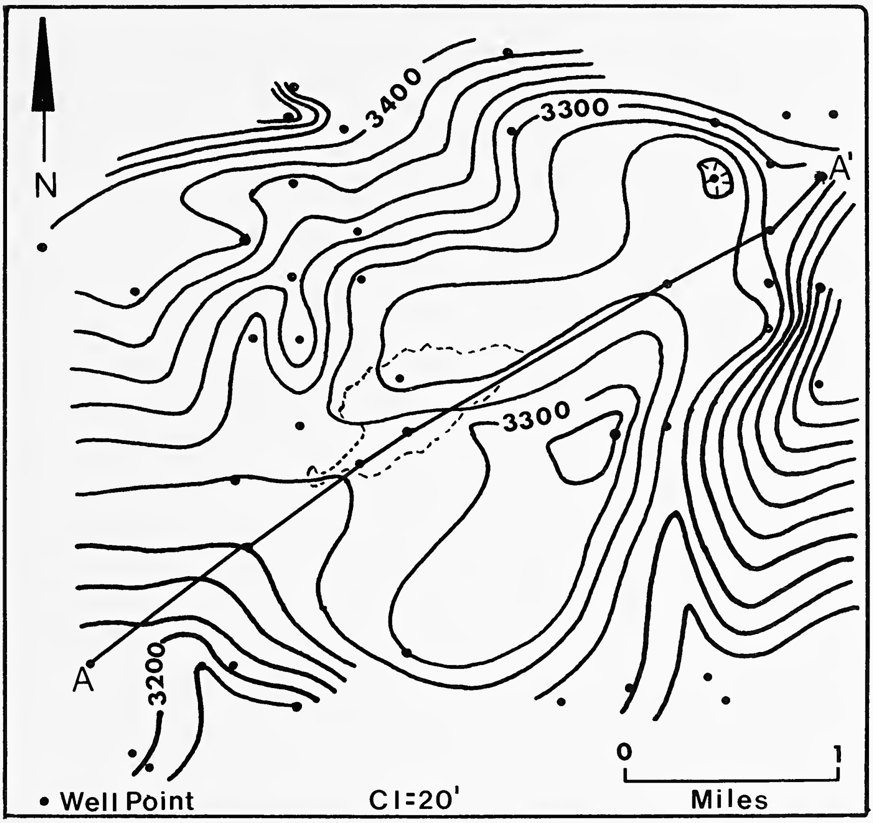

FIGURE 7. Structure map showing elevation, in feet above sea level, of the top of the Rustler Formation. Dashed area represents the location of Cedar Lake Playa.

of this interval is approximately 55 meters and at CL-46 the thickness is about 18 meters.

As shown in Cross Section A-A' (Fig. 5), and as indicated in the geophysical log responses from CL-31 and CL-36, basinward dissolution of the Rustler has occurred, with approximately 75 percent of the Rustler Formation missing at CL-36. Because approximately 50 percent of the Rustler at Cedar Lake Draw is missing from the dissolution of halite, the additional 25 percent (35 meters) of missing Rustler at CL-36 is because of dissolution of anhydrite and dolomite. Thus, it is differential dissolution within the Rustler Formation and subsequent collapse of the overlying Dewey Lake Redbeds, which has resulted in the formation of Cedar Lake Draw.

ACKNOWLEDGMENTS

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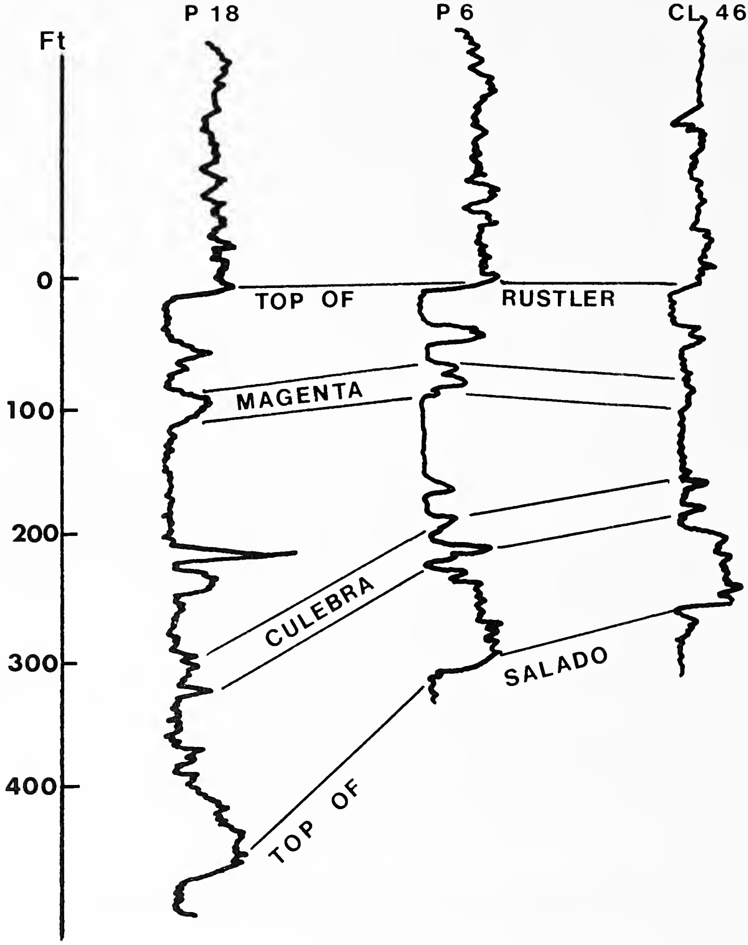

Figure 8. Comparison of geophysical responses from WIPP borings P-6 and P-18 (from Chaturvedi and Channell, 1985) and Cedar Lake Draw well CL-46.

thank Santa Fe Energy, Midland, Texas; Diamond Shamrock, Amarillo, Texas; and the New Mexico Oil Conservation Division, Artesia, New Mexico for granting me access to the well log data used in this study. A grant from Sigma Xi, The Scientific Research Society, provided much appreciated support for portions of the project. I thank Joseph C. Cepeda for his review and helpful commentary. Special thanks are extended to Dr. C. C. Reeves, Jr. for his direction, insight and commentary.

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SHOREBLINE EROSION AT MAD ISLAND MARSH PRESERVE, MATAGORDA COUNTY, TEXAS

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Abstract.—Mad Island Marsh Preserve, located on the shores of Matagorda Bay, Texas, has experienced considerable shoreline erosion along its boundary with the Gulf Intracoastal Waterway (GIWW), since construction of the GIWW in the early 1940's. This study documents long-term shoreline change, based on the analysis of sequential aerial photographs dating from 1930, 1943, 1958, 1978 and 1991. The results indicate that the GIWW widened to about three times its original width over the 48 years studied, and that this widening has been accompanied by rates of shoreline retreat of up to 3.1 meters per year at Mad Island Marsh Preserve. In addition to the loss of Preserve land, the erosion also threatens a number of wetland habitats on the Preserve. Erosion diminished an area of *Spartina* marsh alongside the GIWW from 0.154 km^2 in 1958 to 0.022 km^2 in 1991. Erosive shortening of Mad Island Bayou - a tidal inlet connecting Mad Island Lake to Matagorda Bay - may cause increased salinity within the lake and the consequent loss of freshwater environments. *Key words*: shoreline erosion; wetlands; Gulf Intracoastal Waterway; Matagorda Bay.

Mad Island Marsh Preserve is a 1,274 hectare tract containing the east arm of Mad Island Lake, its associated freshwater and brackish marshes, and surrounding upland prairie and shrubland habitats (Fig. 1). The marshes of Mad Island Lake were once the premier freshwater system on the Texas Mid-Coast, providing a habitat for many species of migratory waterfowl and abundant resident wildlife. Over the past fifty years, saltwater intrusion, reduced freshwater inflows, overgrazing and watershed development have all contributed to the reduction of ecological diversity and abundance. Efforts are now underway, led by the Nature Conservancy of Texas, to restore and enhance both wetland and upland habitats within the Preserve (J. Bergan, Pers. Comm.).

The GIWW, constructed in 1941, cuts through the southern portion of the Preserve and is flanked to the south by man-made islands of dredge spoils (Fig. 1). Considerable wave erosion has occurred, and continues to occur, along the Preserve shorelines bordering the GIWW. Shorelines along the GIWW are eroded by waves generated by barge traffic; a section of the Preserve shoreline is also exposed to waves from the south in Matagorda Bay which pass through the cut in the islands of dredge spoil (Fig. 1).

In addition to causing the loss of Preserve lands, the erosion may threaten the freshwater marsh habitats bordering Mad Island Lake, since erosive shortening of Mad Island Bayou - a tidal inlet connecting the lake to Matagorda Bay - is likely to increase salt water intrusion into the lake.

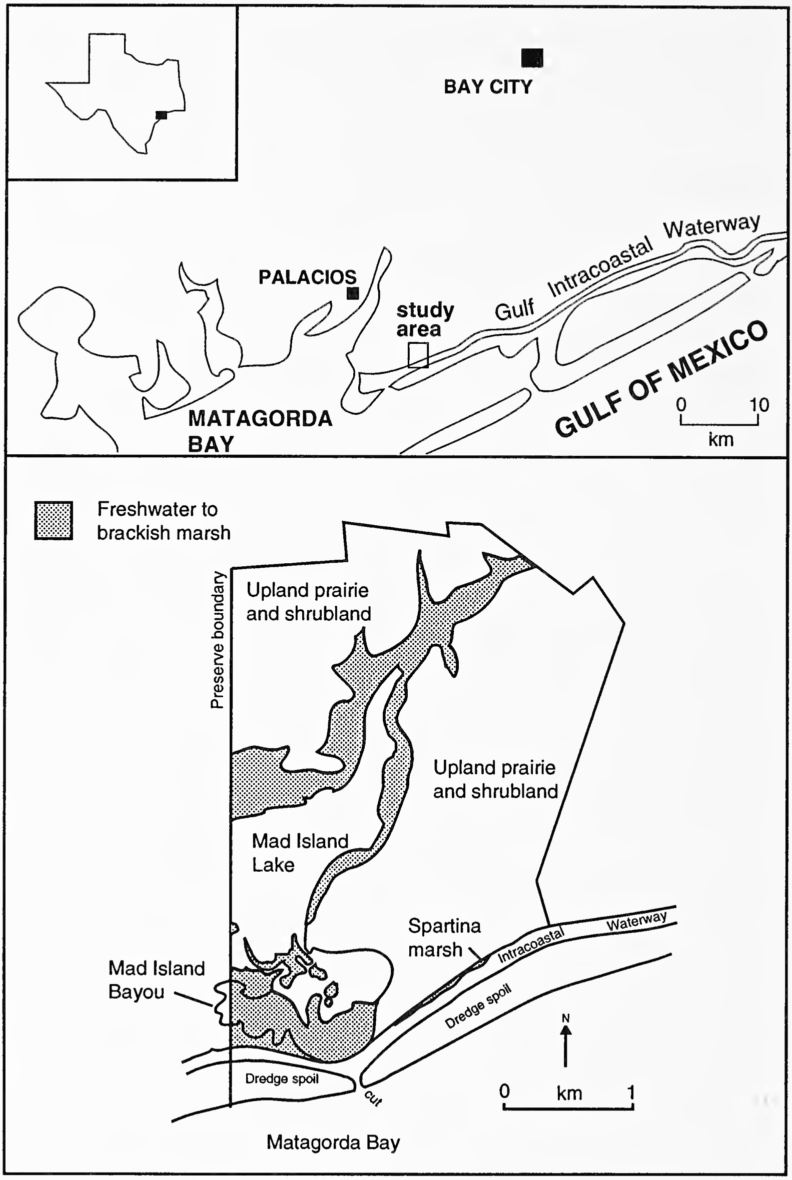

FIGURE 1. Location map: Mad Island Marsh Preserve, Texas.

As a precursor to the implementation of erosion mitigation measures by the Nature Conservancy of Texas, this study was conducted to provide information on the locations and rates of shoreline erosion along the shores of the Preserve over the last fifty years. This information will be used in the targeting of erosion mitigation measures and in the assessment of erosion mitigation effectiveness.

METHODS

Long-term rates of shoreline migration were established by the analysis of sequential aerial photographs. Similar techniques have been used successfully on the Texas coast (Paine and Morton, 1989; McGowen and Brewton, 1975). And, Williams (1991) used the technique to document delta growth in a Texas reservoir. The Nature Conservancy of Texas provided photographs taken in 1930, 1978, and 1991. The Texas Natural Resources Information System (TNRIS) provided photographs from 1943 and 1958.

Field reconnaissance of the study area revealed that much of the shoreline of the Preserve is marked by an erosional scarp. Vegetation extends to the edge of the scarp along most of the shoreline, creating an abrupt boundary which could be readily identified on the aerial photographs. The base of the scarp was either below local water level at the time of observation, or at the back of a narrow shell beach adjacent to the GIWW. Approximately one-third of the Preserve shoreline along the north shore of the GIWW is bordered by *Spartina alterniflora* (smooth cordgrass) marsh which extends into the GIWW (Fig. 1). The marsh edge also consists of an abrupt erosional scarp in many places, making it readily identifiable on the aerial photographs (Fig. 2a, b).

The edge of the erosional scarp was selected to represent the "shoreline" in the study area. The selection of this boundary has several advantages: it is easily identified on the aerial photographs; the position of this boundary does not change with changing tide levels; the scarp itself is the product of erosion, making it well-suited for mapping the progress of erosion along the Preserve shoreline. Other studies have used the vegetation line and beach/water interface for mapping shoreline change; however, vegetation line migration does not always parallel shoreline migration, and the beach/water interface changes position with tides and can be difficult to locate on aerial photographs because the beach often has a similar appearance to the shallow water surf zone (Paine and Morton, 1989).

The shoreline from each photograph was traced onto acetate, along with a number of registration points, such as fence lines and road intersections, which were used to accurately superimpose maps from each year of photography. Beginning with the 1930 photograph, the acetate tracings were transferred onto a single base map using a Goddkin Zoom Transfer Scope. The transfer scope was used to adjust the scale of each image to a uniform scale of 1:8000. To reduce errors due to further processing, all measurements of shoreline migration were made at this stage from the base map. Migration of the shoreline at selected points was measured using a micrometer and converted to meters. Areas were measured on the base map using a Keuffel and Esser Polar Planimeter and were converted into km^2. The completed base map, containing the shoreline locations from each year of photography, was then scanned into a TIFF file format using a Hewlett-Packard ScanJet scanner. The TIFF file was loaded onto a MacIntosh IIx computer for editing and final map production using the Adobe Illustrator 3.0 CAD program.

RESULTS

Maps of shoreline locations in 1943, 1958, 1978 and 1991 are shown in Figure 3. A composite map showing shoreline locations for each year of photography is shown in Figure 4. A comparison of the original shoreline position in 1930 and the shoreline in 1943, shortly after construction of the GIWW, shows that the GIWW cut through the coast in the vicinity of the mouth of Mad Island Bayou; farther east, the GIWW was located about 100 meters offshore from the

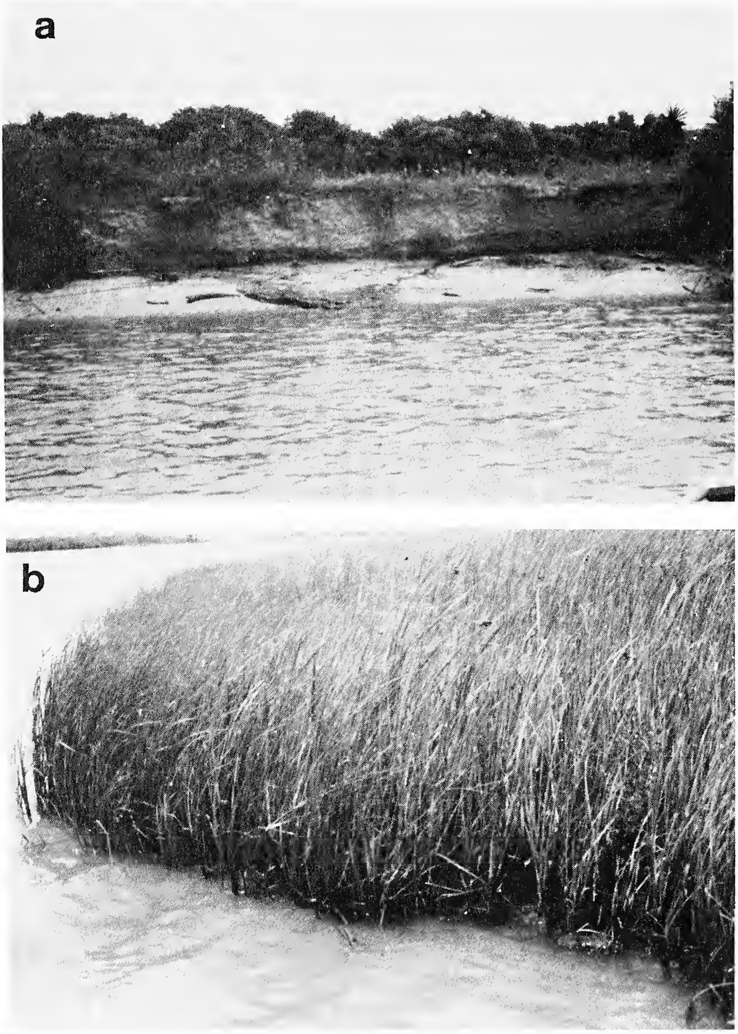

FIGURE 2. Shoreline erosion at Mad Island Marsh Preserve: a. Erosional scarp bordering the Gulf Intracoastal Waterway (scarp is about 1.3 meters high); b. Abrupt edge of the *Spartina* marsh along the northern shore of the Waterway.

original shoreline. The islands of dredge spoil, created during construction of the GIWW, border the GIWW to the south (Fig. 4).

The area of *Spartina* marsh located along the north shore of the GIWW (Fig. 1), appears to have originated as a narrow bank of dredge spoil (Fig. 3). The backwater area located between the original shoreline and this narrow strip of *Spartina* marsh, apparently became infilled by sediments and colonized by marsh plants over subsequent years, such that, by 1958, the area of *Spartina* marsh had grown considerably larger (Fig. 3).

Shoreline migration was measured as the perpendicular distance between successive shorelines (1943-1958, 1958-1978, 1978-1991) at 26 locations selected to cover the entire shoreline of the Preserve. Measurement locations are identified by the letters A through Z on Figure 3 (1991 map). Table 1 contains the total shoreline migration in meters and the mean shoreline migration in meters per year for the periods 1943-1958, 1958-1978, 1978-1991 and 1943-1991.

The width of the GIWW was also measured for each year of photography; but, because the GIWW appears to have widened in a relatively uniform manner, only four measurement locations were deemed necessary to document the changing width. Table 2 contains the width, in meters, measured perpendicular to the adjacent shoreline for the locations numbered 1-4 in Figure 3. The ratio of the 1943 width to the 1991 width, as a percentage, is also included for each location, as well as the mean ratio as a percentage.

The shoreline area eroded or accreted between 1943 and 1991 was calculated for five sections of Preserve shoreline: the shoreline adjacent to Mad Island Bayou, from the western Preserve boundary to location "E" in Figure 3 (indicated by "I" in Fig. 3); the north shore of the western dredge spoil island ("II" in Fig. 3); the south shore of the western dredge spoil island ("III" in Fig. 3); the north shore of the eastern dredge spoil island ("IV" in Fig. 3); and the south shore of the eastern dredge spoil island ("V" in Fig. 3). In addition, the area of *Spartina* marsh eroded from the north shore of the GIWW between 1958 (the greatest extent of the marsh) and 1991 (the least extent of the marsh), was also calculated ("VI" in Fig. 3) (Table 3).

DISCUSSION

The results of the analysis of the aerial photographs show that both erosion and accretion occurred along the shores of the Preserve (Table 1). However, shoreline accretion occurred only on the southern shores of the islands of dredge spoil. This growth was most likely due to the addition of new materials dredged from the GIWW between 1943 and 1991. These spoil island shorelines advanced between 38-254 meters during this period (Fig. 4), gaining an additional 0.257 km^2 and 0.224 km^2 (Table 3; shoreline III and V), respectively.

The shores of the Preserve bordering the GIWW experienced only erosion between 1943 and 1991 (Fig. 4; Table 1). During this 48-year period, the GIWW widened from its original surface width of 46-65 meters in 1943, to 143-181 meters in 1991; a mean change of 282%, or about a three-fold increase in width (Table 2).

