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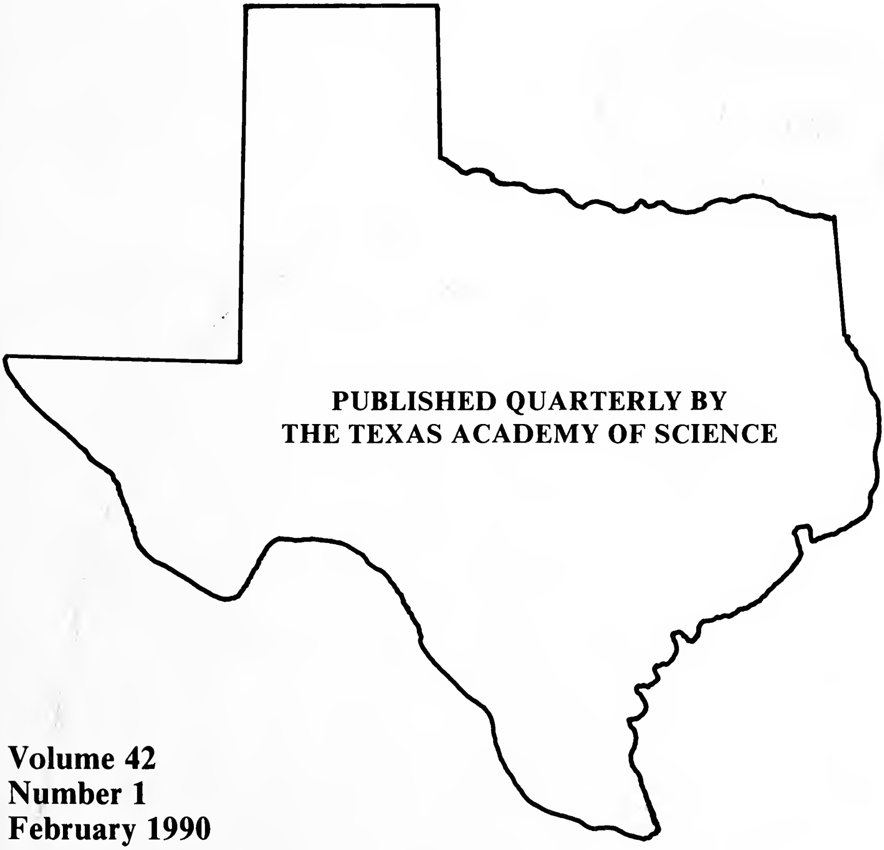

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General Notes

THE TEXAS JOURNAL OF SCIENCE
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FEASIBILITY OF PENAEID SHRIMP CULTURE IN INLAND SALINE GROUNDWATER-FED PONDS

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Abstract.—Saline groundwater in Willacy County of southern Texas was used to polyculture juvenile (1.2 ± 0.18 grams) *Penaeus vannamei* and five-day-old postlarval *P. setiferus* in earthen ponds. Initial stocking densities of 50,700 juvenile *P. vannamei* and 247,000 *P. setiferus* per hectare produced 871.7 ± 14.28 kilograms per hectare for a 120-day grow-out period. Survival of *P. setiferus* was less than one percent. Final size and survival of *P. vannamei* were 19.9 ± 0.71 grams and 86.7 ± 4.53 percent, respectively. Despite the poor performance of *P. setiferus, P. vannamei* production data compared favorably with that of a bay-fed system stocked with *P. vannamei* from the same population, indicating that this particular source of saline groundwater can be used for culture of at least one penaeid species. Use of chemically similar bodies of saline groundwater for mariculture over a more widespread area of Texas is encouraged. *Key words: Penaeus* sp.; saline groundwater; aquifer; mariculture.

World-wide, salt adversely affects more than 30 percent of the rangeland and 27 percent of the cropland by reducing the potential of these areas to produce traditional animal and plant agricultural crops (Rains, 1979; Kelley, 1982). About two-thirds of the continental United States are underlain by saline water (Feth et al., 1965; Feth, 1970). Excluding those coastal areas directly inundated by ocean or bay waters, the major salt-affected areas in the U. S. are associated with the Great Salt Lake basin, interior valleys of California, and with the Colorado and Rio Grande drainage basins (Chapman, 1960). Vast areas of Texas are underlain by saline groundwater in the form of subsurface and near surface aquifers and outcrops. The geology of 29 principal saline aquifers (that is, those containing 3000 parts per million or more of total dissolved solids and that are capable of producing a minimum of 378 liters per minute) have been described in Texas (Winslow and Kister, 1956; Texas Water Development Board, 1972). Mariculture, rather than traditional agriculture, has been suggested as a means of improving productivity of these salt-affected lands (Stickney and Davis, 1981; Issar et al., 1983; Payne, 1983; Sarig, 1984).

The most familiar mariculture-related use of inland saline waters has been the harvesting of *Artemia*. Within a more strict mariculture context, microalgae have been cultured for both pharmacological and aquacultural purposes in Israel (Goldman, 1979; Pasternak, 1982) and the U. S. (Walsh et al., 1985; Goldstein, 1986a). The culture of higher species in inland saline groundwater is limited mainly to studies on tilapia (Granoth and Porath, 1983; Hamza and Zaki, 1987) and gilthead sea bream (Pasternak, 1982) in Israel and Egypt, and, to a lesser extent, oyster (Goldstein, 1986b), rainbow trout, and red drum (J. Davis, Texas Agricultural Extension Service, Texas A&M University, personal communication) in the U. S.

In the 1981 draft of the Texas Aquaculture Plan, saline groundwater was identified as an untapped resource and it was suggested that high priority be given to determining the suitability of such water for mariculture (Stickney and Davis, 1981). Since that report, no formal research investigations have been carried out on the use of Texas saline groundwater for shrimp mariculture. Results of unpublished studies conducted since the early 1970s indicate that saline groundwater in some parts of western Texas may be suitable for crustacean culture on a commercial scale (J. Davis, Texas Agricultural Extension Service, Texas A&M University, personal communication). We examined the growth of penaeids in saline water originating from an inland groundwater source in southern Texas. For the purposes of documentation, the same population of *P. vannamei* was stocked into ponds near Corpus Christi, which received saline water from the Laguna Madre Bay. The bay system acted as a control, not in the true sense of duplication, but rather as a means of assessing the potential of the population to adapt to different conditions.