The most severe erosion occurred along the northern shorelines of the dredge spoil islands; at location "R" (Fig. 3), for example, the shoreline eroded at up to 3.07 meters per year, and the total retreat

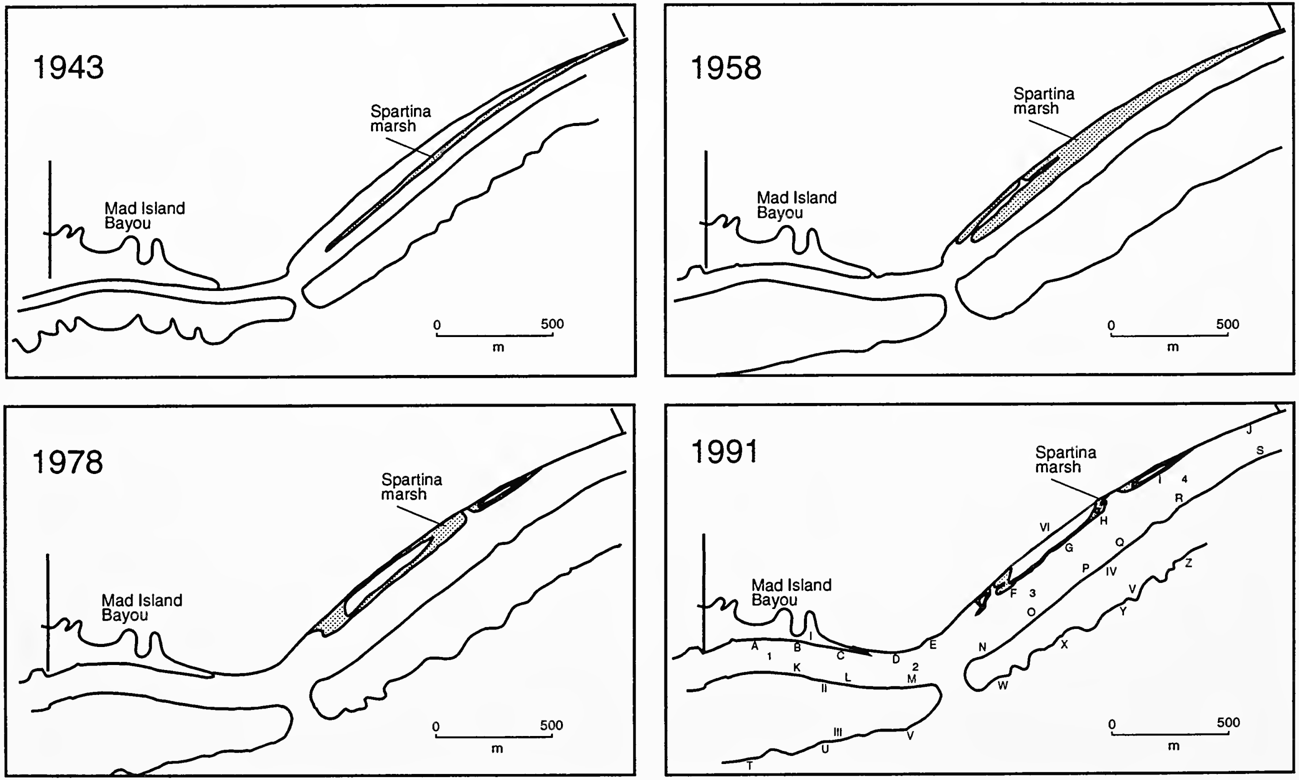

FIGURE 3. Sequential shoreline positions based on 1943, 1958, 1978 and 1991 aerial photographs (see text for explanation of measurement locations shown on 1991 map).

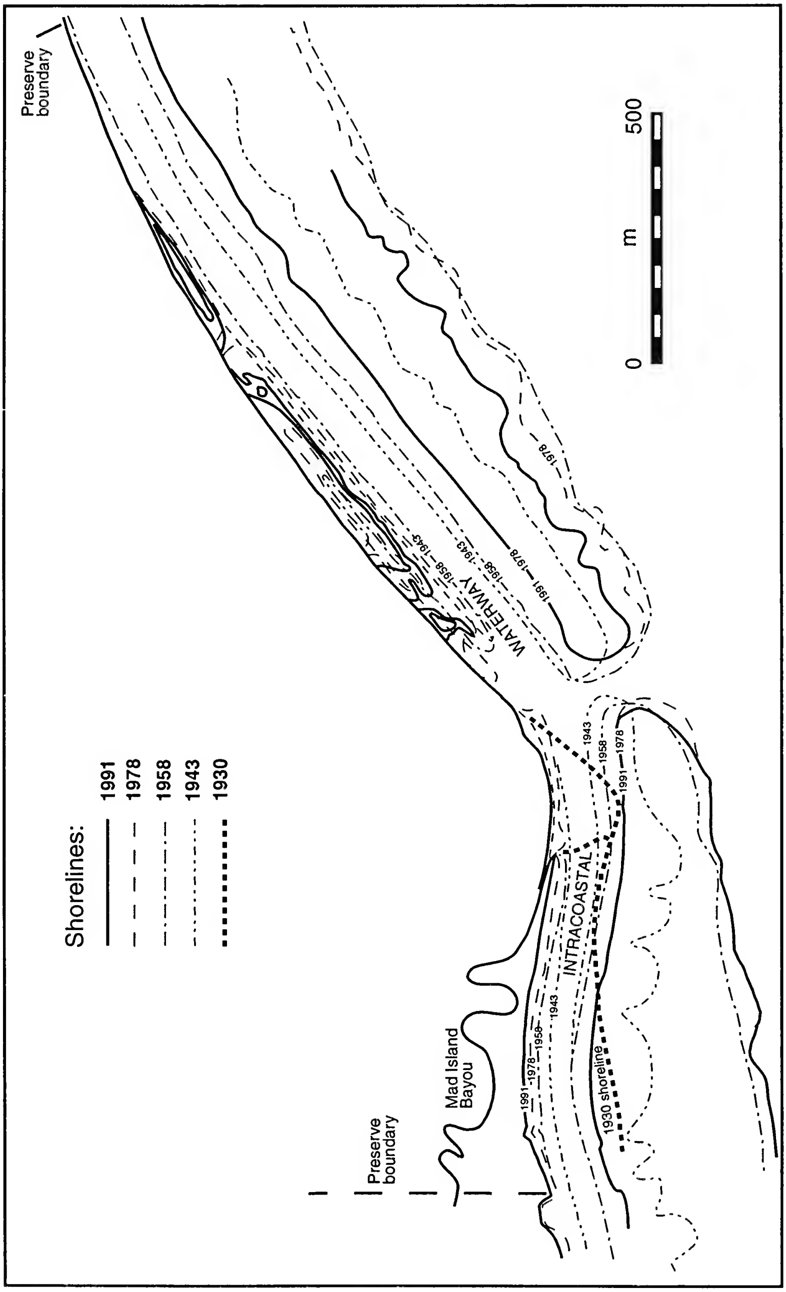

FIGURE 4. Mad Island Marsh Preserve; shoreline migration, 1930 - 1991.

Table 1. Mad Island Marsh Preserve, shoreline migration: 1943-1991. All measurements perpendicular to shorelines. Minus sign indicates shoreline accretion. Site locations A-Z shown on Figure 3.

Site	1943-1958		1958-1978		1978-1991		1943-1991	
	m	m/yr	m	m/yr	m	m/yr	m	m/yr
A	26	1.73	16	0.80	15	1.15	57	1.19
B	27	1.80	13	0.65	16	1.23	56	1.17
C	8	0.53	19	0.95	16	1.23	43	0.90
D	11	0.73	13	0.65	5	0.38	29	0.61
E	0	0.00	27	1.35	24	1.85	51	1.06
F	0	0.00	16	0.80	19	1.46	35	0.73
G	0	0.00	11	0.55	22	1.69	33	0.69
H	0	0.00	9	0.45	22	1.69	31	0.65
I	0	0.00	13	0.65	8	0.62	21	0.44
J	0	0.00	11	0.55	0	0.00	11	0.23
K	15	1.00	27	1.35	0	0.00	42	0.88
L	16	1.06	32	1.60	0	0.00	48	1.00
M	32	2.13	38	1.90	0	0.00	70	1.46
N	13	0.87	48	2.40	0	0.00	61	1.27
O	22	1.47	51	2.55	0	0.00	73	1.52
P	30	2.00	46	2.30	0	0.00	76	1.58
Q	30	2.00	57	2.85	0	0.00	87	1.81
R	46	3.07	43	2.15	0	0.00	89	1.85
S	42	2.80	32	1.60	0	0.00	74	1.54
T	-227	-15.13	-27	-1.35	0	0.00	-254	-5.29
U	-140	-9.33	-41	-2.05	0	0.00	-181	-3.77
V	-108	-7.20	-27	-1.35	0	0.00	-135	-2.81
W	-119	-7.93	35	1.75	46	3.54	-38	-0.79
X	-135	-9.00	32	1.60	65	5.00	-38	-0.79
Y	-191	-12.80	13	0.65	81	6.23	-97	-2.02
Z	-156	-10.40	-11	-0.55	78	6.00	-89	-1.85

over the 48-year period was 89 meters (Table 1). This erosion resulted in the loss of 0.077 km^2 from the western dredge spoil island and 0.202 km^2 from the eastern dredge spoil island (Table 3; shoreline II and IV, respectively). These high rates of erosion apparently ceased during the 13-year period 1978-1991 (Table 1); a comparison of the 1978 and 1991 photographs showed no discernible retreat of these shorelines (Fig. 4). The reasons for this apparent stability are uncertain. It may be that erosion has slowed due to the formation of relatively high (3-5 meter) scarps along these shorelines, such that maintenance of former erosion rates would involve the removal of increasingly larger volumes of material. It was also noted during fieldwork that the GIWW is relatively shallow over a considerable distance offshore from these shorelines; this may be due to the formation of a wave-cut platform, which would tend to dissipate wave energy and reduce its impact on the shore.

Along the shoreline in the vicinity of Mad Island Bayou, erosion

Table 2. Width of Gulf Intracoastal Waterway: 1943-1991. All measurements perpendicular to shorelines. Site locations 1-4 shown on Figure 3.

	Width of Waterway (m)				Ratio:
Site	1943	1958	1978	1991	1991/1943
1	46	70	130	143	311%
2	65	102	154	162	249%
3	65	89	156	181	278%
4	59	108	162	170	288%
					Mean = 282%

averaged between 0.61 and 1.19 meters per year from 1943 to 1991, and showed no indication of slowing or stopping (Fig. 4; Table 1). Total retreat along this section of shoreline has been from 29 to 57 meters, accompanied by the loss of 0.074 km^2 of land (Table 1, sites A-E; Table 3, shoreline I).

Erosion of this part of the shoreline threatens wetland habitats surrounding Mad Island Lake by shortening Mad Island Bayou and thereby increasing the likelihood of saltwater intrusion into the lake. The mouth of the bayou retreated approximately 50 meters between 1943 and 1991 (Fig. 4).

More significantly, erosion threatens to break through the narrow peninsula of land created by retreat of the shoreline (Fig. 4). This would cause abrupt shortening of the bayou, rather than simply a gradual retreat; for example, the peninsula is only 4.7 meters wide in the vicinity of location "C" (Fig. 3 - at the present rate of erosion, 1.23 meters per year - Table 1), this point could be breached within three to four years, abruptly shortening the bayou a further 50 meters. Potential for even greater shortening exists in the vicinity of location "B" (Fig. 3); here, a bend in the Bayou is within about 30 meters of the shore - at the present erosion rate (1.23 meters per year), this point could be breached within about 24 years, shortening the bayou by some 500 meters.

Table 3. Area of shoreline erosion and accretion. Shoreline locations I-VI shown on Figure 3. Minus sign indicates shoreline eroded.

Shoreline	Period	Area eroded or accreted (km^2)
I	1943-1991	- 0.074
II	1943-1991	- 0.077
III	1943-1991	+ 0.257
IV	1943-1991	- 0.202
V	1943-1991	+ 0.224
VI	1958-1991	- 0.132

The area of *Spartina* marsh along the northern border of the GIWW underwent considerable erosion between 1958 and 1991 - erosion which also appears to be continuing at present (Fig. 4). The edge of the marsh retreated at average rates of between 0.44 and 0.73 meters per year during this period. This erosion was accompanied by a reduction in the marsh area from 0.154 km^2 in 1958 to 0.022 km^2 in 1991 - a loss of 85.5% of the 1958 marsh area (Table 3, shoreline VI).

The original 1930 shoreline lies landward of the area of *Spartina* marsh (Fig. 4). This part of the Preserve has remained relatively unchanged over the last 48 years, apparently because the *Spartina* marsh acts as a buffer between it and waves generated in the GIWW. However, with continuing erosion of the marsh, it is likely that this area will also eventually be exposed to wave attack - by 1991, two gaps had already developed in the protective marsh cover along this part of the shore (Fig. 3).

Conclusions

1. The shorelines of Mad Island Marsh Preserve bordering the GIWW were eroded up to 89 meters during the period 1943-1991.
2. During the same period, there was an almost three-fold increase in the width of the GIWW, from 46-65 meters in 1943, to 143-181 meters in 1991.
3. The total area of land lost along the borders of the GIWW during this time amounted to 0.484 km^2 - an average rate of loss of about 0.01 km^2 per year.
4. Along the northern shoreline of the GIWW - the shoreline bordering the main part of the Preserve - there is no indication that erosion is slowing or stopping. The results suggest that erosion here will continue at rates of between 0.38 and 1.85 meters per year.
5. Continued erosion threatens two areas of wetland habitat on the Preserve: in the vicinity of Mad Island Bayou, continued erosion may result in abrupt shortening of the bayou and increase the likelihood of saltwater intrusion into Mad Island Lake and its surrounding freshwater marshes; farther east, an area of *Spartina* marsh bordering the GIWW was reduced from 0.154 km^2 in 1958 to 0.022 km^2 in 1991 - this erosion appears to be continuing, threatening further loss of the marsh habitat and exposure of the adjoining Preserve land to future wave attack.

Acknowledgments

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A NEW SPECIES OF COCCIDIAN (APICOMPLEXA: EIMERIIDAE) FROM *SYNAPTOMYS COOPERI* (RODENTIA: MURIDAE) IN MISSOURI

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Abstract.—A new species of *Eimeria* (Apicomplexa: Eimeriidae) was found in the feces and intestinal contents of the southern bog lemming, *Synaptomys cooperi* Baird, 1858, from St. Charles County, Missouri, USA. Oocysts of this new species are ellipsoidal, 27.7 x 22.1 (24-30 x 17.5-24) μm (N=25); shape index (length/width) 1.26 (1.10-1.53). Micropyle absent; oocyst residuum and polar granule present. Sporocysts are ellipsoidal, 12.6 x 8.6 (10.5-13.5 x 7-9) μm (N=20), with Stieda and substieda bodies; shape index 1.47 (1.39-1.56). Sporozoites each contained a large, ellipsoidal posterior refractile body. This represents the first report of a coccidian from the genus *Synaptomys*. *Key words*: *Synaptomys cooperi*; southern bog lemming; Rodentia; coccidia; *Eimeria*; Apicomplexa.

The southern bog lemming is a small vole that occurs in the northeastern portion of North America, extending as far west as Kansas and Nebraska (Linzey, 1983; Linzey and Cranford, 1984). Habitats frequented by bog lemmings are diverse, and studies have suggested the reason for this may be competitive exclusion of *Synaptomys* by *Microtus* spp. (Linzey, 1981; 1984). Although no species of coccidia have been described from the genus *Synaptomys* previously, we recently were able to examine feces and intestinal contents of select specimens. Herein we report the finding of a new species of the genus *Eimeria* (Apicomplexa).

Materials and Methods

Twenty-two southern bog lemmings, *Synaptomys cooperi*, were collected February-March, 1992 from St. Charles County, Missouri, using Sherman live traps. Animals were transported to the laboratory and euthanized using CO_2 overdose. Intestinal contents and feces were placed in 2.5% (w/v) aqueous $K_2Cr_2O_7$ solution and shipped to Kansas State University. Samples were placed in Petri dishes in a shallow layer of $K_2Cr_2O_7$ solution and allowed to sporulate at room temperature (ca 23°C) for one week. Oocysts were then concentrated by flotation in an aqueous sucrose solution (specific gravity 1.30), and examined and measured using Nomarski interference-contrast optics. Oocysts were measured using a calibrated ocular micrometer and are reported in micrometers as means, followed by the ranges in parentheses.

Results and Discussion

Two of 22 (9.1%) of the samples were found to contain coccidian oocysts, which proved to represent the same undescribed coccidian of the genus *Eimeria*. Below we present a description of the new coccidian.

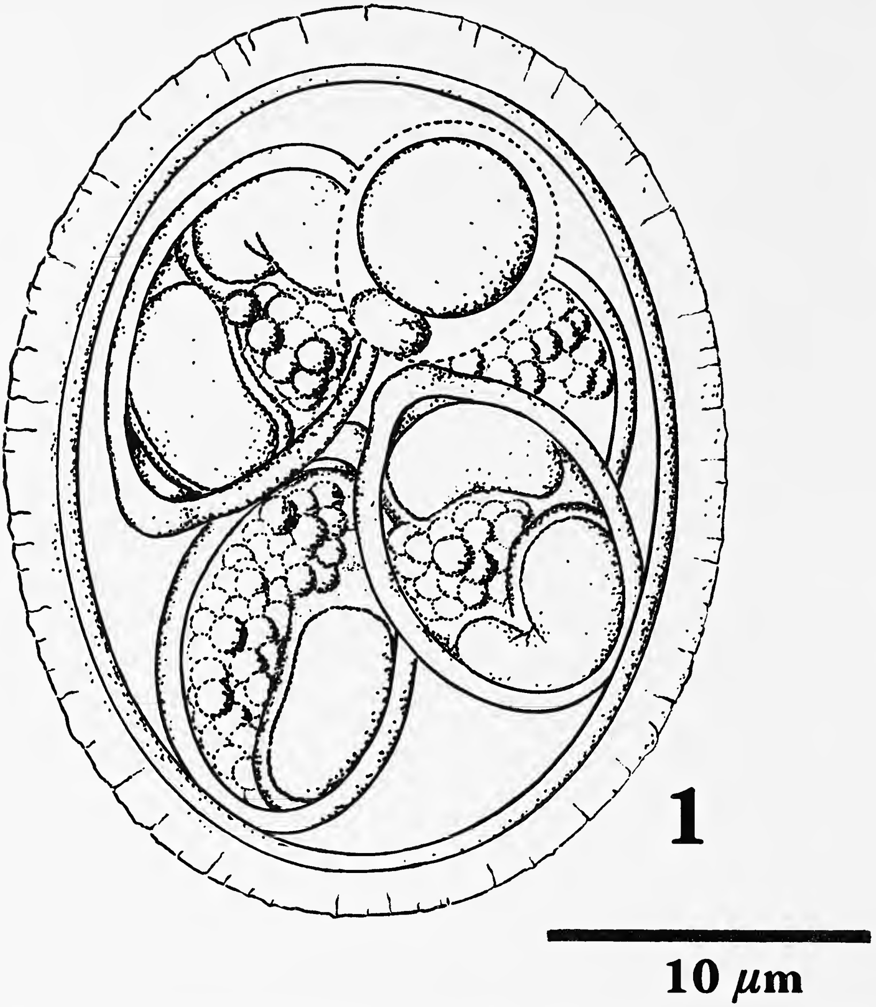
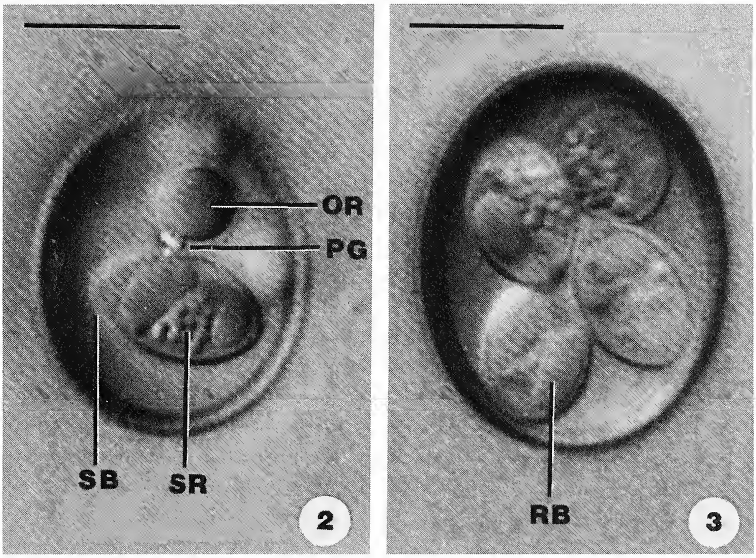


FIGURE 1. Composite line drawing of sporulated oocyst of *Eimeria synaptomys* new species.

TAXONOMIC DESCRIPTION

Eimeria synaptomys new species (Figs. 1-3)
(Apicomplexa: Eimeriidae)

Oocysts ellipsoidal, 27.7 x 22.1 (24-30 x 17.5-24) (N=25); shape index (length/width) 1.26 (1.10-1.53). Wall bilayered, composed of thick, rough outer layer about 1.5 thick and smooth inner layer, about 0.5 thick. Micropyle absent; oocyst residuum present, 5.9 (5-8) (N=20), normally consisting as single homogenous globule but sometimes as 2-many globules enclosed in limiting membrane. Single polar granule



FIGURES 2, 3. Nomarski interference-contrast photomicrographs of sporulated oocysts of *Eimeria synaptomys* new species. Scale bars = 10 μm. Abbreviations: OR, oocyst residuum; PG, polar granule; RB, refractile body; SB, Stieda body; SR, sporocyst residuum.

present, 2.1 (1.5-2.5) (N=20), occasionally fragmented into two pieces and usually enclosed in membrane surrounding oocyst residuum. Sporocysts ellipsoidal, 12.6 x 8.6 (10.5-13.5 x 7-9) (N=20); shape index 1.47 (1.39-1.56). Wall smooth and single-layered, < 1.0 thick. Stieda body present, covered by thin membrane; substieda body present, small, indistinct, and homogenous. Sporocyst residuum present, consisting as numerous, coarse, homogenous granules 0.5-1.5 in diameter scattered among sporozoites. Sporozoites vermiform, 14.5 x 3.4 (13-16 x 3-3.5) (N=20), arranged head-to-tail in sporocyst. Each sporozoite contains single homogenous posterior refractile body, 5.6 x 3.2 (4-7 x 3-3.5) (N=20); anterior refractile body absent. Nucleus located near center of sporozoites.

TYPE HOST: *Synaptomys cooperi* Baird, 1858 ssp. *gossii* Coues, 1877 "southern bog lemming" (Rodentia: Muridae).

TYPE LOCALITY: St. Charles County, Missouri, 3.4 km West Weldon Spring.

PREVALENCE: 2/22 (9.1%) animals were passing oocysts.

SPORULATION: Unknown. Oocysts were fully sporulated upon arrival at Kansas State University.

LOCATION IN HOST: Unknown. Oocysts recovered from intestinal contents and feces.

ETYMOLOGY: The specific epithet represents the host genus.

REMARKS: Although no species of coccidia have been reported from southern bog lemmings previously, nearly 40 species have been collectively reported from related host genera (i.e. *Dicrostonyx, Lemmus, Ellobius, Ondatra, Microtus*; see Levine and Ivens, 1990). Of these, only four (all from the genus *Microtus*) are similar to *Eimeria synaptomys* new species. Oocysts of *E. chetae* Arnastauskene, 1980 from *M. middendorfi* in Russia were reported to lack a Stieda body and discernible sporocyst residuum (Arnastauskene, 1980). Both structures are highly conspicuous in the form we report here. Differences between *E. synaptomys* new species and *E. gomurchaica* Veisov, 1963 from *Microtus arvalis* in Azerbaijan include oocysts of the latter being more spherical, possessing a smooth oocyst wall and a small rather than large sporocyst residuum, and lacking a polar granule (Veisov, 1963). Likewise, oocysts of *E. monocrustae* Veisov, 1963 from the same host in Azerbaijan are more spherical, do not possess a polar ganule, and also have a highly granular wall with unusual inclusions that form a "zig-zag" appearance (Veisov, 1963). In North America, only *E. ochrogasteri* Ballard, 1970 from *M. mexicanus, M. ochrogaster,* and *M. pennsylvanicus* are similar. Oocysts of this species, however, are smaller and possess an anterior refractile body (Ballard, 1970; Vance and Duszynski, 1985).

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REDESCRIPTION OF *EIMERIA BITIS* (APICOMPLEXA) FROM *BITIS ARIETANS* (SERPENTES) FROM NAMIBIA, AFRICA

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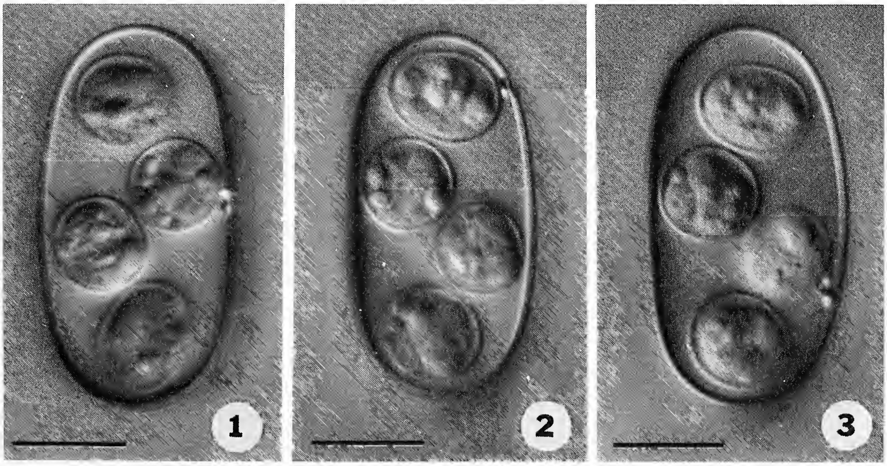
ABSTRACT.—*Eimeria bitis* Fantham, 1932 (Apicomplexa: Eimeriidae), was found in the feces of a puff adder, *Bitis arietans* (Serpentes: Viperidae), from Namibia, southwest Africa. A redescription, line drawing, and photomicrograph of this coccidian are provided. *Key words*: *Eimeria bitis*; *Bitis arietans*; coccidia; puff adder; Namibia; Africa.

Fantham (1932) first described *Eimeria bitis* from the gall bladder and bile ducts of a single puff adder, *Bitis arietans*, near Cape Town, South Africa. Only a brief description of the oocysts was provided, and no photomicrographs or line drawings have ever been published.

During a herpetological collecting trip to Namibia, southwest Africa in May, 1992, feces were collected from two puff adders, *Bitis arietans*. Oocysts were placed in vials containing 2% (w/v) aqueous potassium dichromate solution and shipped to Kansas State University for diagnosis. Coccidian oocysts were observed in one sample, which were concentrated by flotation using an aqueous sucrose solution (specific gravity 1.30) and examined and photographed using Nomarski interference-contrast optics. Measurements were made using a calibrated ocular micrometer and are reported in micrometers as means, followed by the ranges in parenthesis. Oocysts were 6 weeks old at the time of examination.



FIGURES 1-3. Sporulated oocysts of *Eimeria bitis* from *Bitis arietans*. Scale bars = 10 μm.

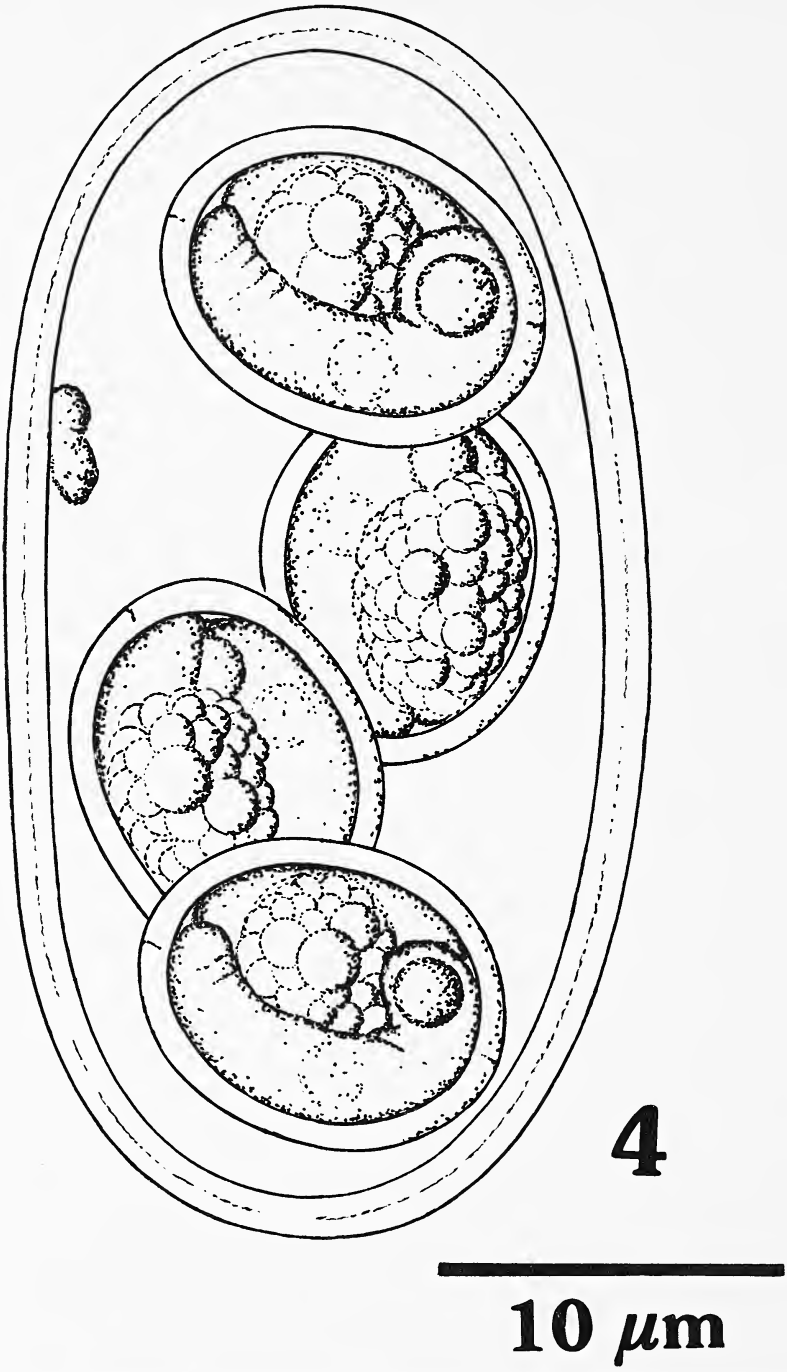


FIGURE 4. Composite line drawing of sporulated oocyst of *Eimeria bitis* from *Bitis arietans*.

TAXONOMIC REDESCRIPTION

Eimeria bitis Fantham, 1932
(Apicomplexa: Eimeriidae)
Figs. 1-4.

Oocysts cylindroidal, 35.4 x 18.5 (34-41 x 17-20) (N=25), often with one side flattened slightly; shape index (length/width) 1.91 (1.71-2.32). Oocyst wall smooth, composed of two layers each about 0.5 thick. Micropyle and oocyst residuum absent; single polar granule present, ellipsoidal or dumb-bell shaped, usually attached to inner surface of oocyst wall. Sporocysts ellipsoidal, 11.2 x 9.2 (10-12 x 8.5-10) (N=20), with smooth, thin, single-layered wall about 0.5 thick; shape index 1.22 (1.10-1.31). Sporocyst residuum spherical or subspherical, 5.6 x 5.4 (5-6.5 x 5-6.5) (N = 10), composed of many homogenous globules of various sizes. Sporozoites elongate, 12.5 x 2.6 (12-14 x 2.5-3) (N = 10) in situ, with posterior ends reflected back along one end of sporocyst. Sometimes transverse striations can be seen on sporozoites anteriorly. Each sporozoite with spherical or subspherical posterior refractile body, 2.5 x 2.3 (2-3 x 2-2.5) (N = 10), and single nucleus slightly posterior to midpoint of body.

Eimeria bitis Fantham, 1932 [syn. *Choleoeimeria bitis* (Fantham, 1932) Paperna and Landsberg, 1989] was described originally from a male puff adder near Cape Town, South Africa (Fantham, 1932). Oocysts were reported as 27.9-36.4 x 17.8-24.3 μm, sporocysts from intact oocysts as spherical or subspherical, 6.5-11.4 μm in diameter, sporocysts ruptured free of oocysts as ellipsoidal, 12.8-11.4 x 8.5-10 μm, and free sporozoites 10-12 x 2.1-2.8 μm. None of the other details provided above have been previously reported. Other records of *E. bitis* include what appears to be a reiteration of the original description (Fantham and Porter, 1950), a report of the parasite from 30/40 (75%) unidentified snakes in Nigeria (Akinboade and Dipeolu, 1982), and what is likely a mis-identification of similar oocysts from *Thamnophis* spp. in Canada (Fantham and Porter, 1954).

ACKNOWLEDGMENT

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TEMPERATURE TOLERANCE AFTER SPAWNING IN FEMALE AND MALE FATHEAD MINNOWS, *PIMEPHALES PROMELAS*

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Abstract.—Possible stress associated with reproduction was bioassayed with the critical thermal maximum (CTMax) method in female and male fathead minnows, *Pimephales promelas*. Temperature tolerances of unspawned females and males were compared with those of similar sized female and male fish which had spawned. Mean CTMax of these four groups (n = 12 to 18) ranged from 36.2° to 36.9°C with standard deviations less than 4% of their respective means. There was no significant interaction between gender and spawning, and neither spawning nor gender significantly effected mean CTMax. And, 73% of test (spawned) fatheads spawned again within five days of temperature tolerance trials. *Key words*: temperature tolerance; CTMax; spawning; reproduction; *Pimephales promelas*.

Several researchers (Markus, 1934; Unger, 1983; Flickinger, 1973) noted high postspawning mortality of fathead minnows, *Pimephales promelas*. For example, between spring stocking and fall harvesting, Flickinger (1973) found mortality rates of fathead minnows as high as 91%. The energetic demand of reproduction has been proposed as a major factor contributing to senescence and death in fishes (Woodhead, 1979).

The objective of our research was to determine if a single spawning event was stressful enough to influence the physiological well-being of fathead minnows. The critical thermal maximum (CTMax) was used to bioassay physiological well-being. Temperature tolerance via the CTMax methodology can be accomplished without death of fish, is relatively easy to determine and the endpoint is scientifically defensible as an ecologically important attribute of fishes (Beitinger and McCauley, 1990). In a CTMax trial, an organism is heated at a constant rate from its acclimation temperature until it exhibits an obvious sublethal but near lethal endpoint, usually loss of equilibrium or onset of muscle spasms. The temperature at which the endpoint occurs is the CTMax. Previous studies by Silbergeld (1973) and Paladino and Spotila (1978) and research conducted in our laboratory (e.g., Watenpaugh and Beitinger, 1985; Watenpaugh et al., 1985; Carrier and Beitinger, 1988; Rutledge and Beitinger, 1989) demonstrated that the CTMax methodology is a sensitive and rapid method to detect the effects of abiotic (particularly chemical) stressors. Many chemicals at sublethal concentrations (e.g., arsenic, cadmium, dieldrin, nickel, nitrite, selenite and zinc) significantly decrease the ability of fishes to tolerate increasing temperatures.

We hypothesize that if a biotic factor or process such as spawning adversely affects internal well being, i.e., homeostasis, it will reduce the ability of an organism to tolerate increasing temperatures. Likewise, we propose that factors responsible for decreases in temperature tolerance would have concomitant effects on other key physiological, ecological, and life-history processes.

Previous research on costs of reproduction have measured reproductive output by the number of gametes produced per parent, the biomass of gametes produced per biomass of parent (Calow, 1979), or have limited food input and measured size and egg production (Wooton, 1977). To our knowledge, no one has measured changes in temperature tolerance, specifically CTMax, to bioassay the effects of reproductive activities on physiological well-being in fishes.

MATERIALS AND METHODS

Fathead minnows were obtained from a culture kept at the University of North Texas. Fish were raised in dechlorinated tap water in aquaria (either 110 or 38 liter) at a controlled temperature of 24 ± 0.5 (range) °C and a photoperiod of LD 18:6 via fluorescent lighting. All fish were sexually mature (more than six months from date of hatch). Aquaria for spawning contained nesting sites consisting of PVC pipe with an internal diameter of seven centimeters (cm) in lengths of about eight cm and cut in half lengthwise. Control fish (not having spawned) were maintained under identical abiotic conditions but at higher densities and without nesting sites. All fish were fed twice daily with flake food supplemented with frozen and freshly hatched brine shrimp, *Artemia.*

Critical thermal maxima were determined for 13 males (mean total length = 5.2 cm, SD = 0.7) and 13 females (mean total length = 4.0 cm, SD = 0.2) which has spawned within the previous 24 hours. Also, control data were collected from 12 males (mean total length = 4.9 cm, SD = 0.8) and 18 females (mean total length = 3.7, SD = 0.1) which had not spawned. CTMax methods were those of Becker and Genoway (1979) with a 0.3°C minute $^{-1}$ rate of temperature increase and first loss of equilibrium as the endpoint (see Hutchison, 1976; Becker and Genoway, 1979; and Beitinger and McCauley, 1990 for discussions of CTMax endpoints). During CTMax trials, water temperature was raised with two circulating heaters and monitored with a calibrated digital thermometer, accurate to 0.01°C. Fish were placed individually in two-liter aquaria after spawning was witnessed or before testing of control fish. Trials occurred between 0900 and 1100 hours and each post-spawn fish was then returned to an aquarium which contained its original mate. No attempt was made to spawn the control fish after CTMax trials. Gender was determined from body coloration, presence or absence of an enlarged urogenital structure (Flickinger, 1969), and the ratio of anal fin length to total length as described by Lewis (1977).

Data were subjected to a parametric two-way analysis of variance after Shapiro-Wilk W tests demonstrated that CTMax values of each group were normally distributed ($p > 0.05$).

RESULTS AND DISCUSSION

Mean CTMax of control (nonspawn) fathead females and males equalled 36.9° and 36.2° C respectively (Table 1). These CTMax values for fathead are about 1° to 1.5°C greater than those previously reported (Watenpaugh and Beitinger, 1985; Carrier and Beitinger, 1988).

TABLE 1. Critical thermal maxima, °C ($\bar{X} \pm$ SD and n in parenthesis) of fathead minnows relative to gender and reproductive status.

	Females	Males
nonspawn	36.9 ± 0.86 (18)	36.2 ± 1.22 (12)
post spawn	36.8 ± 1.40 (13)	36.7 ± 1.38 (13)

Fatheads in the present study were acclimated to 24°C instead of 21°C as in the other two studies. The low variability of the control data as reflected in coefficients of variation of 2.3 and 3.3% for females and males, respectively, make it quite easy to detect statistically significant changes in the mean CTMax of spawned fish. Nevertheless, a parametric two-way ANOVA found no significant interaction between gender and reproductive status ($F = 0.98$, $P = 0.33$) and neither spawning ($P = 0.33$), nor gender ($P = 0.67$) significantly effected mean CTMax. These results confirm that one spawning event did not influence the mean upper temperature tolerance of fathead minnows.

In some cases a stressor not only influences the mean response but also increases the amount of variation in a response variable. For example, fathead minnows exposed to a variety of cadmium concentrations over time, exhibited not only a decrease in mean CTMax, but also an increase in variance at higher doses or longer exposures (Carrier and Beitinger, 1988). Similar increases in the amount of variation in CTMax can be seen in the data of Middaugh, et al. (1975), Watenpaugh et al. (1985) and Watenpaugh and Beitinger (1985). This increase in CTMax variability was not seen in response to spawning activities in our experiments. The variances of spawned and control females and spawned and control males CTMax were not significantly different (variance ratio test, both $P > 0.05$). These results clearly indicate that neither guarding a territory and sperm deposition nor spawning a single clutch of eggs appears to stress either male or female fathead minnows to the extent that an observable difference in thermal tolerance occurs. Nine of 13 males (69.2%) and 10 of 13 females (76.9%) spawned within five days of CTMax testing, suggesting that short-term exposure to CTMax-level temperatures does not impair the future reproductive ability of minnows.

We attempted to use the critical thermal maximum method as an indicator of possible physiological stress due to a biotic process, reproduction. To our knowledge this is the first time that CTMax methodology has been used as a bioassay to assess the effects of stress resulting from a biotic process. Our results show that one spawning event does not decrease thermal tolerance of either male or female fathead minnows. Also, brief exposure to near lethal temperatures does not appear to negatively impact future spawning activities of either female or male fathead minnows.

ACKNOWLEDGEMENTS

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FACTORS INFLUENCING THE GERMINATION OF SEEDS OF *FALLUGIA PARADOXA* (ROSACEAE)

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ABSTRACT.—Freshly matured seeds (achenes) of *Fallugia paradoxa* (D. Don.) Endl. *ex* Torr. (Rosaceae, Apache Plume) appear to be nondormant. Seeds readily germinated without special treatment at 5-10 °C (51 percent) and 20-25 °C (85 percent). When persistent styles were removed and seeds were otherwise placed in the same light and temperature conditions, germination was significantly higher for seeds with detached styles (89 percent) compared to seeds with intact styles (69 percent). In a light gradient, germination decreased as light levels increased. Greatest germination was 32 percent for the lowest light level tested (PPFD 115 μM·m^{-2}·sec^{-1}). At the highest light level tested (PPFD 1291 μM·m^{-2}·sec^{-1}), germination was reduced to 10 percent. For seeds buried in soil at depths of zero, one, two, five, and ten millimeters the greatest emergence was 30 percent at a depth of two millimeters, while only two percent of the seeds buried at ten millimeters reached the surface. For *F. paradoxa*, seed germination soon after dispersal may permit early growth to take place during a period when moisture is most likely to be available; thereby, allowing some seedlings to establish before less favorable moisture and temperature conditions are initiated. Light and soil depth experiments suggest that germination during this period may be favored in microhabitats where light and evaporation levels are at least initially reduced. *Key words*: germination; *Fallugia paradoxa*; Apache Plume; light level; soil depth.

Fallugia paradoxa (D. Don.) Endl. *ex* Torr. (Rosaceae, Apache Plume or Ponil) is a much-branched deciduous or semievergreen shrub found from western Texas and southeastern Colorado through southern Nevada to southeastern California, and southward into northern Mexico (Benson, 1981). Considerable ecotypic variation has been noted in *F. paradoxa*'s appearance, particularly in height which ranges from 0.5 to 2.5 meters (Deitschman et al., 1974). In western Texas, *F. paradoxa* flowers from April to August producing large, white, roselike perfect flowers. Fruits ripen on the plant, changing from a greenish to a reddish color, and are usually dispersed by wind approximately one to two months after flowering begins (Deitschman et al., 1974). The fruit contains a single seed and is a small, hairy achene. Each achene has a persistent style which forms a two to five centimeter feathery tail because of numerous long lateral hairs (Fig. 1). Thirty or more of the long-tailed fruits may result from one flower and form dense clusters that can almost obscure the plant (Benson, 1981).