MATERIALS AND METHODS

Groundwater System

The 0.2-hectare ponds were located west of Raymondville, Texas, in Willacy County, approximately 40 kilometers inland from the Laguna Madre (98°57′ W, 26°28′ N). Willacy County is underlain by the Gulf Coast Tertiary Aquifers, which are uniquely characterized by an abundance of sand and shale, minor amounts of limestone, and lack of carbonates. Salinity varies with depth (zero to 3048 meters) and from less than five to 120 parts per thousand (Texas Water Development Board, 1972). The source of saline water used in this study was an aquifer that flowed over a layer of caliche clay within four meters of the land surface. The ponds were dug directly into the aquifer layer, resulting in a continuous flow of water through all walls and the bottom, which prohibited complete draining and drying of the pond bottom between stockings. Water depth was a constant 4.5 meters.

The ionic composition of this saline (28.3 parts per thousand) groundwater (Table 1) was similar to that of both natural seawater (Sverdrup et al., 1942) and ponds fed from the Laguna Madre Bay system. The saline groundwater was of the sodium chloride type, which typifies groundwater samples in the U. S. having 20,000 parts per million or more of total dissolved solids (Feth et al., 1965). The main differences between the ionic compositions of the saline groundwater and natural seawater were the amounts of calcium and sodium.

Each of the two ponds was stocked with both juvenile *P. vannamei* (50,700 shrimp per hectare) and five-day-old postlarval *P. setiferus* (247,000 shrimp per hectare). *P. setiferus* (less than 0.01 gram) had been reared at the Texas A&M University Larviculture facility in Galveston from wild-caught broodstock that originated from the Gulf of Mexico near Port Aransas. *P. vannamei* (1.2 ± 0.18 grams), spawned from Mexican maturation broodstock, had been reared in a 0.15-hectare nursery pond at the Texas A&M University Pond facility in Corpus Christi for 45 days at a density of 250,000 postlarvae per hectare. Both 0.2-hectare ponds were harvested 120 days after stocking.

TABLE 1. Chemical composition of saline groundwater, Laguna Madre water and natural seawater.

Ion or element	Groundwater mg/l	Groundwater %	Laguna Madre mg/l	Laguna Madre %	Natural SW[a] mg/l	Natural SW[a] %
Calcium	615	6.6[b]	425	3.4[b]	400	3.2[b]
Magnesium	1275	13.7[b]	1148	9.0[b]	1272	10.1[b]
Potassium	152	1.6[b]	371	2.9[b]	380	3.0[b]
Sodium	7291	78.1[b]	10741	84.7[b]	10561	83.7[b]
Bicarbonates	468	2.5[c]	781	3.6[c]	140	0.6[c]
Chlorides	16208	85.6[c]	18425	85.1[c]	18980	87.2[c]
Sulfates	2253	11.9[c]	2441	11.3[c]	2648	12.2[c]
Copper	<0.05		<0.05		0.001-0.01	
Manganese	0.05		0.06		0.001-0.01	
Zinc	<0.05		<0.05		0.005	
pH	8.2		8.0		7.5-8.4	
Salinity (ppt)	28.3		34.3		34.3	

[a] After Sverdrup et al., 1942: 173, 176-177, 194.

[b] Percent of each ion out of the total amount of calcium, magnesium, potassium and sodium in each sample.

[c] Percent of each ion out of the total amount of bicarbonates, chlorides and sulfates in the sample.

The 0.2-hectare ponds were not fertilized prior to, or during, the experiment. Because this was the first stocking into these ponds, any nutrient productivity was related to that occurring naturally in the water, was transferred with shipping water at stocking, or was influenced by artificial feed or proximity to cropland runoff. Salinity (refractometer) and transparency (Secchi disc) were recorded daily; temperature and dissolved oxygen (YSI model 58) were recorded daily at 0600 and 1700 hours. An aeration system consisting of two three-meter-long sections of diffuser hoses connected to an air compressor was installed by the middle of the experimental period and used daily thereafter.

A commercially prepared, pelleted feed (24 percent protein, Texas Farm Products) was fed twice daily. Feeding was suspended whenever the dissolved oxygen level fell below 3.0 parts per million. During the first four weeks of the experiment, the feeding level was determined according to the schedule in Table 2. Thereafter, the rate was determined according to the schedule of Chamberlain et al. (1981), based on weekly samples of 30 individuals. For feeding purposes, survival was estimated to decrease to 93 percent (*P. vannamei*) and 72 percent (*P. setiferus*) by week five, with an additional one and three percent decrease, respectively, each week thereafter.

Bay System

The 0.10 hectare ponds were located at the Texas A&M University Shrimp Mariculture Research facility (described by Conte, 1975) near Corpus Christi, Nueces County, Texas. All ponds were dried and tilled prior to filling. Seawater used to fill and maintain pond levels was pumped through 500-micron filter bags directly from the Laguna Madre Bay. Approximately two weeks prior to stocking, each pond was fertilized with 77 kilograms per hectare of urea, 14 liters per hectare of 54 percent phosphoric acid, and 1360 kilograms per hectare of dried cow manure. Applications of inorganic fertilizers were applied as needed to maintain a Secchi disc depth of 30 centimeters. Freshwater was added as needed to

TABLE 2. Schedule used to determine feeding levels in groundwater-fed ponds during the first four weeks of culture, prior to initiation of weekly sampling.

Species	Week	Assumed % survival	Estimated weight (g)	% body weight
P. vannamei	0	100.00	1.0	—
	1	97.00	1.5	19.0
	2	96.00	2.5	12.4
	3	95.00	3.5	9.4
	4	94.00	4.5	7.6
P. setiferus	0	100.00	0.01	—
	1	93.75	0.10	19.0
	2	87.50	0.20	19.0
	3	81.25	0.35	19.0
	4	75.00	0.60	19.0

TABLE 3. Stocking density of *P. vannamei* and hydrological variables (mean ± SD) in the groundwater-fed ponds and the bay-fed ponds.