Fallugia paradoxa is found in the uplands of the Mojave, Sonoran, and Chihuahuan deserts at 1,070 to 2,290 meters (Benson, 1981). It is an abundant species in some mountain and canyon communities in western Texas, including the foothills of the Chisos Mountains in Brewster County and the Guadalupe Mountains in Culberson County.

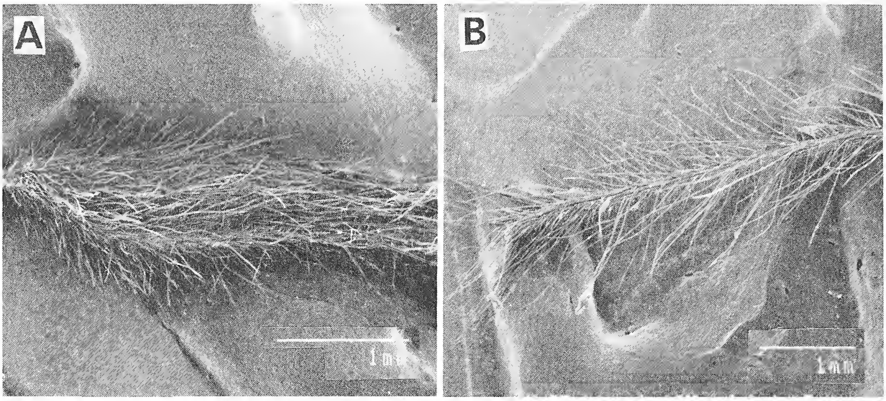

FIGURE 1. Scanning electron micrographs of *F. paradoxa*, achene (A) and persistent style (B), with 20-30X magnification. The bar in the figure is one millimeter. The style of each achene forms a feathery tail two to five centimeters long. Only the base of the tail is shown attached to the achene (A) and the tip (B) with its numerous long lateral hairs.

Fallugia paradoxa is usually found on well-drained gravelly or rocky slopes along mountain trails, roads, or alluvial plains. It may require disturbances for establishment, but no information was found concerning this requirement. In other areas of southwestern North America *F. paradoxa* has been described as an important browse plant for both wild and domestic animals and as an excellent shrub for controlling erosion of arid lands (Deitschman et al., 1974; Benson, 1981). It has been planted to a limited extent for erosion control and ornamental purposes (Anonymous, 1937; Vines, 1960); however, little is known about *F. paradoxa*'s seed germination or seedling development. The purposes of this study were to determine if seeds of *F. paradoxa* are dormant and if cold stratification is necessary for germination. In addition, germination at different light levels and at different soil depths was examined.

METHODS

Fruit of *F. paradoxa* were collected from adult plants growing along dry washes and intermittently flowing streams at the mouth of Pine Springs Canyon in the Guadalupe Mountains, Culberson County, Texas. Fruits were collected in mid-June, 1991, and air-dried for one month before germination experiments were initiated. Fruits (hereafter referred to as seeds) were separated by hand from seed clusters and residual plant material to include seeds with and without styles. In the first experiment, 50 seeds were placed on two layers of filter paper moistened with one milliliter of deionized water in 100 millimeter diameter by 15 millimeter deep, plastic petri plates. The petri plates were placed in cans in the dark, either at 5-10 °C or at 20-25 °C. Five replications with 50 seeds in each replication were used per treatment. Seeds were examined for germination (in the light) on a daily basis. Seeds with a radicle emerged one millimeter were counted as germinated and removed from the petri plate. Deionized water was added as needed to keep the filter paper moist. The experiment was started on 15 July 1991 and completed on 9 September 1991. Seed germination between treatments was statistically compared with a variance ratio test (to determine if differences existing between treatment variances were indicative of a real difference in population variance) followed by a Student's *t*-test (Daniel, 1991).

A second germination experiment was started on 8 August 1991 using fruit collected in June 1991. Seeds were sorted and separated by hand into one of two treatment groups: seeds with styles intact or seeds with styles detached. Seeds from each group were placed on moist filter paper in separate petri plates. All petri plates were stored in one can in the dark at 20-25 °C; otherwise, the seeds were treated in the manner described above. Fifty seeds were used in each replication and there were five replications per treatment. The experiment was terminated on 3 October 1991. A Student's *t*-test was used to statistically compare seed germination between treatments.

A third germination experiment utilized a light gradient. The experiment was conducted in a fiberglass greenhouse with natural sunlight and temperatures ranging from 23-38 °C. Seeds collected in June 1991 were placed on the soil surface in 15 centimeter diameter by 15 centimeter deep plastic pots containing 1,400 grams of air dried, sieved (6.2 millimeter mesh) soil. Soil used was a limestone derived native Patrick series clay-loam soil (Taylor et al., 1966). Fifty seeds were used per pot. Five pots were placed in each of four shade treatments. Shade chambers were constructed with one by one millimeter mesh commercial shade fabric. The number of layers of shade fabric was varied to provide photosynthetically active photon flux densities (PPFDs) of 115 ± 3($\bar{x}$ ± one SD), 487 ± 23, 783 ± 42, and 1291 ± 89 $\mu M{\cdot}m^{-2}{\cdot}sec^{-1}$ (with full sunlight outside the greenhouse at 2065 ± 14 $\mu M{\cdot}m^{-2}{\cdot}sec^{-1}$ at solar noon on 23 August 1991). Light levels were measured with a LiCor® LI-188 integrating quantum sensor. The pots were watered once daily with deionized water as needed to keep the soil surface moist. Seeds were examined daily for germination with the radicle emerged one millimeter as the criterion for germination. The experiment was conducted from 19 August to 10 November 1991. Statistical analyses included a one-way ANOVA with light as the main factor followed by Tukey's HSD (honestly significant difference) multiple comparison test (Daniel, 1991).

A fourth germination experiment was conducted from 19 August to 10 November 1991. Fifty seeds were buried at depths of zero, one, two, five, and ten millimeters in plastic pots containing 1,400 grams of Patrick series soil. The pots were placed on a bench in the greenhouse with the light level at 1291 ± 89 $\mu M{\cdot}m^{-2}{\cdot}sec^{-1}$. Deionized water was added once daily as needed to keep the soil surface moist. The pots were examined daily for emergence of hypocotyls from the soil surface. Seeds with emerged hypocotyls were counted and removed. Statistical analyses included a one-way ANOVA with seed depth as the main factor followed by Tukey's HSD multiple comparison test (Daniel, 1991).

RESULTS

Seeds of *F. paradoxa* readily germinated without special treatment at 5-10 °C and 20-25 °C. Germination started within eight days in the 20-25 °C treatment and on the eleventh day in the 5-10 °C treatment (Fig. 2). Greatest germination was 85 percent at 20-25 °C. This was significantly higher than the 51 percent germination at 5-10 °C (t= 3.71, $P < .0001$).

When seeds were separated into one group without styles and another group with styles, and placed in the same environment,

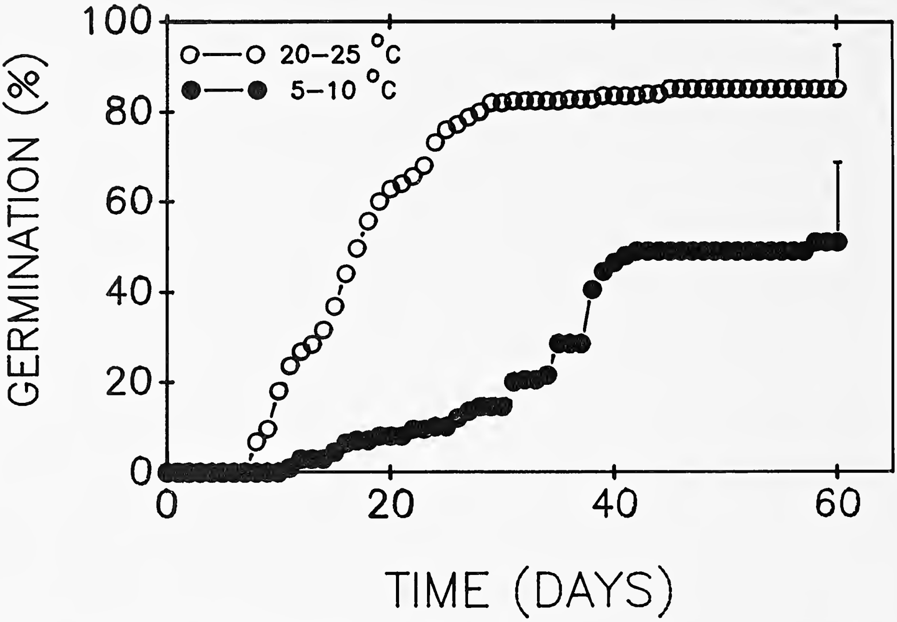

FIGURE 2. Mean percent germination (bar equals a representative standard deviation) of *Fallugia paradoxa* seeds at 5-10 °C and 20-25 °C over 60 days. Germination of seeds at 20-25 °C was significantly higher than at 5-10 °C (Student's t-test, $t = 3.71$, $P < .0001$). The experiment was started on 15 July 1991 and ended on 9 September 1991. Seeds were checked daily and counted as germinated when radicles emerged one millimeter.

germination was significantly higher for seeds with detached styles (89 percent) compared with seeds with intact styles (69 percent) ($t = 4.75$, $P < .0001$, Fig. 3).

In the greenhouse light experiment, germination was much lower on the soil surface compared to the petri plates in the laboratory experiments. In the light experiment, *F. paradoxa* germination tended to decrease as light levels increased (Fig. 4). Germination decreased significantly from 32 percent in the lowest light treatment to 16 and 9 percent, respectively, in the 487 and 783 $\mu M \cdot m^{-2} \cdot sec^{-1}$ treatments, and was 10 percent in the highest light treatment (F= 8.43, HSD= 15.72, $P \leq .05$).

In the soil depth experiment, greatest emergence was 30 percent for seeds placed at a depth of two millimeters (Fig. 5). At zero, one, and five millimeters, emergence was 10, 22, and 10 percent, respectively. Initial emergence from the above planting depths occurred at three to four weeks. For seeds buried at ten millimeters only two percent reached the surface. The time required for reaching the surface from a depth of ten millimeters was six to seven weeks. A significant difference in percent emergence existed only between seeds in the two and ten millimeter depth treatment (F = 4.41, HSD = 26.75, $P \leq 0.05$).

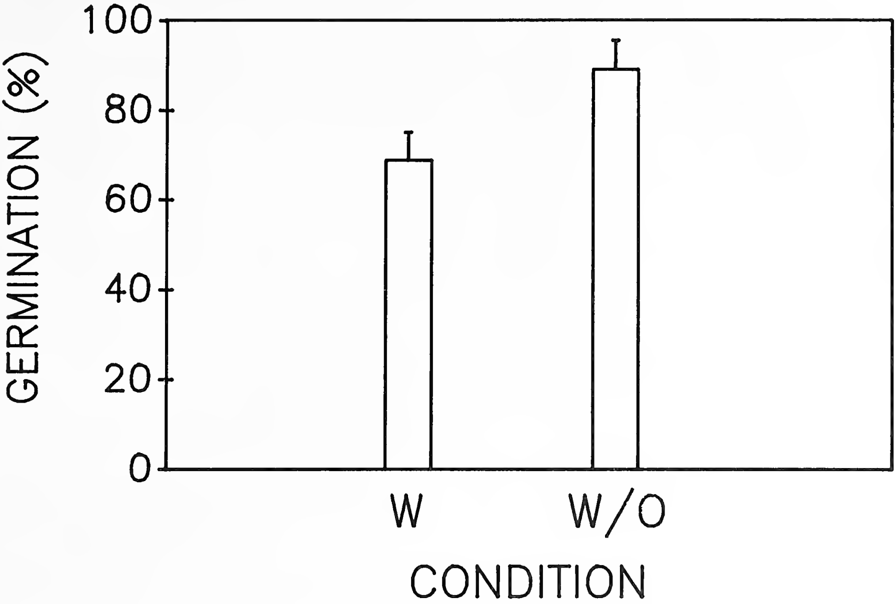

FIGURE 3. Mean percent germination (bar equals one standard deviation) of *Fallugia paradoxa* seeds with and without attached styles. Germination was significantly higher for seeds without styles (Student's *t*-test, $t = 4.75$, $P < .0001$). The experiment was started on 8 August 1991 and ended 56 days later on 3 October 1991. Seeds were examined daily and counted as germinated when radicles emerged one millimeter.

There was no distinction between germination and emergence from the soil in this experiment.

DISCUSSION

Seeds of each plant species respond to a characteristic set of germination requirements. Ideally, seeds respond to a combination of germination factors that have a high probability of being followed by another set of factors favorable for the survival, growth, and reproduction of the seedlings (Fenner, 1985). The timing of germination; therefore, is critical to the subsequent establishment of seedlings. Various internal and external factors regulate the germination of seeds. Three general types of seed dormancy, innate, induced, and enforced dormancy, have roles in regulating germination (Harper, 1977). Fresh seeds are innately dormant if they will not germinate even under conditions normally favorable for growth. They often possess inhibitory mechanisms, including seed coat impermeability, afterripening requirements, or light and temperature sensitivities which must be overcome with specific stimuli or treatments before germination is triggered (Nikolaeva, 1977; Baskin and Baskin, 1991). Seeds that are not innately dormant may be induced

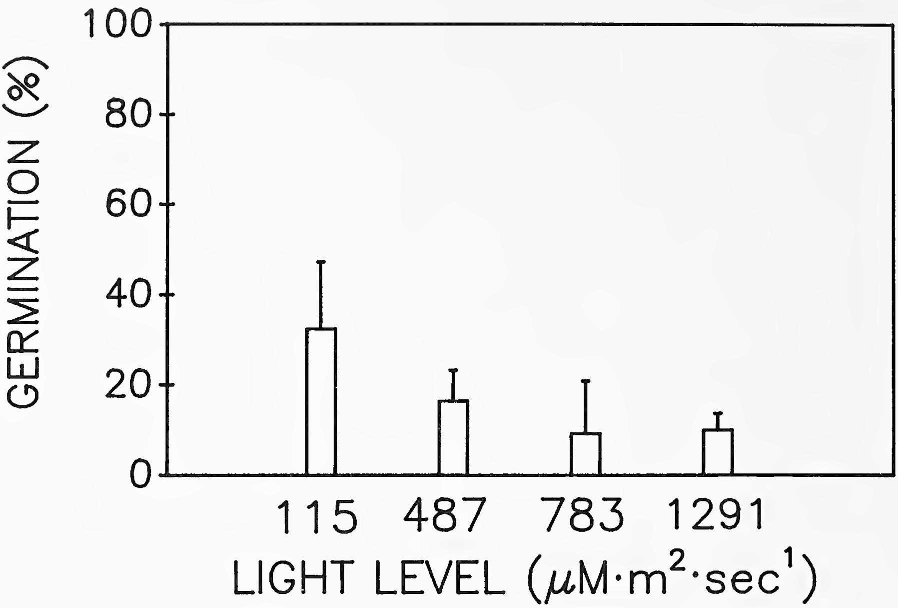

FIGURE 4. Mean percent germination (bar equals one standard deviation) of *Fallugia paradoxa* seeds at four light levels after 83 days of treatment. Germination of seeds at the lowest light level tested was significantly greater than at the three higher light levels (ANOVA, HSD multiple comparison test, F= 8.43, HSD= 15.72, $P \leq .05$). The experiment was conducted from 19 August to 10 November 1991. Seeds were examined daily and counted germinated when radicles emerged one millimeter.

into dormancy by conditions that could reduce survival of seedlings, such as burial in the soil or exposure to light filtered through a canopy (Wesson and Wareing, 1969; Hazebroek and Metzger, 1990). Seeds may also have dormancy enforced upon them by unfavorable environmental conditions. The growth activities of the embryo are suspended, but may be readily resumed with the provision of adequate moisture, oxygen, and/or temperature. These general types of dormancy may occur alone, or one type may succeed another in time in the same seed, or more than one type may occur in different seeds in the same population (Silvertown, 1987).

Limited studies suggested *F. paradoxa* seeds germinate without special treatment (Vines, 1960; Plummer et al., 1969). However, a period of cold stratification is frequently a condition of germination for members of the Rosaceae (Mayer and Poljakoff-Mayber, 1975). One-month-old seeds readily germinated at temperatures of 5-10 °C and 20-25 °C with germination significantly greater at 20-25 °C. Germination of seeds at 5-10 °C (51%) in the present study was lower than germination at 0-3 °C in a previous study using seeds from two Utah sources. In the Utah study, four-month-old seeds were kept at 0-3 °C for 60 days. Mean germination for two seed lots were 60 and 73 percent

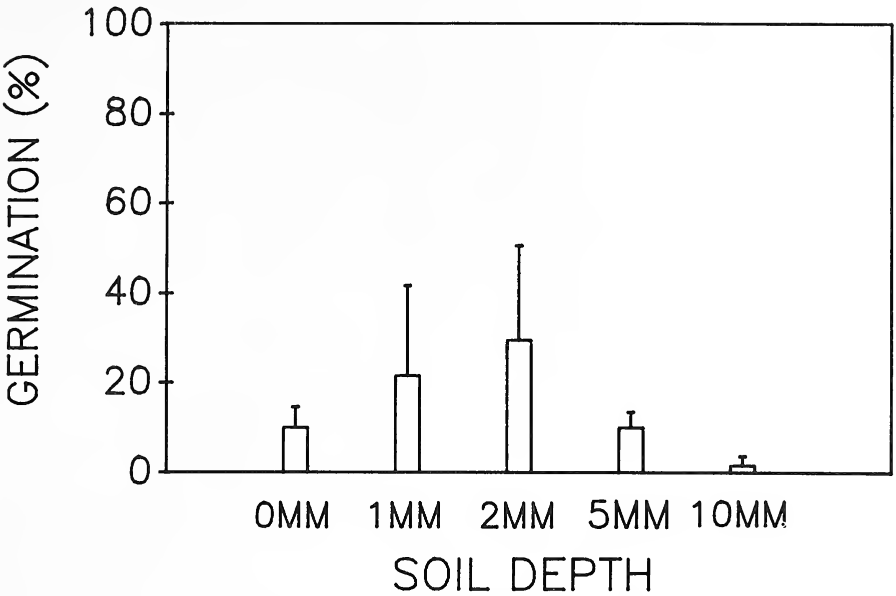

FIGURE 5. Mean percent emergence (bar equals one standard deviation) of *Fallugia paradoxa* seeds at five soil depths after 83 days. Seed emergence from two millimeters in the soil was significantly higher than from ten millimeters of soil depth (ANOVA, HSD multiple comparison test, F= 4.41, HSD= 26.75, $P \leq .05$). The experiment was conducted from 19 August to 10 November 1991. Pots were examined daily and seedlings were counted emerged when the hypocotyl reached the soil surface.

(Plummer et al., 1969). The differences may be due to the additional afterripening of the Utah seeds, differences in preconditioning (Baskin and Baskin, 1973), or the two populations from different parts of the species range may be displaying adaptations to significant locally selective pressures (Thompson, 1981). It is not clear that differences in the two studies indicate a significant ecotypic variation in seed germination; however, Plummer et al. (1969) reported ecotypic differences in *F. paradoxa*'s appearance and tolerance to temperature. It may be that this ecotypic variation extends to seed germination as well.

Removal of the styles from *F. paradoxa* seeds resulted in maximum seed germination (89%). The relatively large, persistent styles and long lateral hairs of *F. paradoxa* appeared to hold the small seeds away from the surface when they were placed on moistened filter paper (Fig. 1). Various studies indicate that the degree of contact between the soil surface and the seed may be a factor in controlling germination (Fenner, 1985). Sheldon (1974) showed that the exact orientation of the seed on the surface can markedly affect the probability of germination.

An alternative explanation for the lower germination of seeds with styles might involve the greater degree of fungal contamination present on seeds with styles. Seeds with large amounts of fungal growth appeared inviable although tetrazolium tests of viability were not done (Baskin and Baskin, 1989).

The tendency of a seed to germinate under specific environmental conditions is generally related to the probability of seedling survival. It appears *F. paradoxa* seeds could germinate at any time after fruit ripening and dispersal if moisture is available. Adult *F. paradoxa* plants growing in western Texas appear to disperse their seeds just prior to months with the highest average temperatures and precipitation for the area, which is June to September (Arbingast et al., 1976). Germination could occur in mid to late summer after significant but intermittent summer showers, permitting early growth to take place when moisture is most likely to be available; thereby, allowing some seedlings to establish before less favorable moisture and temperature conditions of the fall and winter months are initiated.

Between summer rainfall events, light levels and moisture evaporation from the soil surface are likely to be high. The results of the light and soil depth experiments suggest that *F. paradoxa* seeds may germinate where these conditions are partially ameliorated, either slightly below the soil surface or possibly under an adult *F. paradoxa* or other woody species. Adult *F. paradoxa* plants have been observed growing in dense clumps, particularly in dry washes or along streams, as well as singly or in small clumps in open sunny areas. While moisture availability appears to be an important factor for seed germination, additional information on the establishment of *F. paradoxa* seedlings is needed to accurately predict where establishment and growth of *F. paradoxa* will occur in natural communities.

Acknowledgments

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PRODUCTION OF EXTRACELLULAR CELL WALL DEGRADING ENZYMES BY *CURVULARIA SENEGALENSIS*

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Abstract.—The extracellular cellulases of *Curvularia senegalensis* and the effect of different carbon sources on the production of these enzymes were investigated. Production of cellobiohydrolase, endoglucanase and xylanase was induced by all carbon sources tested, except cellobiose that did not induce the production of cellobiohydrolase. Maximum production of cellobiohydrolase was induced when carboxymethyl cellulose (CMC) was used as the carbon source and enzyme inducer. Highest production of endoglucanase was induced by microcrystalline cellulose. Xylan, as carbon source, induced the highest production of xylanase. Results of this study suggest that the production of these enzymes by *C. senegalensis* is, at least in part, constitutive. *Key words*: *Curvularia*; enzymes; cellulases.

Direct penetration of susceptible hosts by the infective hyphae of phytopathogenic fungi is eased by the production of cutinases (Agrios, 1988). Penetration of the host is followed by softening or disintegration of host tissues by cell wall degrading enzymes produced by the pathogen (Kenaga, 1974; Agrios, 1988). Production of these enzymes is induced in many plant pathogenic fungi when these organisms are grown on media containing various sugar polymers (Cooper and Wood, 1973; Pegg, 1981; Ortega, 1990).

C. senegalensis (Speg.) Subram., is primarily a pathogen of cereal crops and grasses including millet, rice, wheat and the grass, *Eragrostis rachitricha* (Cook, 1981; Nyvall, 1989; Khasanov et al., 1990; Sprague, 1950). The main objectives of this work were to study the components of extracellular cell wall degrading enzymes of *C. senegalensis* and to determine the effects of the carbon source on the production of these enzymes by the test fungus.

Materials and Methods

Organism and culture conditions

Stock cultures of *C. senegalensis* were maintained on PDA slants (Difco, B13). The fungus was previously grown in 250-milliliter flasks with 125 milliliters of a medium containing: 0.02 percent $MgSO_4.7H_2O$, 0.01 percent $Ca(NO_3)_2.4H_2O$, 0.1 percent Peptone, 0.2 percent yeast extracts, 2.0 percent glucose in Na-citrate buffer at pH 4.8. After four days growth at 26 C, five milliliters of mycelium inoculum was washed twice in distilled water and used to inoculate the cellulolytic growth medium. The medium for the production of cellulases contained: 0.15 percent NH_4NO_3, 0.24 percent K_2PO_4, 0.08 percent $MgSO_4$, 0.08 percent Ca $(NO_3)_2.4H_2O$, 0.72 ppm Fe $(NO_3)_3.9H_2O$, 0.44 ppm $ZnSO_4.7H_2O$, 2.0 ppm $MnSO_4.4H_2O$, 0.40 ppm $ZnCl_2$, 0.1 percent Peptone, 0.1 percent yeast extract, 1.0 percent carbohydrate. The carbohydrates used as carbon sources and cellulase inducers were: microcrystalline cellulose (Sigma Chemical Company, type 50), sodium carboxymethyl cellulose (CMC, Aqualon Company, type 7HF), xylan (Aldrich

Chemical Company) and cellobiose (Sigma Chemical Company). The control cultures had glucose as carbon source. The pH of the growing medium was adjusted to 4.8. Incubation of the cultures was carried out for seven days in covered 250-milliliters flasks on an orbital shaker at 100 rpm and 26°C.

Enzyme preparation and assays

Culture fluids were collected after seven days of growth by centrifugation (4500 rpm, 30 minutes, 10°C). The supernatant was subsequently used for the determination of extracellular enzyme activity. For simplification, the collected supernatant is hereafter referred to as the enzyme. All tests were replicated four times. It has been shown before (Mandels et al., 1976; Saddler, 1982; Ortega and Baca, 1985) that maximum enzyme activity of fungal cellulase systems is obtained when the pH of the reaction mixture is 4.8 to 5.0.

Cellobiohydrolase (1, 4-B-D-glucan cellobiohydrolase, EC 3.2.1.91). Cellobiohydrolase activity was measured by combining in separate test tubes one milliliter of enzyme with 20 milligrams of microcrystalline cellulose in one milliliter of 0.05 M sodium citrate buffer (pH 4.8) and incubating the reaction mixture for two hours at 50°C. The tubes were stirred several times during incubation. After centrifugation, the concentration of reducing sugars in the supernatant was determined by the dinitrosalicylic acid method of Miller (1959).

Endoglucanase (CM-cellulase, carboxymethyl cellulase, EC 3.2.1.4). Endoglucanase activity was measured by combining one milliliter of enzyme with one milliliter of 0.8 percent carboxymethyl cellulose in 0.05 M sodium citrate buffer, pH 4.8. The reaction mixture was incubated at 50°C for 30 minutes. The concentration of reducing sugars in the reaction mixture was measured by the dinitrosalicylic acid method of Miller (1959).

Xylanase (EC 3.2.1.32). Xylanase activity was measured by combining 10 milligrams of xylan in one milliliter of 0.05 M sodium citrate buffer, pH 4.8, with one milliliter of enzyme. The reaction mixture was incubated at 50°C for 30 minutes. After centrifugation, the concentration of reducing sugars in the supernatant fluid was determined by the dinitrosalicylic acid method of Miller (1959).

Protein determination

Extracellular protein in the crude supernatants was determined with the bicinchoninic acid (BCA) reagent (Pierce Chemical Company) using bovine serum albumin as standard.

Data analysis

All enzyme activity tests and protein determinations were replicated four times. The results were expressed as units of specific enzyme activity and represent means plus or minus the standard deviation of four replications. Each unit of enzyme activity is the amount of enzyme that liberates one micromole of glucose or xylose (or their reducing sugar equivalents) from their respective substrates per minute under the assay conditions. Statistical analysis of experimental data was made with Student's *t*-test. The Michaelis constant (Km) of the enzymes studied in this investigation were determined with Lineweaver-Burk plots of the reciprocals of the initial reaction rate (1/v) versus substrate concentration (1/Cs).

RESULTS AND DISCUSSION

Cellobiohydrolase

Production of cellobiohydrolase was induced in cultures with crystalline cellulose, CMC, xylan and glucose as carbon sources and enzyme inducers. No cellobiohydrolase activity was detected in the

TABLE 1. Effect of different carbon sources on the specific activities [1] of extracellular cell wall degrading enzymes produced by *Curvularia senegalensis*.

	Enzymes			
Carbon source	Cellobio-hydrolase	Endoglucanase	Xylanase	Extracellular protein[2]
Microcrystalline cellulose	21.84±0.51	83.16±2.24*	15.27±0.27	0.271±0.005
CMC	39.71±2.90*	70.52±1.52	14.33±0.23	0.369±0.016
Xylan	21.60±0.98	46.42±1.92	93.37±1.63*	0.584±0.028
Cellobiose	0.00	50.99±1.24	8.07±0.44	0.503±0.007
Glucose	10.68±0.75	50.01±1.26	8.00±0.04	0.549±0.012

[1] U/min/mg of protein. Mean ± SD of four replications.

[2] mg/ml.

* Using Student's *t*-test, significantly different ($P < 0.001$) from the control.

fluids of cultures of the test fungus with cellobiose as carbon source. Maximum cellobiohydrolase activity (39.71 U) was measured in fluids obtained from cultures with CMC as carbon source and enzyme inducer (Table 1). This activity was significantly higher ($P < 0.001$) than the activities of the enzyme measured in fluids of the control cultures. The activities of this enzyme measured in the fluids collected from cultures containing microcrystalline cellulose or xylan (21.84 and 21.60 U respectively) were significantly higher ($P < 0.001$) than the activities measured in fluids from cultures containing glucose (10.68 U, Table 1). Cellobiohydrolase activity (39.71 U, Table 1) measured in the fluids taken from cultures with CMC as carbon source were significantly higher ($P < 0.01$) than the activities determined in fluids from cultures with microcrystalline cellulose or xylan (21.84 and 21.60 U, respectively). The lowest cellobiohydrolase activity (10.68 U) was recorded in fluids harvested from the control cultures (Table 1). The Km constant of cellobiohydrolase for microcrystalline cellulose was 0.17 mg (Fig. 1). The cellobiohydrolase activity measured in fluids of the control cultures suggests that *C. senegalensis* may produce a small amount of this enzyme in a constitutive manner. It was found before (Ortega, 1990) that production of this enzyme is induced in cultures of *Fusarium oxysporum* f. sp. *lycopersici* with CMC as carbon source.

Endoglucanase

Production of endoglucanase was induced by all carbon sources tested in this investigation. Maximum endoglucanase activity (83.16 U) was measured in fluids harvested from cultures with microcrystalline cellulose as the carbon source and enzyme inducer (Table 1). This activity was 66.29% more than the endoglucanase activity measured in fluids collected from the control cultures. Endoglucanase activities

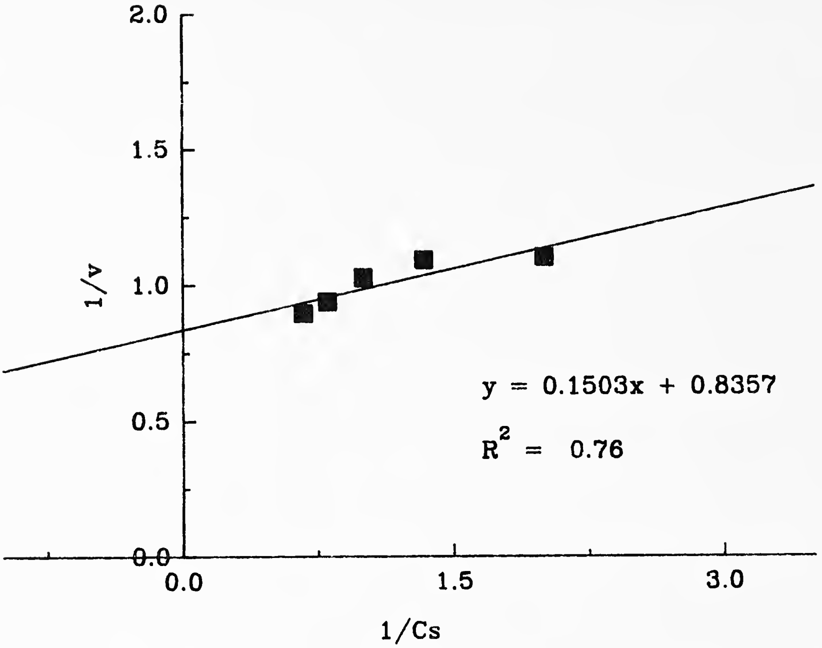

FIGURE 1. Determination of the Michaelis constant (Km) of cellobiohydrolase. Lineweaver-Burk plot of the reciprocals of initial reaction rates (1/v) versus different concentrations of microcrystalline cellulose (Cs, mg/ml).

measured in fluids obtained from cultures with xylan or cellobiose (46.42 and 50.99 U respectively) were not significantly different from the activities (50.01 U) measured in the fluids of the control cultures (Table 1). The activity (70.52 U) of this enzyme measured in fluids obtained from cultures with CMC as carbon source was significantly higher ($P < 0.01$) than the activity determined in the fluids of the control culture. The lowest endoglucanase activity (46.42 U, Table 1) was measured in fluids harvested from cultures with xylan as carbon source. The Km constant of endoglucanase for CMC was 1.64 mg (Fig. 2). The endoglucanase activity measured in the fluids collected from the control cultures suggests that this enzyme is produced constitutively by *C. senegalensis,* its production enhanced by the presence of microcrystalline cellulose (Table 1). It was found before (Ortega, 1990; 1992) that *Fusarium oxysporum* f. sp. *lycopersici* and *Alternaria brassicae* cultivated under similar conditions, produced constitutively small amounts of endoglucanase. Cooper and Wood (1973) have shown that *F. oxysporum* f. sp. *lycopersici* and *Verticillium albo-atrum* grown with the proper enzyme inducers produce endoglucanase plus galactosidase and polygalacturonase.

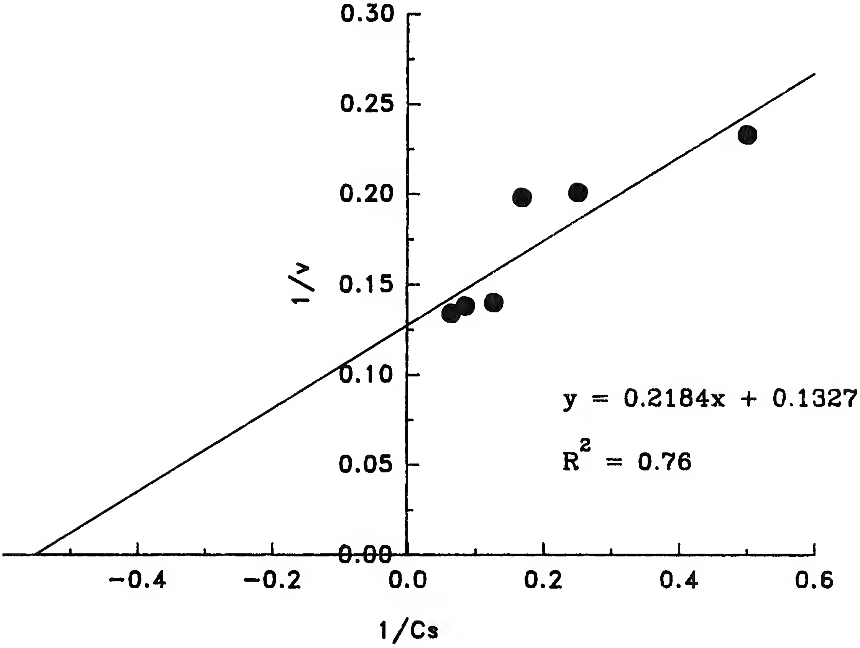

FIGURE 2. Determination of the Michaelis constant (Km) of endoglucanase. Lineweaver-Burk plot of the reciprocals of initial reaction rates (1/v) versus different concentrations of CMC (Cs, mg/ml).

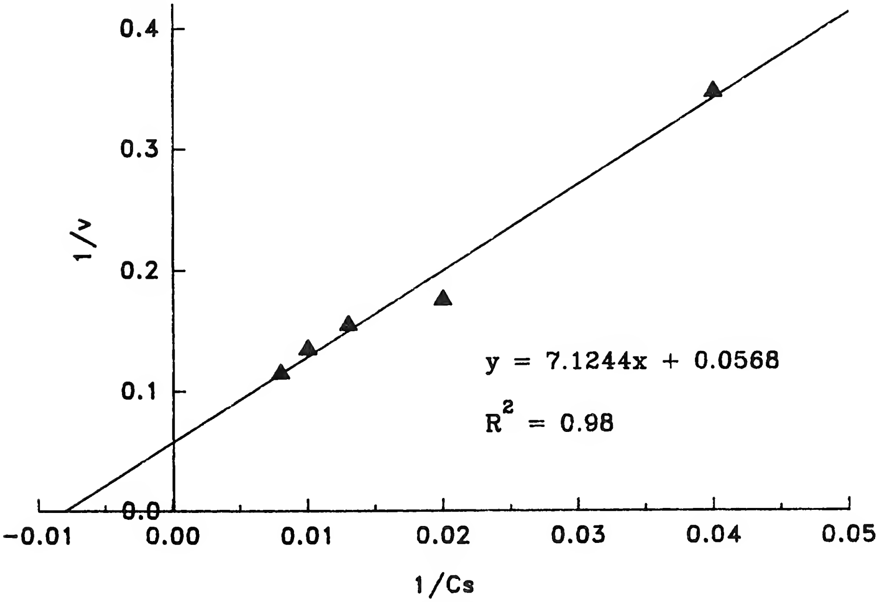

FIGURE 3. Determination of the Michaelis constant (Km) of xylanase. Lineweaver-Burk plot of the reciprocals of initial reaction rates (1/v) versus different concentrations of xylan (Cs, mg/ml).

Xylanase

Production of xylanase by the test fungus was induced in all cultures (Table 1). Maximum activity of this enzyme (93.37 U) was found in fluids collected from the cultures that had xylan as carbon source. This activity was significantly higher ($P < 0.001$) than the activities induced by the other carbon sources tested (Table 1). Xylanase activities measured in fluids of cultures with microcrystalline cellulose and CMC (15.27 and 14.33 U, respectively) were significantly higher than the xylanase activity found in fluids obtained from cultures with cellobiose and glucose (8.07 and 8.00 U, respectively). The Km constant of xylanase for xylan was 125.42 mg (Fig. 3). It was shown before (Ortega, 1990) that CMC induces the production of xylanase by *Fusarium oxysporum* f. sp. *lycopersici.* Cooper and Wood (1973) used D-xylose to induce the production of xylanase in cultures of *F. oxysporum* f. sp. *lycopersici* and *V. albo-atrum.*

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HABITAT UTILIZATION AND POPULATION SIZE ESTIMATE OF FOUNTAIN DARTERS, *ETHEOSTOMA FONTICOLA*, IN THE COMAL RIVER, TEXAS

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Abstract.—Fountain darters (*Etheostoma fonticola*) were sampled in the Comal River, Texas, to determine their habitat utilization and population size. Sampling grids were established along transects to characterize the vegetative community and depth regimes. Fountain darters, collected within these grids, were found in greatest densities in filamentous algae. The mean population estimate for the Comal River upstream of Torrey Mill Dam was 168,078 with 95% confidence limits of 114,178 and 254,110. *Key words: Etheostoma fonticola*; fountain darter; Comal River; Edwards Aquifer; endangered fishes.

Listed as endangered by the U.S. Fish and Wildlife Service (USFWS) (35 FR 16047; October 13, 1970) fountain darters (*Etheostoma fonticola*: Percidae) are endemic to the Comal and San Marcos rivers (USFWS, 1984). Both rivers originate from springs fed by the Edwards Aquifer.

Reduced spring flows have impacted the fountain darter population at Comal Springs in the past and are a continual threat to the species' viability. A severe drought from 1950-1956 greatly reduced the aquifer level and spring discharges. During 1956, Comal Springs ceased to flow for five months (Buckner and Shelby, 1990) as total well pumping increased to 321,100 acre-feet, while recharge decreased to 43,700 acre-feet (U.S. Geological Survey [USGS], 1991). A less severe drought in 1984 resulted in minimum daily spring flows of 24 cubic feet per second (cfs; Buckner et al., 1986). Annual recharge in 1984 was 197,900 acre-feet and total well discharge was 529,800 acre-feet (USGS, 1991). Several years later, another drought reduced minimum daily spring flows to 46 cfs in 1990, compared to a mean spring flow discharge (1933-1990) of 292 cfs (Buckner and Shelby, 1990).

Since 1970, well withdrawal has averaged 422,000 acre-feet per year (USGS, 1991). Given the relationship between aquifer recharge and precipitation and the increasing trend in well pumpage, Comal Springs is likely to cease flowing again (Guyton and Associates, 1979; USFWS, 1984; Edwards Aquifer Research and Data Center [EARDC] and Southwest Texas State University [SWTSU], 1988).

The 1950's drought and subsequent cessation of flows from the Comal Springs is presumed to have caused the Comal River fountain darter population to be extirpated (Schenck and Whiteside, 1976). This population had been impacted in the early drought during renovation efforts of Landa Lake in 1951 when the piscicide, rotenone, was applied to remove exotic Rio Grande cichlids (*Cichlasoma cyanoguttatum*) (Ball et al., 1952). Renovation efforts did not eliminate the fountain darter population, because individuals were seined and held in a protected area prior to the rotenone application (Ball et al., 1952; C. Hubbs, pers. comm.); however, it probably made the population more vulnerable to extirpation. The Comal River was restocked in 1975 and 1976 with 457 fountain darters taken from the San Marcos River (USFWS, 1984).

Schenck and Whiteside (1976) reported that fountain darters predominantly inhabit vegetated areas, and estimated the population at 102,966 individuals in the San Marcos River between Spring Lake Dam and the outfall of the San Marcos Wastewater Treatment Plant (river area of 102,633 m^2). Until now, no such work had been conducted in the Comal River. This study was designed to determine fountain darter habitat utilization, the amount of habitat available, and to estimate the number of fountain darters in the Comal River. Study results will assist future efforts to determine spring flow requirements necessary to protect the Comal River ecosystem.

Study Area

The Comal River, Comal County, Texas, originates from numerous springs fed by the Edwards Aquifer and flows eastward for about five kilometers before joining with the Guadalupe River (Fig. 1). The headwaters of the river were dammed in the late 1880's (D. Whatley, pers. comm.), forming Landa Lake (about 84,280 m^2). Water exits the lake at two points, the "old" and "new" channels. Most of the water is diverted through the new channel, a channelized run formerly used for cooling an electrical power generating plant (Ottmers, 1987). The remainder flows through the old channel which rejoins the new channel about 2.5 kilometers downstream of the lake.

The physical and chemical properties of the Comal River are relatively stable; water temperature remains near 25° C year-round and water clarity is high (Brune, 1981; Ottmers, 1987). The Comal River supports a large quantity and variety of aquatic macrophytes (Table 1), and is heavily utilized for contact and non-contact recreation by area residents and visitors.