		Groundwater system		Bay system	
		Pond A	Pond B	n=3	n=3
Stocking density (number per hectare)		50,000	50,000	25,000	75,000
Salinity (ppt)		32±2	23±1	25±2	25±2
Temperature (C)	AM	24.8±2.5	24.7±2.4	25.9±2.4	25.9±2.5
	PM	27.8±2.2	28.1±1.6	29.3±3.0	29.4±3.0
Dissolved oxygen (ppm)	AM	3.4±1.6	3.5±1.2	4.9±0.9	5.0±0.8
	PM	7.0±2.7	9.4±1.9	0.4±1.2	9.2±1.1
Transparency (cm)		54.3±16.3	38.3±7.8	40.2±12.5	43.6±13.0

maintain salinity near 25 parts per thousand. Hydrological data (temperature, salinity, dissolved oxygen and transparency) were monitored as described for the groundwater system.

Juvenile *P. vannamei* (1.60 ± 0.28 grams), from the same population used to stock the groundwater system, were stocked into ponds, in triplicate, at 25,000 and 75,000 shrimp per hectare (Table 3). Feed was distributed at a rate of eight kilograms per hectare per day for the first two weeks. Thereafter, feed was distributed according to the schedule of Chamberlain et al. (1981), based on weekly subsamples of about 0.3 percent of the initial stocking density and assuming a survival of 70 percent. Feeding was suspended when dissolved oxygen levels fell below 3.0 parts per million. Ponds were harvested 115 days after stocking.

Differences in mean values between systems were analyzed by general linear regression using the 1988 version of PC-SAS (Statistical Analysis System, Cary, Indiana) and considered significant at the five percent level.

RESULTS

Hydrology

Hydrological data from both the groundwater and bay systems are summarized in Table 3. Generally, hydrological conditions in groundwater-fed pond B more closely resembled conditions in the bay-fed ponds than did those in pond A. The almost 10 parts per thousand difference in salinity between the groundwater-fed pond A (32 ± 2 parts per thousand) and pond B (23 ± 1 parts per thousand) was due to the proximity of pond A to an area of saline surface deposits. No attempt was made during the experiment to adjust salinity in the groundwater-fed ponds. Mean water temperatures were similar between the two systems. During weeks 10, 13, and 15, water temperatures in the groundwater-fed ponds dropped an average 10, 5, and 9° C, respectively, in response to cold fronts. Up to 10 days were required for temperatures to return to pre-cold front levels. Corresponding drops in the bay-fed ponds were less severe (3 to 6° C) and recovery occurred within three to five days. Dissolved oxygen levels were similar between the two systems. Low (less than 3.0 parts per million) dissolved oxygen levels occurred on 44 mornings in groundwater-fed pond A and on 33 mornings in pond B, with nearly half of those levels between 1.0 and 2.0 parts per million. Dissolved oxygen levels in the bay-fed ponds were more stable than those in the groundwater-fed ponds, partly due to the more efficient aeration system. Lowest measured dissolved oxygen level in the bay-fed ponds was 2.3 parts per million. Levels between 2.0 and 3.0 parts per million occurred in isolated ponds on two occasions. Natural productivity, estimated using Secchi values, was substantially lower in pond A than in pond B. Transparency was more stable in the bay system than in the groundwater system, due to the strict fertilization regime.

Production

Despite hydrological differences, mean growth and final weight of *P. vannamei* and *P. setiferus* did not differ significantly between the two groundwater-fed ponds (Fig. 1). Mean final weight of *P. setiferus* (8.0 ± 0.50 grams, n=2) was significantly lower than that of *P. vannamei* (19.9 ± 0.71 grams, n=2). Survival of *P. setiferus* in the groundwater system, however, was less than one percent and the contribution of this species to the final production was negligible (about 2.0 kilograms per hectare).

Mean survival and final size of *P. vannamei* grown in the groundwater-fed ponds were not significantly different from those of *P. vannamei* cultured in the bay-fed ponds (Table 4), although growth rate of shrimp stocked in the groundwater system more closely resembled that of shrimp stocked at the higher density in the bay system (Fig. 2). Production of *P. vannamei* from the groundwater system stocked at 50,000 shrimp per

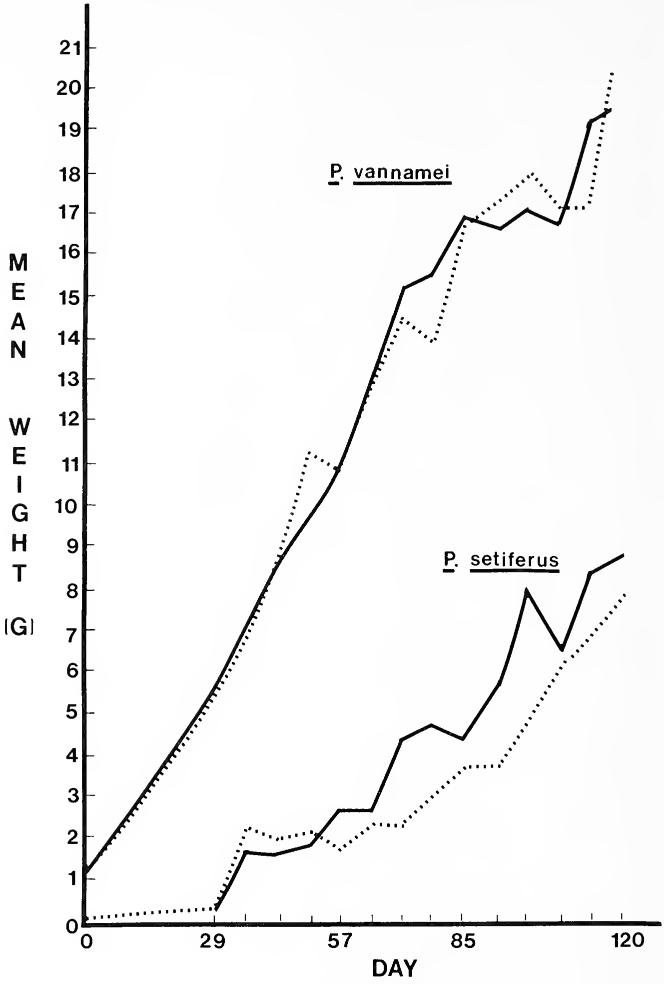

FIGURE 1. Apparent growth of *P. vannamei* and *P. setiferus* in saline groundwater-fed pond. A (solid line) and B (dotted line).

hectare was within the expected range of the bay system stocked at lower (25,000 shrimp per hectare) and higher (75,000 shrimp per hectare) densities. Food conversion ratio was better in the groundwater-fed system than in the bay-fed system.