Materials and Methods

In August 1990, 30 cross-channel transects were systematically placed at 200 meter intervals beginning at three random starting points—one in Landa Lake, one in the new channel, and one in the old channel (Fig. 1). No transects were established below Torrey Mill Dam, as instream vegetation appeared patchy and few fountain darters were collected during reconnaissance sampling. Permanent markers were established at each

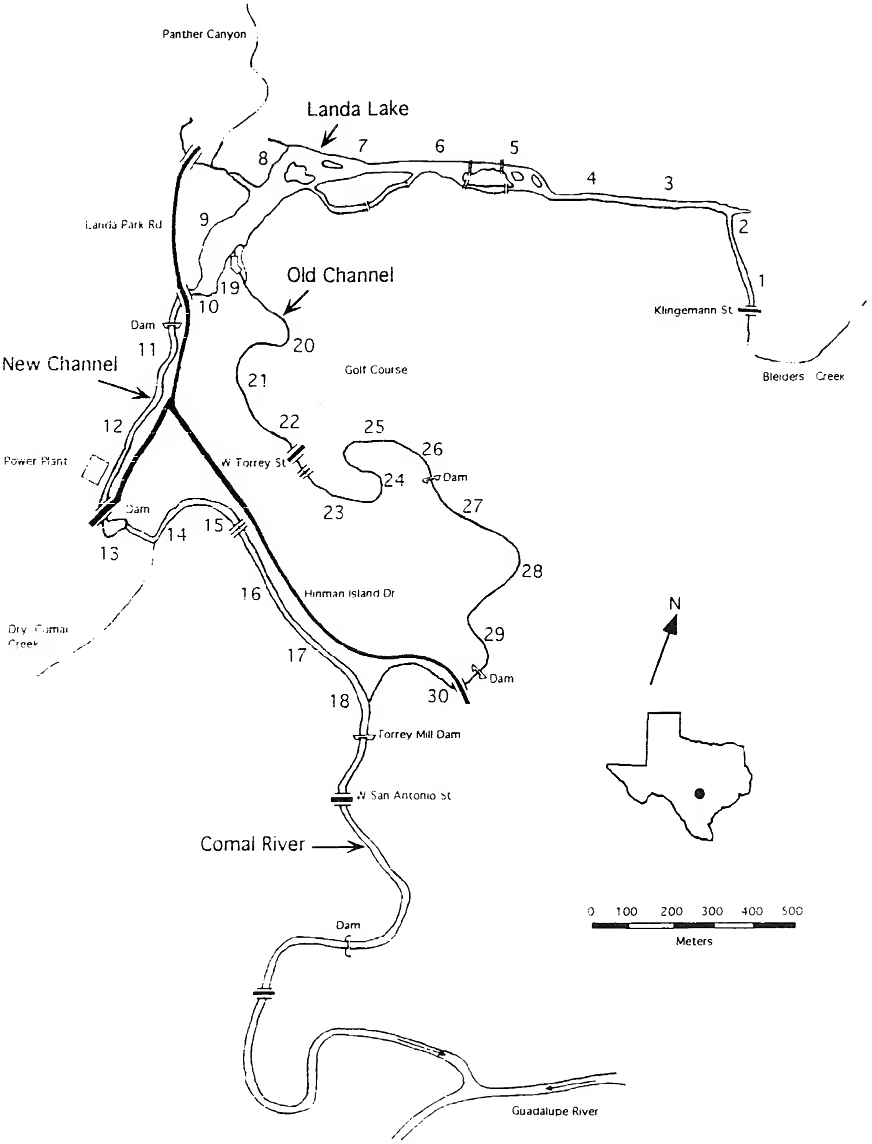

FIGURE 1. Map of the Comal River illustrating the transect locations. Modified from Brune (1981).

transect. Two rows of 10 m^2 cells constructed of nylon rope were stretched across the water at each transect (one on each side of the transect line) to form a sampling grid.

Habitat types within each cell were identified (Correll and Correll, 1975; Tarver et al., 1986) and classified into a series of cover classes, where class one represented 0-5% cover, two (5-25%), three (25-50%), four (50-75%), five (75-95%), and six (95-100%). To estimate area covered by each habitat type over the entire system, the midpoint of each cover class (i.e. 15% for cover class two) for each habitat type within each cell was multiplied by the cell area. Values for the habitat types were summed and divided by the total area sampled. These values were then multiplied by the total area of the system. Depth was recorded for each cell.

Fountain darters were sampled in each cell of transects 6, 8, 10, 11, 13, 15, and 17 in August 1990, and in each cell of transects 2, 4, 20, 22, 24, 26, 28, and 30 in June 1991 using square dip nets (0.09 m^2 and 0.37 m^2) with 1.6 millimeter mesh. Each dip consisted of pushing the net the length of the net opening over the substrate and lifting up through the water column. All fountain darters were counted and released.

Densities of fountain darters within all habitat types exhibited a skewed distribution due to a large proportion of dips yielding no fountain darters. Based upon inspection of untransformed residuals, the distribution resembled a negative binomial. Generalized Linear Interactive Modelling was used to calculate mean fountain darter density within each habitat type for estimating population size (Atkin et al., 1990). Differences in fountain darter densities among habitat types and depths were analyzed using a two-way analysis of variance followed by a multiple range test (Zar, 1984). Given the non-normal distribution, raw density data were log transformed prior to analysis.

The fountain darter population was estimated by summing the products of mean density by the estimated area of each habitat type. Total area represented in the population estimate was approximately 161,000 m^2.

Results and Discussion

Table 1 presents the estimated areas occupied by each habitat type recorded in this study. *Vallisneria americana* and *Cabomba caroliniana* were the dominant plants in Landa Lake; *Ludwigia* sp. and *Cabomba caroliniana* were dominant in the new channel; and *Ludwigia* sp. and filamentous algae were dominant in the old channel. The new channel had the greatest percentage of non-vegetated area (46%), followed by Landa Lake (33%) and the old channel (24%).

Fountain darters were found in greatest densities in filamentous algae (Table 2). Similarly, Schenck and Whiteside (1976) found fountain darters in the San Marcos River preferred areas where vegetation grew close to the substrate; specifically in *Rhizoclonium* sp. (filamentous algae).

Greater utilization of filamentous algae by fountain darters may result from a combination of factors. First, filamentous algae appears to provide protective cover for young and probably adults as well. Strawn (1956) spawned fountain darters in aquaria containing filamentous algae and found that few if any of the eggs laid in filamentous algae were eaten, whereas eggs laid on the sides of the tank frequently disappeared. He speculated that adults ate the eggs, and observed adults eating newly-hatched larvae. In aquaria crowded with adults, fountain darters hatched and grew to maturity when dense vegetation was provided. Additionally, filamentous algae may harbor food organisms. The diet of fountain darters consisted mainly of small aquatic invertebrates in the San Marcos River (Schenck and Whiteside, 1977a). During the present study, large numbers of aquatic invertebrates were consistently observed in filamentous algae.

TABLE 1. Estimated area (m^2) for each habitat type in the Comal River during the summer of 1990 (number of cells sampled in parenthesis).

Vegetation	Landa Lake (268)	Old Channel (135)	New Channel (105)	Total (508)
Amblistegium sp.	28	0	0	28
Bryophyta	669	0	358	1027
Cabomba caroliniana	16,606	69	3,927	20,602
Ceratopteris thalictroides	121	244	66	431
Chara sp.	1,497	68	0	1,565
Egeria densa	0	9	0	9
Filamentous algae	1,381	14,636	372	16,389
Hydrilla verticillata	0	0	19	19
Hydrocotyle sp.	0	9	0	9
Justicia americana	1,060	1,189	9	2,258
Ludwigia sp.	7,787	17,025	8,824	33,636
Ludwigia sp./filamentous algae	0	44	2,127	2,171
Myriophyllum sp.	0	44	0	44
Nuphar luteum	1,103	154	0	1,257
Potamogeton illinoensis	949	0	1,851	2,800
Riccia sp.	38	0	0	38
Sagittaria sp.	0	18	0	18
Typha latifolia	0	95	0	95
Utricularia sp.	25	0	0	25
Vallisneria americana	25,138	8	182	25,328
No vegetation	27,878	10,637	15,058	53,573
	84,280	44,249	32,793	161,322

A statistically significant difference ($P<0.0001$) was observed between fountain darter densities at 2.7 meters and all other depths. Significant depth by plant species interaction was also observed ($P<0.0001$); but, only two observations were associated with that depth in a single plant type (*Cabomba caroliniana*). Consequently, we concluded that the differences were not biologicially meaningful.

The mean population estimate for the Comal River upstream of Torrey Mill Dam was 168,078 with 95% confidence limits of 114,178 and 254,110. This seems reasonable given the fountain darter's fecundity and spawning characteristics, and the population size estimated for the San Marcos River by Schenck and Whiteside (1976). The population estimate indicates that the reintroduction effort was successful. Reproductive success was noted a few months after reintroduction when offspring were collected in the vicinity where adult fountain darters had been released (USFWS, 1984). Fountain darters appear to spawn throughout the year (Strawn, 1956; Schenck and Whiteside, 1977b). Schenck and Whiteside (1977b) collected females with mature ova throughout the year in the San Marcos River

TABLE 2. Mean fountain darter densities (fish/m^2) calculated for various habitat types in the Comal River during the summers of 1990 and 1991 (sample size in parenthesis). Significant differences ($P<0.05$) in density are followed by different letters. Densities reported for the San Marcos River (Schenck, 1975) are included for comparison.

Vegetation	Comal	San Marcos
Filamentous algae	4.99 (28) a	4.68
Chara sp.	2.15 (10) b	—
Ludwigia sp./filamentous algae	1.74 (31) b	—
Cabomba sp.	1.44 (84) b	0.69-3.15
Ludwigia sp.	0.88 (209) b	0.00-2.58
Ceratopteris sp.	0.54 (5) b	—
No vegetation	0.26 (126) b	0.00-0.90
Vallisneria sp.	0.21 (65) b	0.71
Justicia sp.	0.18 (15) b	—
Nuphar sp.	0.00 (4) b	—
Potamogeton sp.	0.00 (12) b	1.36

and reported two major spawning periods annually, one in August and another in late winter to early spring. In regards to fecundity, Brandt et al. (in press) reported a daily mean of 19.3 eggs released per female on days when eggs were released, and a maximum of 60 eggs released over a 24 hour period. Over a 54 day period, the mean number of days an individual deposited eggs was 13.5 (25%), and ranged from five (9%) to 27 (50%). Taking a conservative approach with their data in assuming eggs are released on nine percent of the days each year, and on each of these days a mean of 19 eggs are released per female, a total of 624 eggs would be released each year per female. Assuming the 457 fountain darters reintroduced to the Comal River had a male to female ratio of 1.39:1 (Schenck and Whiteside, 1977b), the 191 restocked females would have released 119,184 eggs the first year. Fountain darters reach sexual maturity at a relatively early age. Eggs were collected from fish about six months of age during laboratory spawning, and mature ova were found in fountain darters estimated at 3.5 months of age from the San Marcos River (Brandt et al., in press; Schenck and Whiteside, 1977b).

Despite the successful reintroduction effort, other factors might preclude it being replicated should the springs cease to flow again. During the 1950's drought when Comal Springs ceased to flow for five months, enduring pools sustained some segment of the aquatic plant community, providing a base for reestablishment. Should another drought cause cessation of spring flow, the assumption enduring pools will once again provide a source of aquatic plants is no longer valid. Since the introduction of giant rams-horn snails (*Marisa cornuarietis*) around 1983, plants in many areas of Landa Lake have been denuded of leaves or even grazed to the bottom (Horne et al., 1992). The snail population significantly increased during the low flows associated with the 1988-90 drought, leading researchers to conclude that spring flow may influence their numbers (T. Arsuffi, pers. comm.). If this is the case, low flow conditions may allow grazing by giant rams-horn snails to more severely impact or even eliminate the fountain darter habitat.

If another severe drought occurs, given present groundwater pumping rates, Comal Springs will again stop flowing, but for a longer period than in 1956 (Guyton and Associates, 1979). They also state that if pumpage from wells continues to increase, Comal Springs will go dry even without a major drought, since average withdrawals are slowly approaching average recharge. Lowering the water levels of the aquifer below the historic lows of 1956 could also result in intrusion of water with high dissolved solids from formations adjacent to the southern or down slope boundaries of the aquifer (Guyton and Associates, 1979; EARDC and SWTSU, 1988). An extended period without spring flow, the possibility of a shift in water quality, and the presence of giant rams-horn snails makes the likelihood of another successful reintroduction of fountain darters unlikely.

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GENERAL NOTES

OCCURRENCE AND SOUNDS OF FRASER'S DOLPHINS (*LAGENODELPHIS HOSEI*) IN THE GULF OF MEXICO

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Fraser's dolphin, *Lagenodelphis hosei*, is one of the least-known cetacean species. From its original description in 1956 (Fraser, 1956) to its "rediscovery" in 1973, it was known only from a single skeleton collected in Sarawak (Borneo). Perrin et al. (1973) provided the first description of external appearance and confirmed a tropical distribution in the Indian and Pacific oceans, based on seven new records. Since 1973, information on the biology of this species has accumulated slowly [summaries by Jefferson and Leatherwood (1993) and Perrin et al. (1993)]. Published accounts include only eight records from the Atlantic Ocean (three strandings and one sighting), and adjacent Caribbean Sea (three fisheries takes) and Gulf of Mexico (one mass stranding) (Fig. 1), and contain no information on sounds produced by these dolphins. This paper presents details of the first five observations of free-ranging animals in the Gulf of Mexico, describes sounds recorded during one of those observations, and presents details of a recent stranding on the Florida Gulf Coast.

A cooperative program on cetaceans of the northern Gulf of Mexico (Gulfcet) is being undertaken (1991-1993) by Texas A&M University, the U.S. Minerals Management Service, and the National Marine Fisheries Service through two of its southeastern laboratories. Data for this investigation are being collected during vessel and aerial surveys along preplanned transects. Visual searches with 25-power, pedestal-mounted binoculars are supplemented on many cruises by acoustic recordings using the Texas Institute of Oceanography's 183-m long linear towed array (Thomas et al., 1986) and an eight-channel Raycal V-Store tape recorder. The array consists of fore and aft high-frequency stations, with multiple hydrophone (Benthos AQ 20) traces centered at 5, 10 and 15kHz bandwidths. The tape recorder is operated at 9.53 cm per second, resulting in a 12.5 kHz bandwidth.

Four groups of Fraser's dolphins (including one tentative indentification) were encountered during Gulfcet cruises, two in 1992 and two in 1993, and a fifth was seen during a Gulfcet aerial survey in 1993. The first sighting was made from the Texas A&M University research vessel *Gyre* at 0925 on 24 May 1992, at 25° 13.978′N, 96°09.196′W. Water depth at the location was 1,750 meters, surface water temperature 26.4°C. A tight group of approximately 180-220 animals was detected through the binoculars at a bearing of 340° and an estimated distance of 300 meters from the vessel. During the next 10 minutes, as the vessel continued on course, the dolphins maintained tight ranks as they first approached the vessel from the eleven o'clock position, swam briskly in the opposite direction of the ship's heading until they were about 50 meters astern, and then turned and crossed beneath the towed array. Sounds were detected

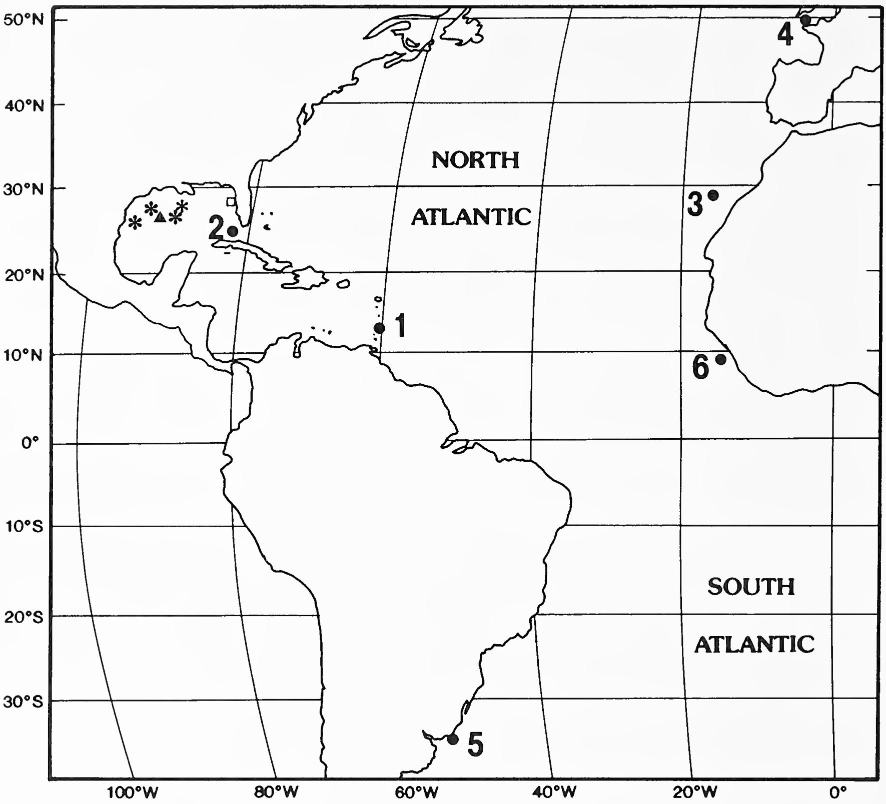

FIGURE 1. Records of Fraser's dolphins in the Atlantic Ocean, Caribbean Sea and Gulf of Mexico: (1) single animals harpooned off St. Vincent, Lesser Antilles, 2 October 1972 and 15 and 18 May 1976 (Caldwell et al., 1976); (2) 17 + stranded on Marquesas Key, Florida, in November 1981 (Hersh and Odell, 1986); (3) single animal stranded at the Canary Islands in August 1983 (Vonk and Martel, 1990); (4) 11 stranded in Brittany, France, on 29 May 1984 (Duguy, 1985; van Bree et al., 1986); (5) 4 animals stranded in Uruguay in March 1991 (Praderi et al., 1992); (6) sighting of 40 animals from a research vessel off West Africa (Tormosov et al., 1980); previously-unpublished sightings (asterisks); previously-unpublished tentative sighting (triangle); and previously-unpublished stranding (square) from the Gulf of Mexico.

and recorded. The vessel was then turned and slowed and the milling dolphin group approached for closer observation. Three large animals came to the ship and briefly rode the bow wave. Two had dark eye-to-anus stripes, but the third did not. The group appeared to contain individuals of various size-classes, but no obvious newborns were noted. By the time observation was terminated at 1010, the dolphins were in a tight formation swimming hurriedly away from the vessel with frequent leaping.

Sound recordings from the encounter were analyzed on a Kay model 5500 digital sonograph with a DC to 16 kHz frequency range. After the sounds were captured on the sonograph, they were passed to another computer for bandpass filtering using the Interactive Laboratory Software (ILS). The signals were anti-alias filtered and digitized at 35,000 samples/second. The eight whistles recorded were of two basic types: relatively long duration (0.4 - 0.5 seconds) single calls centered at either 11.4 - 13.4 kHz (Fig. 2A) or 7.64 - 8.88 kHz (Fig. 2B) and

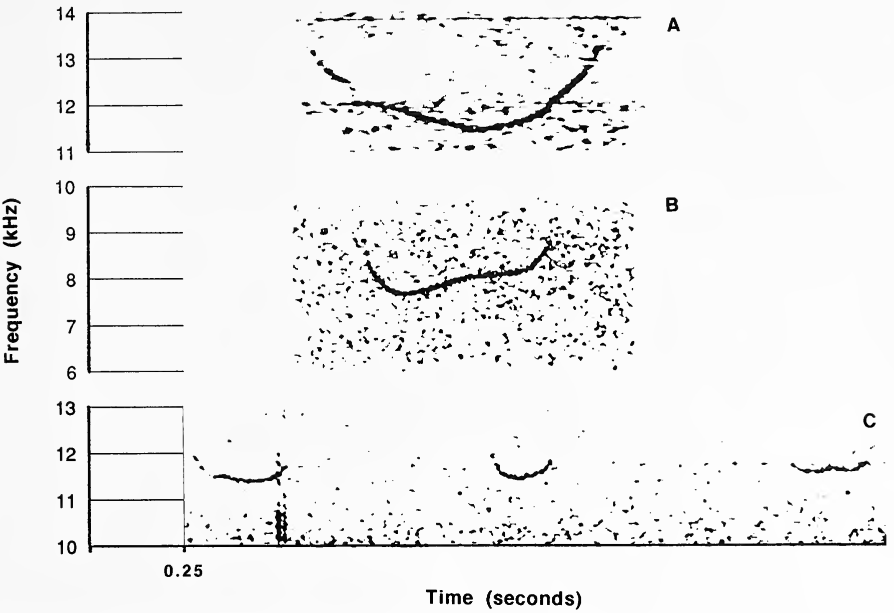

FIGURE 2. Whistles recorded in the presence of a group of 180-220 Fraser's dolphins on 24 May 1992. Single calls (0.4-0.5 s duration) 11.4-13.4 kHz (A), single calls (0.4-0.5 s duration) 7.64-8.88 kHz (B), 3 to 5 calls (0.2 s duration) 11.4-12.8 kHz (C).

groups of 3-5 relatively short duration (0.2 seconds) calls centered between 11.4 and 12.8 kHz (Fig. 2C). Overall, the whistles were relatively stereotyped. We do not know if they are representative of the repertoire of Fraser's dolphin. Compared to whistles recorded to date during the Gulfcet project, they are higher in frequency than typical whistles recorded from bottlenose dolphins, *Tursiops truncatus*, but similar in frequency to whistles of dolphins of the genus *Stenella*. Pulsed vocalizations, presumably used for echolocation, were also recorded. Unfortunately, the recording system was too bandlimited to permit any conclusions about the frequency content of those signals.

The second sighting was made from the NOAA Ship *Oregon II* at 1757 hr on 4 June 1992 at 26°22.34′N, 91°00.08′W. It involved a large (approximately 135 animals), mixed-species group of Fraser's dolphins (25%) and melon-headed whales, *Peponocephala electra* (75%), first detected through 25-power binoculars at a bearing of 9° and an estimated distance of 8 kilometers. Surface water temperature was 26.5 °C and depth was 2,057 meters. Initially, the animals were leaping and splashing. During the next few minutes, several small Fraser's dolphins came to the bow and rode the bow wave briefly before returning to the herd. The eye-to-anus stripe was evident on only a few of the Fraser's dolphins (Fig. 3A). The larger and more numerous melon-headed whales trailed the Fraser's dolphins throughout the observation.

The third sighting was made from the Louisiana Universities Marine Consortium's research vessel *Pelican* at 1913 hr on 1 June 1993 at 27°26.71′N, 94°09.95′W. A mixed-species group was detected through 25-power binoculars at an estimated 3.7 kilometers ahead of the vessel. The herd was overtaken in 9 minutes and observed at close range for 25 minutes. The aggregation contained an estimated 30-55 Fraser's dolphins, some of which rode the bow wave, and 105-195 melon-headed whales, which did not (although some did surf in the vessel's wake). In the fading light and rough seas, it was not possible to describe subtle details of the Fraser's dolphins' color pattern, but most of the animals seen well had only faint eye-to-anus stripes.

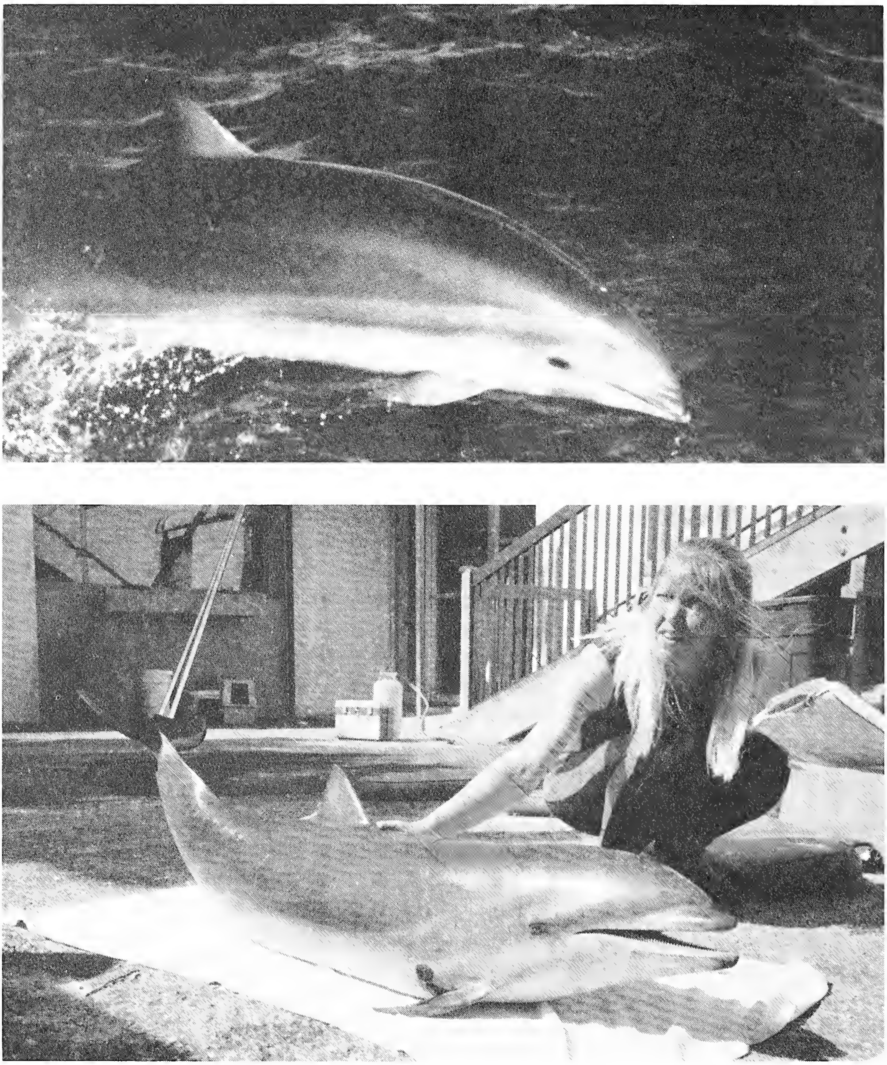

FIGURE 3. Fraser's dolphins in the Gulf of Mexico; a live animal at 26°22.34′N, 91°00.08′W, 4 June 1992 (A); and a 142.3cm male live-stranded at 28°05. 0′W, 82°49.0′W on 23 February 1993 (B). Note the subdued eye-to-anus stripe. [Scott R. Benson (A); courtesy of Clearwater Marine Science Center Aquarium Museum (B)].

Tape recordings were made using the towed array described above. The analyses of those tapes are not reported here, however, because it was not possible for us to ascertain for certain which of the sounds were produced by Fraser's dolphins and which were by melon-headed whales.

A fourth group, consisting of 17 Fraser's dolphins including three calves, was sighted during Gulfcet aerial surveys on 16 May 1993 at 27°47.4′N, 90°19.9′W at a depth of 835 meters. The Fraser's dolphins were identified by their small size, short beak, and the black eye-to-anus stripe that was clearly visible on some individuals. The loosely-aggregated subgroups of 2-3 Fraser's dolphins were leaping and traveling fast in a long line. They were along the western perimeter of a group of approximately 400 melon-headed whales, in widely dispersed groups of 5-10. A group of 13 rough-toothed dolphins, *Steno bredanensis*, was on the northeast perimeter. There were large east-to-west patches of *Sargassum* sp. along portions of both the northern and southern perimeters of the cetacean complex.

The fifth sighting took place on 4 September 1993, at 26°39.49′N, 93°30.23′W, during a survey aboard the *Pelican*. A group of about 20 dolphins was first observed at 312° and approximately 400 meters from the boat. Despite several attempts to approach the group for closer observation, the dolphins were very elusive and appeared to avoid the vessel. Very short beaks, robust bodies, small triangular dorsal fins, and some evidence of side stripes were observed on some animals. These animals are tentatively referred to *L. hosei*; however, we could not positively confirm species identification.

On 23 February 1993, a 142.3 cm Fraser's dolphin stranded alive on the northeastern tip of Honeymoon Island, Pinellas County, Florida (28°05.0′N, 82°49.0′W) (Fig. 3B). It died during transport to the Clearwater Marine Science Center Aquarium Museum in Clearwater, Florida, where it was measured and necropsied. The dolphin, a 42.6 kg male, had enlarged lymph nodes with white foci and showed signs of chronic pancreatitis. There were unidentified tapeworms internally and gooseneck barnacles, *Xenobalanus* sp., on the flukes. The stomach was empty. The most important external measurements (in cm - following Norris, 1961) are: snout to center of eye 26.9, to apex of melon 3.6, to center of blowhole 27.9, to flipper 35.6, to tip of dorsal fin 84.5, to center of umbilicus 77.5, to genital slit 99.0, and to anus 114.3; flipper anterior length 20.3, posterior length 13.3, and maximum width 5.0; dorsal fin height 11.4, and base 21.5; fluke width 30.4, and length 10.8; girth at axilla 81.2, at eye 66.0, maximum 85.0, at anus 46.9, and 30 cm anterior to fluke notch 35.5; projection of lower jaw < 0.6; length of gape 22.9; eye to gape 5.0, and to center of blowhole 17.7; blowhole length 1.0, and width 2.5; length of anal slit 3.7, and of genital slit 10.5. The tooth count was 37 (UL), 35 (UR), 39 (LL), 40 (LR). The skull, post-cranial skeleton, gonads, and miscellaneous tissues (muscle, blubber, liver, kidney, and brain) were saved (Specimen CMSC-04-93) (Terri Hepburn, *in litt.*, 10 August 1993).

Fraser's dolphins have now been found, albeit at apparent low densities, in all tropical oceans where there have been intensive and systematic surveys for cetaceans (Jefferson and Leatherwood, 1993). The Gulfcet program represents the first such surveys in oceanic waters of the northern Gulf of Mexico. Thus, it is not surprising that Fraser's dolphins have only recently been added to the list of diverse marine mammalian fauna documented to occur in the Gulf of Mexico, or that specimens of this species have occasionally been found stranded on Gulf beaches.

Participation of the Texas A&M University authors on the *Gyre* and *Pelican* cruises was supported by Texas A&M University and the Gulfcet project, under contract number 14-35-001-30619 from the Minerals Management Service. The use of trade names of commercial products does not constitute endorsement of recommendation for use. The authors thank the officers and crew of the *Gyre, Oregon II* and *Pelican* for their cheerful and competent assistance, the other marine mammal observers who participated in the cruises, and the Clearwater Marine Science Center, especially Terri Hepburn, for providing the data and photograph of the unpublished stranding. This represents Contribution No. 13 of the Marine Mammal Research Program, Texas A&M University.

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THE GRAY FOX, *UROCYON CINEREOARGENTEUS*, ON THE LLANO ESTACADO OF NEW MEXICO

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The gray fox (*Urocyon cinereoargenteus*) occurs widely in New Mexico and Texas where it is primarily associated with broken terrain or forested areas below the spruce-fir zone (Davis, 1974; Findley et al., 1975). Specimen records from New Mexican grasslands have been few and are apparently limited to areas where rock outcrops occur or juniper (*Juniperus* spp.) woodland encroaches (Findley et al., 1975). Aday and Gennaro (1973) reported no specimens from the grasslands of the Llano Estacado in eastern New Mexico, but provided a record from the western escarpment of the plain in Chaves County. Records for northwestern Texas (Packard and Bowers, 1970; Jones et al., 1987) include localities at the eastern and northern limits of the Llano Estacado in that state where the High Plains are delimited by broken terrain and stream valleys. Conversely, recent collections of gray foxes from Andrews and Midland counties, Texas (Choate et al., 1992), are from grassland habitat in the southern part of the Llano Estacado. Herein we provide additional records for the southern Llano Estacado in New Mexico.

On 3 October 1992 a vehicle-killed gray fox was collected at the junction of U.S. Highway 83 and State Highway 132, 21 km. E of Lovington, Lea County, New Mexico. The specimen, a young adult male, was collected about 50 kilometers northeast of the nearest part of the escarpment marking the southwestern boundary of the Llano Estacado. Habitat at the site is mesquite-grassland which is typical of much of eastern Lea County where rangeland has not been converted to cotton and sorghum farms. No stream valleys, rock outcrops, or other natural broken terrain were observed in the area of the collecting site nor are such features apparent on topographic maps of this part of the county.

We also examined a gray fox collected at 6.4 km. N of Hobbs, Lea County, in July 1989. The specimen, a very young juvenile female (total length, 532 mm; mass, 550 g), was acquired in an emaciated condition by the Hobbs animal shelter (S. C. Peurach, personal communication). Habitat at this collecting site is similar to that of the previous locality. Juvenile gray foxes have been reported to travel more than 80 kilometers from their natal area (Sheldon, 1953); animals on the Llano Estacado, therefore, could be individuals dispersing from distant den sites in rocky or wooded habitat. However, the immaturity of the Hobbs specimen suggests that a reproducing population of gray foxes probably exists in the grasslands of eastern Lea County.

Elsewhere within its range the gray fox is known to occur in semi-developed areas where it often does well around human habitations (e. g., Schmidly, 1983). Small caliche quarries and abandoned homesites with hedgerows occur throughout the Hobbs-Lovington area and these features may provide den sites in terrain that otherwise seems to offer little habitat for the species. Packard and Bowers (1970) suggested that the extensive eradication of the coyote (*Canis latrans*) on and near the Texas High Plains may have permitted incursions by the gray fox which apparently increases in numbers in the absence of coyotes (Davis, 1974). Perhaps the presence of the gray fox on the southern Llano Estacado is due to both rural development and predator-control activities that have favored colonization from more typical habitats adjacent to the plain.

Specimens collected in Lea County in 1989 and 1992 are preserved in the Museum of Southwestern Biology, University of New Mexico (MSB 61619 and 64939, respectively). We thank J. K. Frey and N. J. Scott, Jr. for comments on an earlier version of the manuscript, and W. L. Gannon and S. C. Peurach for technical assistance.

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REDESCRIPTION OF *EIMERIA SCELOPORIS* (APICOMPLEXA: EIMERIIDAE) FROM A NEW HOST *SCELOPORUS JARROVII* (SAURIA: PHRYNOSOMATIDAE)

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The Yarrow's spiny lizard, *Sceloporus jarrovii* Cope, 1875, inhabits rocky outcroppings in mountainous woodlands in southern Arizona, southwestern New Mexico and northern México (Stebbins, 1985). It has recently been placed in the family Phrynosomatidae (Frost and Etheridge, 1989). Previous parasitological studies on this lizard have examined gastrointestinal helminths (Goldberg and Bursey, 1990, 1992; Bursey and Goldberg, 1991a, b, 1992); malaria (Telford, 1970a; Mahrt, 1987; 1989) and ectoparasites (Goldberg and Holshuh, 1992, 1993; Goldberg and Bursey, 1993). Recently, we had an opportunity to examine this host for coccidian parasites.

We collected six *S. jarrovii* during June, 1989, near the Southwestern Research Station, Chiricahua Mountains, Cochise County, Arizona (31° 53'N, 109° 12'W, 1645 m elevation). Two of these were placed in the herpetology collection of the American Museum of Natural History (AMNH) (134218-134219). Thirty additional specimens, collected October, 1991, were examined from Kitt Peak, Baboquivari Mountains, Pima County, Arizona (31° 95'N, 111° 59'W, 1889 m elevation). Twenty of these were placed in the herpetology collection of the Natural History Museum of Los Angeles County (LACM) (140490-140509). Lizards were sacrificed and intestinal contents from each lizard were placed in individual vials of 2.5% (w/v) aqueous potassium dichromate solution. Oocysts were concentrated by flotation in sucrose solution (specific gravity 1.30) and examined using Nomarski interference-contrast optics. Twenty-five parasites were used for each measurement, which were made with a calibrated ocular micrometer and are presented as means in micrometers (μm), followed by the ranges in parentheses.

Coccidian oocysts were found in 2/6 (33%) *S. jarrovii* from the Chiricahua Mountains and 9/30 (30%) animals from Kitt Peak. The overall prevalence was 11/36 (31%) *S. jarrovii* passing oocysts. No other species of coccidian was found. Because we noted several morphologic details not reported in the original description, we present a description of this coccidian from this new host: Oocysts are ellipsoidal, 28.6 x 23.2 (25.6-31.2 x 20.0-27.2); shape index (length/width) 1.24 (1.03-1.50). Wall smooth, bilayered, 1.2-1.4 thick; outer layer 0.8-1.0; inner layer ca. 0.4. Micropyle, oocyst residuum, and polar granule absent, although numerous highly refractile granules of various sizes representing remnants of polar granules sometimes present and scattered among sporocysts. Sporocysts ellipsoidal, 10.1 x 7.9 (8.8-11.2 x 6.4-8.8); shape index 1.29 (1.10-1.47); wall smooth, single-layered, 0.5-0.6 thick. Stieda and substieda bodies absent. Irregular to ellipsoidal sporocyst residuum present, 5.5 x 3.9 (4.0-8.0 x 2.4-6.4), as compact mass composed of granules of various sizes. Sporozoites vermiform, tapered anteriorly, 10.0 x 3.1 (8.0-12.0 x 2.4-4.0) in situ, normally arranged head-to-tail in sporocyst with posterior ends reflexed. Spherical to subspherical anterior refractile body present, 1.9 x 1.7 (1.2-2.4 x 1.0-2.4); ellipsoidal posterior refractile body present, 3.5 x 2.5 (2.4-5.0 x 1.6-3.2). Nucleus situated between refractile bodies.

Oocysts of the coccidian reported herein are morphologically indistinguishable from those reported originally for *E. sceloporis* by Bovee and Telford (1965). We found sporocyst mean length to be slightly higher than in the original description, but this difference most likely represents measurements of many sporocyst length measurements taken from end-on views in the original description. We noted both anterior and posterior refractile bodies, not presented in the original description.

Eimeria sceloporis appears to have little species specificity within the genus *Sceloporus* as it has been reported previously to infect *Sceloporus clarki* Baird and Girard, 1852 from México, *S. occidentalis* Baird and Girard, 1852 from southern California and central Washington, *S. magister* Hallowell, 1854, from southern California, and *S. variabilis* Wiegmann, 1834 from México (Telford and Bovee, 1964; Bovee and Telford, 1965; Telford, 1970b; Clark and Colwell, 1973; Matuschka and Bannert, 1987; McAllister and Upton, 1989). *Sceloporus occidentalis* also harbors *Eimeria ahtanumensis*, which thus far has only been reported from Ahtanum Canyon, Yakima County, Washington (Clark, 1970; Clark and Colwell, 1973). This species is easily distinguished from *E. sceloporis* by its longer and more cylindrical oocysts.

There is little information on the prevalence of *E. sceloporis*. Clark and Colwell (1973) reported (72%) 101/140 adult and (82%) 31/38 juvenile *S. occidentalis* from Washington were infected with *E. sceloporis*. McAllister and Upton (1989) reported (100%) (2/2) prevalence for *E. sceloporis* in *S. variabilis* from Veracruz, México.

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ADDITIONAL RECORDS OF THE PLAINS HARVEST MOUSE (*REITHRODONTOMYS MONTANUS)* FROM THE EDWARDS PLATEAU, TEXAS

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The plains harvest mouse (*Reithrodontomys montanus*) reaches distributional limits in Texas along the southeastern portion of the Edwards Plateau and in eastern Texas (Schmidly, 1983). Apparently, *R. montanus* prefers prairie habitats with dense stands of weeds and grasses.

During fieldwork on the Edwards Plateau on 21 February 1993, we trapped a female *R. montanus* (TTU 63027) along a grassy fencerow adjacent to mesquite pastureland 7.5 mi. N, 10 mi. W London, in Menard County, Texas. Vegetation in this small valley consisted of Johnsongrass (*Sorghum halepense*), prickly pear (*Opuntia* sp.), live oak (*Quercus virginiana*), and mesquite (*Prosopis glandulosa*). The only other mammals collected at this locality were four *Sigmodon hispidus*.

Five additional specimens of *R. montanus* from the Edwards Plateau were found in the Collection of Recent Mammals, The Museum, Texas Tech University. Four of these mice (TTU 43919, 43920, 43921, 43922) were taken in Schleicher County, 3 mi. S Eldorado on 17 March 1986; and one (TTU 59294) was collected in Nolan County, 7 mi. S, 4 mi. E Sweetwater on 2 February 1991. Field notes from J. Knox Jones, Jr., include a description of the Schleicher County locality as a fencerow bordering a plowed field and mesquite pasture. Vegetative cover was described as "grassy and weedy". In these respects, the Schleicher County locality resembles the Menard County location approximately 55 miles to the east. Another *R. montanus* specimen of interest was discovered in the Midwestern State University Collection of Recent Mammals (MWSU 9254). This harvest mouse was taken from 10 mi. WSW Brady, McCulloch County.

These specimens represent the first reported occurrences of the plains harvest mouse from McCulloch, Menard, Nolan, and Schleicher counties, Texas. Additional records of *R. montanus* from Coke County (Simpson and Maxwell, 1989) and Tom Green County (Davis, 1974) help to fill a distributional gap for the species on the Edwards Plateau as reported by McAllister and Earle (1991).

Although plains harvest mice are trapped rarely on the Edwards Plateau and in the Big

Bend area of western Texas, they have been reported from several scattered localities (Davis, 1974; Jones, et al., 1993). Thus, habitats for *R. montanus* may be patchy, as proposed by McAllister and Earle (1991). Collecting efforts have only rarely been published for this large region and further collecting in suitable habitats may result in additional information on distribution and ecology of the species.

We thank Fred Stangl for access to the Collection of Recent Mammals at Midwestern State University, Wichita Falls, Texas and Clyde Jones for assistance with the manuscript. We are grateful to Robert C. Dowler and Terry C. Maxwell for providing additional records of the plains harvest mouse and for critically reviewing the manuscript.

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A RINGTAIL (*BASSARISCUS ASTUTUS*) RECORDED FROM SAN PATRICIO COUNTY, TEXAS

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Although ringtails (*Bassariscus astutus*) are common in central Texas, the southeastern distribution is unclear. Bailey (1905; pg. 182) reported "the civet cat is common all over Texas except the open plains country of the western half from Brownsville, Corpus Christi, Seguin, Austin, Brownwood and Grady westward". Hall (1981) interpreted this statement to mean that the range extended to Corpus Christi, although Bailey (1905) did not indicate whether any specimens had been recorded for those cities. Recently, Jones and Jones (1992) indicated the southern limit of the ringtail distribution occurs at the Rio Grande Valley and Coastal Plains of South Texas.