DISCUSSION

Inasmuch as this was the first attempt to culture shrimp in saline groundwater from this particular source, the primary concern was to assess the potential of the system by documenting growth and survival of a penaeid species. Juvenile *P. vannamei* proved to be a successful species for culture in this saline groundwater system. Despite differences in

TABLE 4. Stocking and production data for *P. vannamei* in the groundwater and bay systems.

	Saline water source		
	Groundwater	Bay	
Density (number per hectare)	50,000	25,000	75,000
Percent survival, mean ± SD	86.7±4.53	84.8±18.42	91.0±8.73
Final size, mean ± SD (g)	19.9±0.71	20.8±2.14	17.6±1.90
Production, mean ± SD (kg/ha)	869.7±14.3*	461.5±89.9	1191.3±45.5
Count/pound, range	46-56	46-56	57-66
FCR	2.15:1	3.5:1	2.4:1
n	2	3	3

*Does not include contribution from *P. setiferus*.

hydrology, nutrient input, and pond design between the two systems, it is important to note that performance of *P. vannamei* stocked at 50,700 shrimp per hectare in the groundwater-fed ponds was consistent with that of shrimp from the same population stocked into Laguna Madre Bay-fed ponds near Corpus Christi at 25,000 and 75,000 shrimp per hectare. The fact that the groundwater-fed ponds were not fertilized makes their performance all the more noteworthy. Although the bay-fed pond system could not act as a control in the true sense of system and design replication, it did serve as a means of documenting the relative growth potential of *P. vannamei* in the groundwater-fed system. Improvements in pond design and aeration, as well as the initiation of a fertilization regime, may increase future yields from this system.

Postlarval *P. setiferus* did not prove to be a successful species under these experimental conditions. The larger size of *P. vannamei* at stocking plus its ability to tolerate high density culture conditions (Chamberlain et al., 1981) are possible explanations for the much greater production of *P. vannamei* compared to *P. setiferus*. Although salinity and temperature ranges recorded during this study were within those reported for wild *P. setiferus*, Lindner and Cook (1970) proposed that the rapidity of temperature change is more critical to survival of *P. setiferus* than actual temperature extremes. The rapid drop in water temperature due to cold fronts coupled with the low morning dissolved oxygen levels observed for several days may have influenced mortality losses of *P. setiferus* from the groundwater-fed ponds. Oxygen levels between 1.0 and 2.0 parts per million occurred on 20 days in the groundwater-fed experimental system

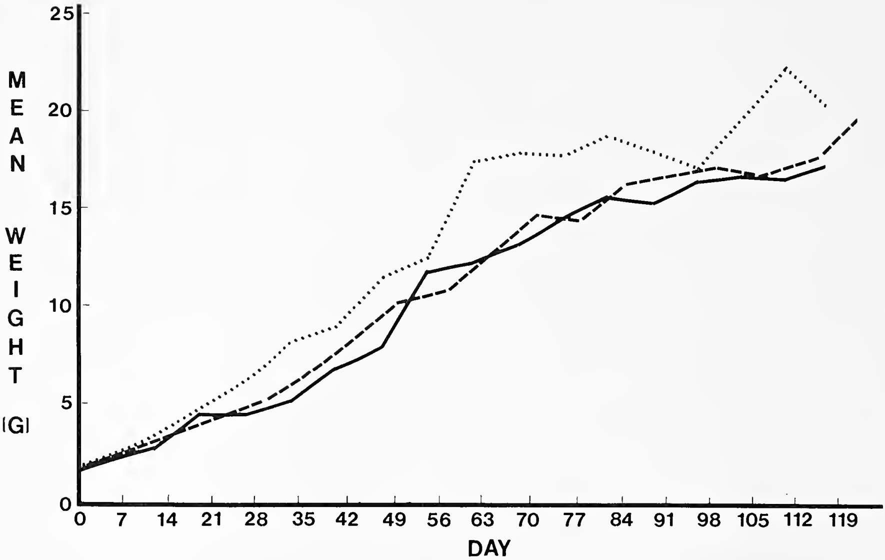

FIGURE 2. Apparent growth of *P. vannamei* stocked into the saline groundwater system at 50,000 shrimp per hectare (dashed line), and into the bay system at 25,000 (dotted line) and 75,000 (solid line) shrimp per hectare.

and fell below 1.0 parts per million on four days. Seidman and Lawrence (1985) suggested a conservative estimate for critical dissolved oxygen level for growth to be 1.91 parts per million for juvenile *P. vannamei* and 2.22 for *P. monodon*. Levels above 2.0 parts per million have been recommended for pond culture of *P. aztecus* (Kraner, 1975). The suitability of *P. setiferus* in this system should be readdressed under different stocking conditions.

Sarig (1984) credited the use of marginal saline waters unsuitable for agricultural irrigation as one reason for the general success of aquaculture in Israel. Although there are reports of experimental aquarium systems relying on saline water derived from wells or aquifers (Clark and Eister, 1971; Nakamura, 1971; Strasburg, 1971), U. S. researchers, in general, have been slow in recognizing the potential of saline groundwater for aquaculture. Goldstein (1986a, 1986b) reported successful culturing of *Spirulina* sp. and *Crassostrea* sp. in New Mexico saline groundwater. The Aquaculture Research Corporation, located at the mouth of the Barnstable Harbor in Cape Cod, Massachusetts, uses saline water pumped from an aquifer located about 20 meters below the complex to culture microalgae required to feed *Mercenaria* (Walsh et al., 1985).

Since 1973, members of the Texas Agricultural Extension Service and county extension agents, working with private individuals, have been investigating the commercial potential of stocking penaeids into western

Texas ponds using saline groundwater sources (J. Davis, Texas Agricultural Extension Service, Texas A&M University, personal communication). Small farms presently are located in seven Texas counties (Dawson, Fisher, Howard, Kent, Martin, Pecos, and Ward) and areas near the Salt Fork of the Red and Brazos rivers also are being examined. Reasonably good success has been obtained in recent years with the availability of good seedstock. For example, one farm in Howard County produced approximately 1345 kilograms of live heads-on *P. vannamei* per hectare in 1988 (27 count, tails). Results from our research strongly suggest that saline groundwater in southern Texas also can be used to culture at least one penaeid species. The formal examination of other chemically similar bodies of saline groundwater in Texas for penaeid mariculture is encouraged.

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BATS FROM THE COASTAL REGION OF SOUTHERN TEXAS

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Abstract.—A complete literature review revealed a paucity of information regarding chiropteran distribution and habitat along the southern coast of Texas. This survey describes distributional and ecological observations for 13 species of bats from that region.
Key words: Chiroptera; distribution; natural history; Texas.

The coastal region of southern Texas offers a diversity of habitats suitable for bats, yet few surveys of their distribution in that region have been undertaken. In an unpublished survey of Texas mammals and birds, Lloyd (1891) reported several observations of bats in southern Texas, but identified only two species. Bailey (1905) recorded four species from Cameron and Hidalgo counties, only a small part of coastal southern Texas as here defined. Mulaik (1943) subsequently found five species in Hidalgo County. In his survey of Texas biotic provinces, Blair (1950) included only two bats from coastal southern Texas. Little information has been published on the distribution of bats in the region since Blair's (1952) survey. Davis (1974) reported 11 species from the coastal region of southern Texas, but as Schmidly et al. (1977) noted, this reference lacks exact collecting localities and a listing of institutions where specimens are deposited.

To provide a more complete picture of distribution and seasonal abundance of the bat fauna of the coastal region of southern Texas, 438 specimens from 12 counties were examined. These included collections from field work in Cameron, Nueces, San Patricio, and Willacy counties from April 1987 until October 1988. Wherever possible, pertinent life history observations also are recorded.

Region Studied

The study area defined herein as "southern coastal Texas" includes those counties along the Gulf of Mexico from Refugio and Bee counties south to México (Fig. 1). The western boundry includes Live Oak, Jim Wells, Brooks, and Hidalgo counties.

Coastal southern Texas is situated in the Tamaulipan biotic province of Texas (Blair, 1950). Oberholser et al. (1974) referred to the habitats in the Tamaulipan province from San Antonio to the Rio Grande as South Texas brush country and coastal prairie. A part of this province, including Cameron, Willacy, Hidalgo, and Starr counties is designated as the Matamoran district (Blair, 1950), from which Blair (1952) reported seven species of bats. Included in the Matamoran district are approximately 14 hectares of Rio Grande palmetto palms (*Sabal texana*), which occur naturally in a grove southeast of Brownsville, Cameron County. Resident populations of *Lasiurus ega* and *L. intermedius* may occur in this palm grove. The remainder of the Tamaulipan province is referred to as the Nuecian district (Blair, 1952).

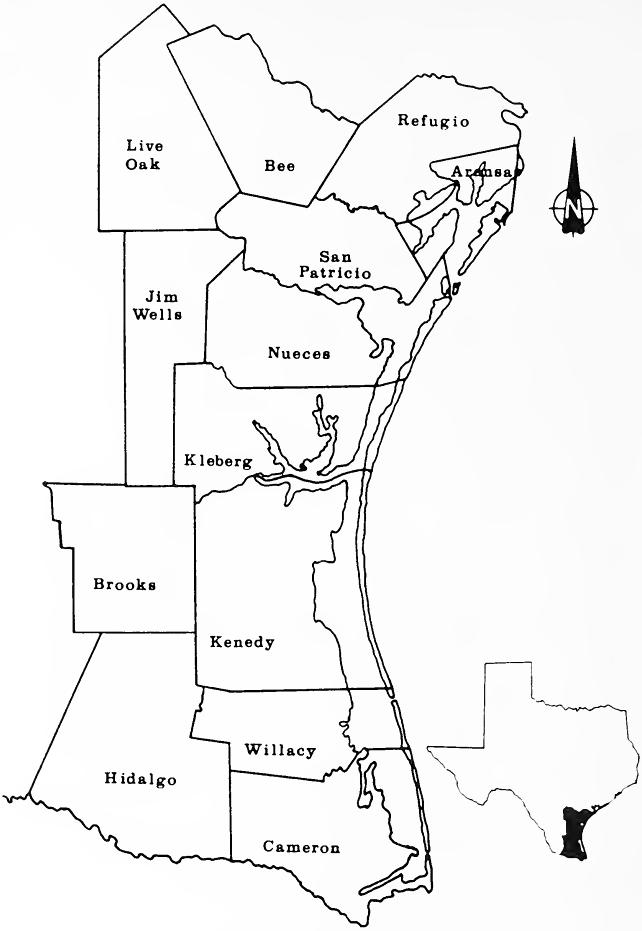

FIGURE 1. The study region in southern coastal Texas.

Bats were collected in Cameron County at the Fort Brown Hotel in Brownsville. Vegetation surrounding the hotel included Washington fan palms (*Washingtonia robusta*) and Rio Grande palmetto palms. Specimens were taken from the decorative columns on the second story of the hotel. These columns were composed of pumice rocks held in place by mortar. Bats were removed from gaps in the mortar using forceps.

One collection site in Nueces County was located 1.6 km. S Driscoll. A discription of the site is provided in Spencer et al. (1988). Bats were removed with insect nets from Washington fan palms. Bats also were collected from the Corpus Christi Public Compress cotton warehouses in Nueces County. Using forceps, bats were removed from gaps between wooden beams and concrete walls inside the warehouses.

Rob and Bessie Welder Wildlife Foundation was used as the collection site in San Patricio County. This refuge is located in a transitional zone between the Gulf Prairies and Marshes and the South Texas Plains (Thomas, 1975). The area where bats were taken was described by Drawe et al. (1978) as a Woodland-Spiny Aster complex. Specimens were taken over Moody Creek using mist nets.

The study site for Willacy County was located on the Yturria Ranch, La Chata Division. Specimens were collected by setting mist nets and trip wires over an earthen cattle tank. The vegetation surrounding this site was dominated by large honey mesquite trees (*Prosopis glandulosa*) and mixed brush.