Anderson and Holzem (1992) reported a vehicle-killed ringtail in Refugio County, Texas. Although a ringtail had been sighted in this county in 1954 (Halloran, 1961), this was the first specimen collected southeast of Bee County (Anderson and Holzem, 1992). Almost two years before their discovery, on 21 March 1990, I captured a ringtail on the Rob and Bessie Welder Wildlife Foundation Refuge, San Patricio County, Texas (13.3 km. NE Sinton). This is the first record of a ringtail for that county.

The ringtail, a male weighing 1.2 kilograms, was captured in a wire-mesh, box livetrap baited with canned fish. It was released at the capture site after sexing and weighing. The event was recorded with photographs and witnessed by D. L. Drawe (Assistant Director, Rob and Bessie Welder Wildlife Foundation) and C. McDonough (University of California-Davis). Photographs have been verified by E. K. Fritzell (University of Missouri-Columbia) and J. G. Teer (Director, Rob and Bessie Welder Wildlife Foundation).

The trap was set in a riparian woodland community (Drawe et al., 1978) next to a fallen hackberry (*Celtis laevigata*). Two years of subsequent trapping (2,657 trap-nights) failed to produce additional ringtail captures, suggesting that local population densities were low or that the captured animal was a transient. Interviews with nearby residents indicated this was probably not a pet or recently released captive animal.

The capture site was approximately 16 kilometers west of the vehicle-killed ringtail reported by Anderson and Holzem (1992). This report provides additional information as to the status and distribution of ringtails in southeastern Texas. Comments on an earlier draft by J. T. Anderson and an anonymous reviewer improved the manuscript. Funding was provided by the Rob and Bessie Welder Wildlife Foundation, Edward K. Love Foundation, and the Missouri Cooperative Fish and Wildlife Research Unit. This paper is a contribution of the Missouri Cooperative Fish and Wildlife Research Unit (U. S. Fish and Wildlife Service, Missouri Department of Conservation, and University of Missouri-Columbia, cooperating).

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NEW DISTRIBUTIONAL RECORDS OF AMPHIBIANS AND REPTILES FROM TITUS COUNTY, TEXAS

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Dixon (1987) presented detailed range maps for Texas' amphibians and reptiles. For Titus County, in northeast Texas (Fig. 1), he reported that museum records existed for seven amphibian and 19 reptile species. In this note, new county records are reported for an additional seven amphibian species (six families, six genera) and nine reptile species (three families, eight genera) from Titus County. All specimens were collected by the author and are housed in The University of Texas at Arlington Collection of Vertebrates (UTA). Identifications were confirmed by P. D. Klawinski. Specimens are listed below, followed by common name (Collins, 1990), locality data, date of capture, and museum catalogue number.

CAUDATA: SIRENIDAE

Siren intermedia nettingi Goin, 1942 (Western Lesser Siren). 2 km (air) NE Winfield, Texas Utilities Monticello Lignite Mining Area (TUMLMA), Winfield North Mining Area (Winfield North), pond AR-32, (33° 10′ 23″ N, 95° 05′ 07″ W). 25 October 1992. UTA A-39593.

CAUDATA: AMPHIUMIDAE

Amphiuma tridactylum Cuvier, 1827 (Three-toed Amphiuma). 6 km (air) NE Winfield,

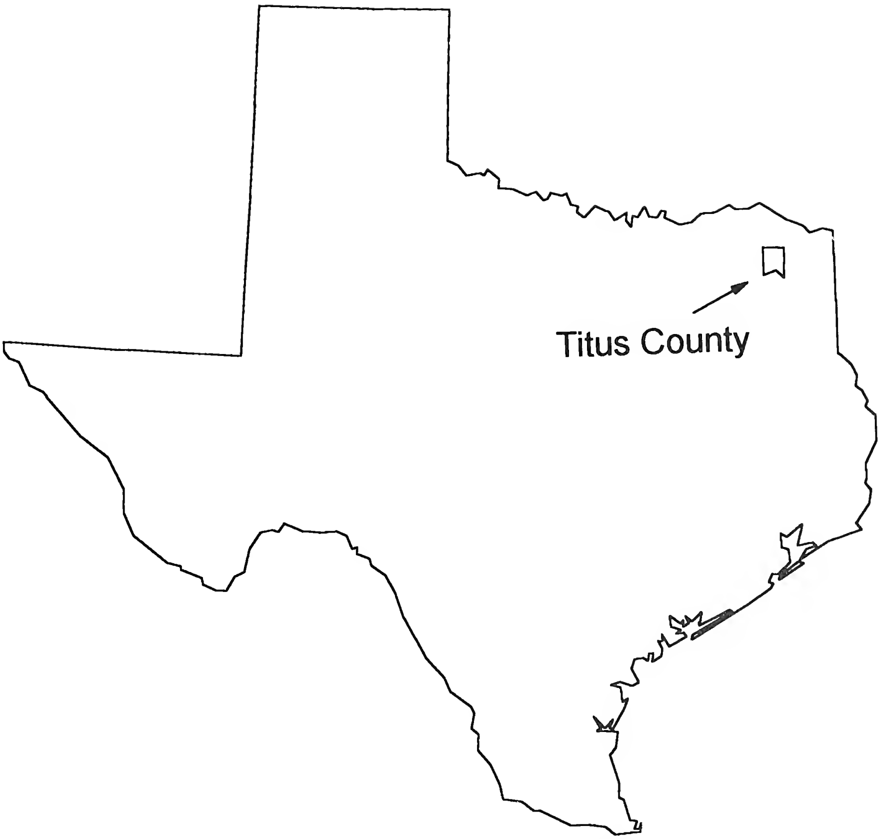

FIGURE 1. Location of Titus County, Texas.

TUMLMA, Winfield North, pond B-12, (33° 11′ 45″ N, 95° 02′ 20″ W). 23 June 1992. UTA-Live Collection.

ANURA: BUFONIDAE

Bufo americanus charlesmithi Bragg, 1954 (Dwarf American Toad). On County Road (Co. Rd.) NW 18, 1.3 rd. km E of junction with Co. Rd. NW 3, (33° 13′ 11″ N, 95° 06′ 31″ W). 11 June 1991. UTA A-37934.

Bufo woodhousii velatus Bragg and Sanders, 1951 (East Texas Toad). On Co. Rd. NW 18, 2.1 rd. km E of junction with Co. Rd. NW 3, (33° 13′ 06″ N, 95° 06′ 05″ W). 12 June 1991. UTA A-37930.

ANURA: HYLIDAE

Acris crepitans crepitans Baird, 1854 (Northern Cricket Frog). 2 km (air) NE Winfield, TUMLMA, Winfield North, pond AR-24, (33° 10′ 41″ N, 95° 05′ 36″ W). 11 July 1991. UTA A-37763.

ANURA: RANIDAE

Rana clamitans clamitans Latreille, 1801 (Bronze Frog). 2 km (air) NE Winfield, TUMLMA, Winfield North, pond AR-24, (33° 10′ 41″ N, 95° 05′ 36″ W). 12 Aug. 1992. UTA A-39590.

ANURA: MICROHYLIDAE

Gastrophryne carolinensis (Holbrook, 1836) (Eastern Narrowmouth Toad). On Co. Rd. NW 18, 0.6 rd. km E of junction with Co. Rd. NW 3, (33° 13′ 23″ N, 95° 06′ 51″ W). 11 June 1991. UTA A-37928.

TESTUDINES: EMYDIDAE

Pseudemys concinna metteri Ward, 1984 (Missouri River Cooter). 2 km (air) NE Winfield, TUMLMA, Winfield North, pond AR-32, (33° 10′ 23″ N, 95° 05′ 07″ W). 12 Oct. 1992. UTA R-34117.

Terrapene ornata ornata (Agassiz, 1857) (Ornate Box Turtle). On Farm to Market (FM) Rd. 1734, 0.5 rd. km N of junction with Co. Rd. NW 13, (33° 11′ 22″ N, 95° 05′ 38″ W). 18 May 1991. UTA R-30144.

SQUAMATA: SERPENTES: COLUBRIDAE

Elaphe obsoleta lindheimerii (Baird and Girard, 1853) (Texas Rat Snake). 4.2 km (air) NE Winfield, TUMLMA, Winfield North, 0.2 km NW of pond B-6, (33° 12′ 01″ N, 95° 04′ 14″ W). 23 July 1992. UTA R-33945.

Heterodon nasicus gloydi Edgren, 1952 (Dusty Hognose Snake). Dead on road (DOR) at junction of Co. Rd. NW 13 and FM Rd. 1734, (33° 11′ 26″ N, 95° 05′ 44″ W). 15 May 1991. UTA R-32669.

Masticophis flagellum flagellum (Shaw, 1802) (Eastern Coachwhip). DOR on Co. Rd. NW 15, 1.3 rd. km N of junction with FM Rd. 1734, (33° 12′ 19″ N, 95° 04′ 40″ W). 22 Oct. 1991. UTA R-32657.

Nerodia erythrogaster flavigaster (Conant, 1949) (Yellowbelly Water Snake). 3.2 km (air) NE Winfield, TUMLMA, Winfield North, pond AR-3, (33° 11′ 04″ N, 95° 04′ 28″ W). 12 April 1991. UTA R-32680.

Nerodia fasciata confluens (Blanchard, 1923) (Broad-banded Water Snake). On Co. Rd. NW 13, 2.6 rd. km N of junction with FM Rd. 1734, (33° 12′ 42″ N, 95° 05′ 34″ W). 14 May 1991. UTA R-32679.

Storeria dekayi texana Trapido, 1944 (Texas Brown Snake). 3.2 km (air) NE Winfield, TUMLMA, Winfield North, 0.1 km W of pond A-13, (33° 10′ 35″ N, 95° 04′ 14″ W). 23 Sept. 1991. UTA R-32688.

SQUAMATA: SERPENTES: VIPERIDAE

Agkistrodon piscivorus leucostoma (Troost, 1836) (Western Cottonmouth). Found dead. 4.4 km (air) NE Winfield, TUMLMA, Winfield North, pond BR-18, (33° 11′ 45″ N, 95° 04′ 03″ W). 19 June 1992. UTA R-34124.

Texas Utilities Services provided financial support during my studies in Titus County. Stephen W. Shackleford, of the Texas Department of Transportation, helped determine coordinates for many of the localities.

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NEW LOUISIANA RECORDS FOR FRESHWATER MUSSELS (UNIONIDAE) AND A SNAIL (PLEUROCERIDAE)

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Freshwater mussels (Bivalvia: Unionidae) and snails (Gastropoda: Viviparidae and Pleuroceridae) are often illusive and difficult to discover even with years of search. Louisiana has been searched for mussels for more than 100 years (Vidrine, 1985; 1993), and it possesses a relatively diverse fauna. During a fish survey in Bayou Bartholomew, the senior author discovered a large mussel bed in the river. The water level in the river remained high all summer, in 1992, but September and October provided a low water period convenient for a rather extensive search for freshwater mollusks. The Louisiana portion of Bayou Bartholomew had apparently never been searched extensively for freshwater mussels and snails.

Bayou Bartholomew, a tributary of the Ouachita River, drains a relatively large area of southeastern Arkansas and most of a single parish, Morehouse Parish, in northern Louisiana. The system drains an intensively farmed area, in which cotton is a major crop. Portions of the Bartholomew drainage in Arkansas were studied by Gordon et al. (1980). Species reported were : *Megalonaias nervosa* (Rafinesque, 1820), *Amblema plicata* (Say, 1817), *Plectomerus dombeyanus* (Valenciennes, 1827), *Pleurobema pyramidatum* (Lea, 1840), *Pyganodon grandis* (Say, 1829), *Obliquaria reflexa* Rafinesque, 1820, *Obovaria olivaria* (Rafinesque, 1820), *Leptodea fragilis* (Rafinesque, 1820), *Potamilus purpuratus* (Lamarck, 1819), *Lampsilis teres* (Rafinesque, 1820), *Lampsilis siliquoidea* (Barnes, 1823), and *Lampsilis hydiana* (Lea, 1838). The only records from Bayou Bartholomew in the state of Louisiana known to the authors were those of Moore (1909) and Vanatta (1910). Moore (1909) reported three species from Indian middens: *P. purpuratus*, *L. teres* (a small vessel), and *M. nervosa* (a shell hoe). The first was from Keno Plantation, while the latter two were from Ward Place. Both locations are within Morehouse Parish. Vanatta (1910) reported *P. dombeyanus* at Seven Pine Landing on Bayou Bartholomew in Morehouse Parish.

Hand searching for freshwater mussels and snails was primarily done in a 6.0 km stretch of Bayou Bartholomew extending from the western edge of Chemin A Haut State Park downstream to approximately 1.5 km downstream from the intersection of the bayou with Rte. U.S. 425, north of Log Cabin, Morehouse Parish, Louisiana. Further searching was done approximately 15 river km upstream and downstream. Mussels were relatively scarce at these upstream and downstream localities, so collecting was concentrated in the 6.0 km stretch. Mussels were aggregated in beds among gravel riffle zones and mud/sand zones, and snails were commonly dispersed among the mussels.

We employ the mussel and snail names of the most recent fisheries list for North America (Turgeon et al., 1988), with the exception that the genus *Pyganodon* as resurrected by Hoeh (1990) is used in place of *Anodonta*. Voucher specimens of the mussel species and *Pleurocera canaliculata* (Say, 1821) were deposited in the Mississippi Museum of Natural Science, Jackson, MS. The mollusk specimens were identified by the authors and verified by Paul Hartfield (Endangered Species Office, Jackson, MS) and John Harris (Highway and Transportation Department, Little Rock, AR).

Twenty-nine species of freshwater mussels were found in this portion of Bayou Bartholomew. Five species are reported for the first time in Louisiana and three species are recorded for only the second time in Louisiana. The five new state records are: *Lampsilis abrupta* (Say, 1831), *Lampsilis cardium* (Rafinesque, 1820), *Lampsilis siliquoidea* (Barnes, 1823), *Obovaria olivaria* (Rafinesque, 1820), and *Ptychobranchus occidentalis* (Conrad, 1836). *Lampsilis abrupta* is a federally listed endangered species (USFWS, 1982). Three species, *Quadrula*

TABLE 1. Freshwater mussels, _Corbicula_, and snails found in a 6.0 km stretch of Bayou Bartholomew at Rte. U. S. 425, north of Log Cabin, Morehouse Parish, Louisiana, September-October 1992. Numbers in parentheses represent the numbers of specimens examined for parasitic mites.

- Unionidae
  - Anodontinae
    - _Pyganodon grandis_ (Say, 1829) (1)
    - _Arcidens confragosus_ (Say, 1829) (7)
  - Ambleminae
    - Amblemini
      - _Amblema plicata_ (Say, 1817) (7)
      - _Megalonaias nervosa_ (Rafinesque, 1820) (8)
      - _Plectomerus dombeyanus_ (Valenciennes, 1827) (6)
      - *_Quadrula cylindrica cylindica_ (Say, 1817) (3)
      - *_Quadrula metanevra_ (Rafinesque, 1820) (12)
      - _Quadrula pustulosa_ (Lea, 1831) (17)
      - _Quadrula quadrula_ (Rafinesque, 1820) (10)
      - _Tritogonia verrucosa_ (Rafinesque, 1820) (8)
    - Pleurobemini
      - _Elliptio dilatata_ (Rafinesque, 1820) (27)
      - _Fusconaia ebena_ (Lea, 1831) (20)
      - _Fusconaia flava_ (Rafinesque, 1820) (18)
      - _Pleurobema pyramidatum_ (Lea, 1840) (7)
    - Lampsilini
      - *_Ellipsaria lineolata_ (Rafinesque, 1820) (1)
      - ***_Lampsilis abrupta_ (Say, 1831) (2)
      - **_Lampsilis cardium_ (Rafinesque, 1820) (2)
      - _Lampsilis hydiana_ (Lea, 1838) (2)
      - _Lampsilis satura_ (Lea, 1852) (4)
      - **_Lampsilis siliquoidea_ (Barnes, 1823) (1)
      - _Lampsilis teres_ (Rafinesque, 1820) (6)
      - _Leptodea fragilis_ (Rafinesque, 1820) (4)
      - _Obliquaria reflexa_ Rafinesque, 1820 (1)
      - **_Obovria olivaria_ (Rafinesque, 1820) (2)
      - _Potamilus purpuratus_ (Lamarck, 1819) (4)
      - **_Ptychobranchus occidentalis_ (Conrad, 1836) (5)
      - _Truncilla donaciformis_ (Lea, 1828) (0)
      - _Truncilla truncata_ Rafinesque, 1820 (5)
      - _Villosa lienosa_ (Conrad, 1834) (2)
- Corbiculidae
  - _Corbicula fluminea_ (Mueller) (5)
- Viviparidae
  - _Campeloma decisum_ (Say, 1816) (5)
  - _Viviparus subpurpureus_ (Say, 1829) (5)
- Pleuroceridae
  - **_Pleurocera canaliculata_ (Say, 1821) (5)

* not reported in Louisiana since Moore (1908) and Vanatta (1910)
** new state records (Louisiana)
*** new state record (Louisiana) and federally listed as an endangered species

cylindrica cylindica (Say, 1817), *Quadrula metanevra* (Rafinesque, 1820), and *Ellipsaria lineolata* (Rafinesque, 1820), have not been reported in Louisiana since 1910 (Vanatta, 1910) and are new records for Bayou Bartholomew. All of the species found are listed in Table 1 with annotation regarding the new and repeat state records. *Corbicula fluminea* (Mueller) (Bivalvia: Corbiculidae), an introduced Asian clam, was common in this portion of Bayou Bartholomew.

Three species of large snails were found among the mussels in the 6.0 km section of Bayou Bartholomew: *Campeloma decisum* (Say, 1816), *Viviparus subpurpureus* (Say, 1829), and *P. canaliculata*. No records of pleurocerid snails from the state of Louisiana were known (Burch, 1989). Thus, the *P. canaliculata* is a new state record for the species and the family.

Varied sized lots of the different mussels, *Corbicula*, and snails (212 specimens, 32 species) were searched for parasitic mites (Acari: Unionicolidae: *Unionicola* and Najadicolinae: *Najadicola*). No mites were found in the specimens. The numbers of individual specimens searched are listed in Table 1. Typically a diverse community of freshwater mussels has approximately 60.0% of its mussels infested with mites (Vidrine, 1989; 1990; Vidrine and Wilson, 1991). We do not know why mites are absent at this locality, but their absence may be linked to agricultural chemicals used in the intensive cotton farming in the drainage.

The mussel and snail assemblage of Bayou Bartholomew at this station closely resembles that described for the Saline River in Arkansas (Gordon 1981; Harris and Gordon, 1987; 1990), and may indicate that Bayou Bartholomew represents, zoogeographically, the southern tip of the Ozarkian subprovince of the Mississippi Interior Basin. Bayou Bartholomew is the host for a possible relict community of freshwater mussels and snails. We suggest that this river and indeed all of northeastern Louisiana receive intensive survey to disclose the biotic diversity in this area.

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INDEX TO VOLUME 45 (1993), THE TEXAS JOURNAL OF SCIENCE

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This index has separate subject and author sections. Key (or other important) words or phrases are followed by an abbreviated title and initial page number of each article in which they appeared. Scientific names of organisms have been indexed only to genus, followed by the initial page number of each article in which that generic name was mentioned. Generic names selected by authors as key words or used in titles, however, were treated as all other key words indexed. Specific geographic areas or localities used by authors in titles or as key words were entered as index headings with the exception of Texas, because the majority of articles in the *Journal* dealt with that state. All states (or countries) other than Texas appear as separate headings in the index. Vernacular names of biological species, ordinal and familial names, and chemical compounds were indexed only if used in titles or as key words.

The author index includes the names of all authors, each followed by the initial page number of the appropriate article. Also included is a list of the names of colleagues, with the exception of the editorial committee, who kindly served as reviewers of articles submitted for this volume of the *Journal*.

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Davis, G. L. 1975. The mammals of the Mexican state of Yucatan. Unpublished Ph.D. dissertation, Texas Tech Univ., Lubbock, 396 pp.

Jones, T. L. 1971. Vegetational patterns in the Guadalupe Mountains, Texas. Amer. J. Bot., 76:266-278.

———. 1975. An introduction to the study of plants. John Wiley and Sons, New York, xx+386 pp.

Jones, T. L., A. L. Bain, and E. C. Burns. 1976. Grasses of Texas. Pp. 205-265, *in* Native grasses of North America (R. R. Dunn, ed.), Univ. Texas Studies, 205:xx+1-630.

Smith, J. D. 1973. Geographic variation in the Seminole bat, *Lasiurus seminolus.* J. Mamm., 54:25-38.

Smith, J. D., and G. L. Davis. 1985. Bats of the Yucatan Peninsula. Occas. Papers Mus., Texas Tech Univ., 97:1-36.

Consecutively-paged journal volumes and other serials should be cited only by volume number and pagination. Serials with more than one number and that are not consecutively paged should be cited by number as well (Smiths. Misc. Coll., 37(3):1-30).

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