Accounts of Species

Specimens examined were preserved either as skins accompanied by skulls or in alcohol and deposited in the following collections (museum abbreviations given in parentheses): Corpus Christi State University Vertebrate Collection (CCSU); Texas A&I University Vertebrate Collection (A&I); Pan American Univeristy Vertebrate Collection (PAU); Texas Cooperative Wildlife Collection, A&M University (TCWC); Texas Natural History Collection, University of Texas at Austin (TNHC); The Museum, Texas Tech University (TTU); U. S. National Museum of Natural History (USNM); American Museum of Natural History (AMNH); Welder Wildlife Foundation Collection (WWF). The arrangement of species and use of vernacular names follows Jones et al. (1988).

Mormoops megalophylla Peters, Ghost-faced Bat

The ghost-faced bat, referable (Smith, 1972) to the subspecies *M. m. megalophylla*, is known from Cameron and Hidalgo counties in the coastal region of southern Texas (Mulaik, 1943; Constantine, 1961; Davis, 1974; Hall, 1981; Jones et al., 1988). No additional specimens were collected or examined during this survey although this species may range along the Texas coast (Barbour and Davis, 1969).

This bat occupies a range of diverse habitats from desert scrub to tropical forests (Barbour and Davis, 1969). In Edinburg, Texas, four specimens were captured in January and February while hanging from a rough plaster ceiling in a junior high school (Davis, 1974). Apparently, ghost-faced bats do not hibernate, but no information is available on the subject (Jameson, 1959; Barbour and Davis, 1969).

Choeronycteris mexicana Tschudi, Mexican Long-tongued Bat

This species is known by a single record from Hidalgo County, represented by photographs only (LaVal and Shifflett, 1972). Jones et al. (1988) reported that this record probably represents an accidental northward occurrence. *Choeronycteris mexicana* is a monotypic species (Hall, 1981).

Mexican long-tongued bats occupy a range from tropical lowlands to montane habitats (Villa-R., 1967; Matson and Patten, 1975). The specimen from Hidalgo County was taken in December 1970 from a garage in the Santa Ana National Wildlife Refuge. The refuge was described by LaVal and Shifflett (1972) as mostly subtropical riparian forest.

Myotis velifer (J. A. Allen), Cave Myotis

The cave myotis is known only from Hidalgo County in the southern coastal study region (Hayward, 1970; Jones et al., 1988). The subspecies is *M. v. incautus* according to Hall, 1981.

These bats are usually cave dwellers, although they also roost in old, abandoned buildings and mine tunnels (Hayward, 1970; Davis, 1974; Schmidly, 1983). The species occupies a variety of habitats (Blair, 1952; Davis and Russell, 1952; Baker, 1956; Hayward, 1970; Davis, 1974; Schmidly, 1983). Some populations of cave myotis are known to hibernate (Hayward, 1970; Schmidly, 1977), whereas others probably migrate (Davis et al., 1962; Hayward, 1970).

Pipistrellus subflavus (F. Cuvier), Eastern Pipistrelle

Reports of this bat, referable to the subspecies *P. s. subflavus*, from the coastal counties are rare. It has been reported previously from Kleberg, Bee, and Cameron counties (Bailey, 1905; Davis, 1959; Zehner, 1985). Zehner (1985) recorded a specimen found in August in a building on Padre Island National Seashore. Additional specimens reported from the study region were collected in April. This bat hibernates (Davis, 1974), but no information is available on seasonal movements.

Specimens examined (2).—BEE CO.: 2 mi. N Beeville on U. S. Hwy. 181, 1 (CCSU). KLEBERG CO.: 2.4 mi. S Padre Island National Seashore, 1 (CCSU).

Lasiurus borealis (Müller), Eastern Red Bat

Red bats have been collected from Aransas, Refugio, Bee, Nueces, Hidalgo, and Cameron counties in the coastal region of southern Texas (Miller, 1897; Mulaik, 1943; Blair, 1952; Raun, 1966; Davis, 1974). This species also occurs in San Patricio and Kleberg counties. *Lasiurus borealis* is a monotypic species according to Baker et al. (1988).

According to Schmidly et al. (1977), red bats occur in all major vegetation regions. Museum specimens examined from coastal Texas were collected from May through October. Texas populations of this species may be migratory (Davis, 1974; Hall, 1981), although Schmidly et al. (1977) reported that this bat has been collected in the eastern part of the state in all seasons of the year.

Specimens examined (7).—BEE CO.: Beeville, 1 (TNHC). ARANSAS CO.: Rockport, 2 (AMNH). SAN PATRICIO CO.: Sinton, 2 (WWF). KLEBERG CO.: Kingsville, A&I campus, 2 (A&I).

Lasiurus cinereus (Palisot de Beauvois), Hoary Bat

The hoary bat, referable to the subspecies *L. c. cinereus*, has been reported from Cameron and Hidalgo counties (Bailey, 1905; Mulaik, 1943; Davis, 1974; Hall, 1981). Examination of museum collections also revealed a specimen of this species from Kleberg County.

Hoary bats have been found roosting in wooded areas hanging in the open from a branch or twig (Davis, 1974). One specimen (A&I 172) collected in Kleberg County was found roosting approximately one meter above the ground in a grapefruit tree. Specimens have been collected in the study region in January, April, May, September, and October. This species migrates southward in winter (Stones and Wieber, 1965; Davis, 1974), but probably does not hibernate (Findley and Jones, 1964; Stones and Wieber, 1965).

Specimens examined (11).—KLEBERG CO.: Kingsville, 1 (A&I); 7.5 mi. S Kingsville in South Pasture, 1 (A&I). HIDALGO CO.: 1.25 mi. SE Edinburg, 1 (PAU); 5 mi. S Pharr, 1 (PAU); Weslaco, 1 (PAU). CAMERON CO.: Brownsville, 6 (USNM).

Lasiurus ega (Gervais), Southern Yellow Bat

This species, previously believed to be rare in southern Texas, had been reported only from Cameron County (Baker et al., 1971). Recent collections show that southern yellow bats are common in Nueces County (Spencer et al., 1988). The species also has been collected in Kleberg and Hidalgo counties.

Southern yellow bats, referred to the subspecies *L. e. panamensis* by Baker et al., 1971, have been collected in the coastal region of southern Texas in most months of the year. In Brownsville, this species roosts in natural palm groves where it is considered to be a permanent resident (Baker et al., 1971; Davis, 1974). All specimens collected in Nueces County were found roosting in Washington fan palms (Spencer et al., 1988). Although most bats in the genus *Lasiurus* are solitary, many of the specimens from Nueces County were found roosting with *Lasiurus intermedius*. Most specimens from Nueces County were collected in March; however, this species has been observed flying and roosting there from February until November. Persons at the Driscoll study site reported having seen these bats there in all months of the year for many years, even though this species is thought to be migratory (Barbour and Davis, 1969).

Specimens examined (100).—NUECES CO.: 1 mi. S Driscoll, 4 (CCSU); Corpus Christi, 2 (CCSU). KLEBERG CO.: Kingsville, A&I campus, 1 (A&I). HIDALGO CO.: no precise locality, 1 (PAU). CAMERON CO.: 5 mi. SE Brownsville, 91 (1 A&I, 90 TTU); Brownsville, 1 (AMNH).

Lasiurus intermedius (H. Allen), Northern Yellow Bat

This species may be a common resident in coastal southern Texas. It was known previously from San Patricio, Kleberg, Cameron, and Hidalgo counties (Bailey, 1905; Taylor and Davis, 1947; Davis, 1974; Hall, 1981). During field work, this species, referable to *L. i. intermedius* according to Hall and Jones (1961), also was collected in Nueces County (Spencer et al., 1988).

Northern yellow bats have been collected from January to September in the study area. In Cameron County, they have been taken from the dead fronds of tall palms (Barbour and Davis, 1969; Baker et al., 1971). Most specimens from Nueces County were collected from Washington fan palms (Spencer et al., 1988). Although several bats of this species have been found roosting together in dead fronds (Barbour and Davis, 1969), *L. intermedius* had not previously been reported roosting with other bat species. At the Driscoll Ranch study site, northern yellow bats were found roosting with southern yellow bats (Spencer et al., 1988).

Specimens examined (48).—San Patricio Co.: Sinton, 1 (TNHC). Nueces Co.: 1 mi. S Driscoll, 5 (CCSU); Corpus Christi, 4 (CCSU); Kleberg Co.: Kingsville, Texas A&I campus, 20 (17 A&I, 1 TCWC, 2 TTU). Cameron Co.: no precise locality, 1 (TCWC); 5 mi. SE Brownsville, 5 (TCWC); Brownsville, 12 (4 AMNH, 8 USNM).

Lasiurus seminolus (Rhoads), Seminole Bat

The seminole bat has been reported only from Cameron County in coastal southern Texas (Hall, 1981). Although this species may range along the coast through Texas into México (Barkalow and Funderburg, 1960; Barbour and Davis, 1969), we collected no specimens, and the one record from the region may be an extralimital occurrence or possibly represents a mididentified *L. borealis*. In any event, Jones et al. (1988) did list southern Texas as within the range of the seminole bat.

Spanish moss and pine-oak and long-leaf pine forests are favored roosting sites (Schmidly, 1983). Specific habitats in southern Texas remain unknown. These bats probably are active throughout the year (Davis, 1974). Although migratory patterns are not known, Barbour and Davis (1969) reported a definite distributional shift southward in autumn. The occurrence of this species in Cameron County is in need of verification.

Nycticeius humeralis (Rafinesque), Evening Bat

Evening bats have been reported from San Patricio, Bee, Kenedy, Refugio, Cameron, and Hidalgo counties in coastal southern Texas (Miller, 1897; Mulaik, 1943; Blair, 1952; Davis, 1974; Hall, 1981). In addition, we have examined museum specimens from Kleberg County and individuals have been collected in Willacy County.

This bat, referable to the subspecies *N. h. humeralis*, was observed roosting in gaps under loose bark and cavities in mesquite trees (*Prosopis glandulosa*) in Willacy County. Several specimens also were taken from between decorative rocks at a hotel in Cameron County. Specimens from coastal southern Texas have been taken from January to September. Migration and hibernation abilities of this species are unknown.

Specimens examined (181).—BEE CO.: Mineral, 1 (A&I); 8 mi. N Beeville, 1 (TNHC). REFUGIO CO.: Woodsboro, 1 (TCWC). SAN PATRICIO CO.: 8 mi. N Sinton, 1 (TCWC); Welder Wildlife Foundation, Sinton, 4 (WWF). KLEBERG CO.: Kingsville, 4 (A&I). KENEDY CO.: Encino Division, King Ranch, 3 (A&I); Rudolph, Norias Division, King Ranch, 14 (TCWC); 6 mi. ESE Rudolph, Norias Division, King Ranch, 5 (PAU). HIDALGO CO.: Bentson State Park, 5 (TCWC). WILLACY CO.: 5.75 mi. N Raymondville, U. S. Hwy. 77, Bakke-Esparanza Ranch, 6 (TCWC); Yturria Ranch, La Chata Division, 80 (CCSU). CAMERON CO.: Southmost Nursery, Brownsville, 2 (A&I); Southmost Ranch, Brownsville, 1 (A&I); Brownsville, 1 (AMNH); Brownsville, Fort Brown Hotel, 4 (CCSU); 5 mi. SE Brownsville, 48 (5 A&I, 43 TTU).

Antrozous pallidus (Le Conte), Pallid Bat

Pallid bats apparently are rare in coastal southern Texas and are known only from Cameron County (Davis, 1974; Hall, 1981). Specimens from this area are referable (Martin and Schmidly, 1982) to the subspecies *A. p. pallidus*.

Pallid bats are primarily cave dwellers, but have been captured roosting in man-made structures such as attics, barns, and abandoned buildings (Davis, 1974). The specimen examined from Cameron County was netted in September in a natural Rio Grande palmetto grove. Possibly this was a migrant, because pallid bats probably undertake seasonal movements (Vaughan and O'Shea, 1976).

Specimens examined (1).—CAMERON CO.: 5 mi. SE Brownsville (TTU).

Tadarida brasiliensis (Saussure), Brazilian Free-tailed Bat

This bat, presumably referable to the subspecies *T. b. mexicana*, is common throughout the study region. It has been reported from Bee, San Patricio, Refugio, Jim Wells, Hidalgo, and Cameron counties (Bailey, 1905; Mulaik, 1943; Blair, 1952; Short et al., 1960; Davis, 1974). Based on specimens collected and examined, this species also occurs in Aransas, Nueces, and Kleberg counties.

This bat utilizes man-made structures as roosting sites in coastal southern Texas (Barbour and Davis, 1969). In Nueces County, specimens were collected and others examined at the cotton warehouse study site every month from April 1987 through August 1988. Bats were taken in Cameron County from the Fort Brown Hotel in the same manner as described for *N. humeralis*. This species is known to migrate.

Specimens examined (87).—BEE CO.: 6 mi. E Beeville, Hwy. 202, Medio Creek Bridge, 5 (CCSU); Poesta Creek, Beeville, 1 (CCSU). ARANSAS CO.: Rockport, 1 (CCSU). SAN

Patricio Co.: Sinton, 23 (TCWC); Welder Wildlife Foundation, Sinton, 1 (WWF). Nueces Co.: Corpus Christi, 26 (24 CCSU, 2 USNM). Kleberg Co.: Kingsville, Texas A&I campus, 14 (A&I); Kingsville, 2 (TCWC); Padre Island National Seashore, 1 (CCSU). Hidalgo Co.: 13 mi. S Edinburg, 4 (TCWC); 5 mi. S Mission Anzaldouas Dam, 1 (TCWC); Edinburg, Pan American University campus, 5 (PAU); Santa Anna Wildlife Refuge, 1 (USNM). Cameron Co.: Fort Brown Hotel, Brownsville, 2 (CCSU).

Tadarida macrotis (Gray), Big Free-tailed Bat

The only record of the big free-tailed bat in the southern coastal region is that of a male found hanging from a screen door in San Patricio County (Raun, 1961). The habitat surrounding the collection site was described by Drawe et al. (1978) as a live oak-chaparral community. Although little information is available, Davis (1978) suspected that this species hibernates in the Big Bend region of Texas.

Specimens examined (1).—San Patricio Co.: Welder Wildlife Foundation, Sinton, (WWF).

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A NUTRITIONAL ANALYSIS OF DIET AS REVEALED IN PREHISTORIC HUMAN COPROLITES

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Abstract.—Nutritional analysis of archaeological material has not been extensively conducted. The main reasons for the lack of such studies include the problems inherent in archaeological preservation of dietary remains, and the lack of information on the nutritional content of prehistoric foods. Coprolites (dessicated human feces), however, are unique resources for determining the prehistoric diet of archaeological populations. This paper presents a nutritional analysis conducted on 38 coprolites approximately 1000 years old that were excavated from a dry, limestone rockshelter in Val Verde County, Texas. The nutritional analysis indicates that the prehistoric diet of these people was relatively nutritious, although other archaeological information from the botanical, faunal, and human remains needs to be assessed before a complete nutritional statement can be made.
Key words: nutrition; coprolites; diet.

Nutritional analyses provide insights into the health of a population, supplying answers to previous unanswered questions, pinpointing nutritional deficiencies, and possibly exposing cause and effect relationships of specific dietary deficiences and health problems. Such cause and effect relationships include the lack of vitamin C in the diet and the development of scurvy (Ortner and Putschar, 1985), and the increase in osteoporosis with a calcium-deficient diet (Robson, 1972). The low quality of diet obtained after alkali treatment of corn (which is deficient in niacin and a niacin precursor, tryptophan) also is realized with such work (Wing and Brown, 1979). However, nutritional studies have been conducted mainly on modern populations, and references pertaining to such studies are directed mostly toward modern American diets.

Nutritional analyses in prehistoric archaeological settings have mainly been ignored (Yesner, 1980). One reason for the lack of such studies stems from the problems that researchers face in the initial phases of such analyses and with the subsequent interpretation of data. Archaeological data of any kind are a limiting factor. Samples recovered from an archaeological excavation are most likely the best preserved and most resilient of such samples, and so do not reflect the frequencies with which food items may have been used by the prehistoric population. This is especially true for archaeological food remains, both faunal and floral (Carbone and Keel, 1985). Another major problem with analyzing prehistoric food remains is determing what actually was used as a dietary resource and what was used in some other fashion, or is a contaminant.

This paper will discuss a nutritional analysis based on 38 coprolites excavated from Baker Cave, Val Verde Co., Texas. This analysis is unique in that it is an initial step in determining the nutrition of a prehistoric population. Coprolites are an excellent source of information for nutritional analyses because the contents are what was most likely eaten. Coprolites, however, will yield an underestimate of the amount of animal protein consumed by a group of people, as it has been estimated that all animal protein is digested, and larger animal bone remains generally are not ingested. Trace elements and minerals found in the water supply also will be underestimated. A nutritional analysis of coprolite samples thus is only a partial statement of the nutrition of a prehistoric group because coprolites only reflect one portion of the diet. Other aspects that need to be analyzed for a complete nutritional statement include food items represented in faunal and floral archaeological material, and prehistoric human remains.

Sample Location

Baker Cave is located in a cultural area known as the lower Pecos region. This region is situated in southwestern Texas and northern Coahuila, México, specifically centering around the Pecos and Devils rivers and their confluence with the Rio Grande (Fig. 1). The environment in this area is semiarid, leading to increased preservation of prehistoric cultural material found in rockshelters and open sites. Baker Cave is specifically located in an ecotonal environment at the eastern edge of the Chihuahuan Biotic Province, bordered by the mesquite-chaparral zone of southern Texas, the oak-cedar zone of the Edwards Plateau to the east, and the sotol-lechuguilla zone to the west (Chadderdon, 1983).

Prehistoric occupation began in the lower Pecos region at least 9000 years ago (Shafer and Bryant, 1977; Shafer, 1981, 1986). Subsistence patterning was centered around the arid environment from which a conservative foraging adaptation was mainly followed (Williams-Dean, 1978; Dering, 1979; Stock, 1983; Lord, 1984; Sobolik, 1988*a*). Agriculture was not practiced in this region mainly due to the inhospitable environment, to the time-consuming nature of the practice, and to the relative success of the inhabitants in a hunting-gathering subsistence (Lee and DeVore, 1968).

The nutritional analysis of the food items observed in the Baker Cave coprolites is the first of its kind conducted on an actual sample of coprolites.

The most extensive nutritional analysis of the area (Winkler, 1982) included a review of ethnobotanical and coprolite research in the lower Pecos area as well as some nutritional values of a few of the botanical dietary items recovered.

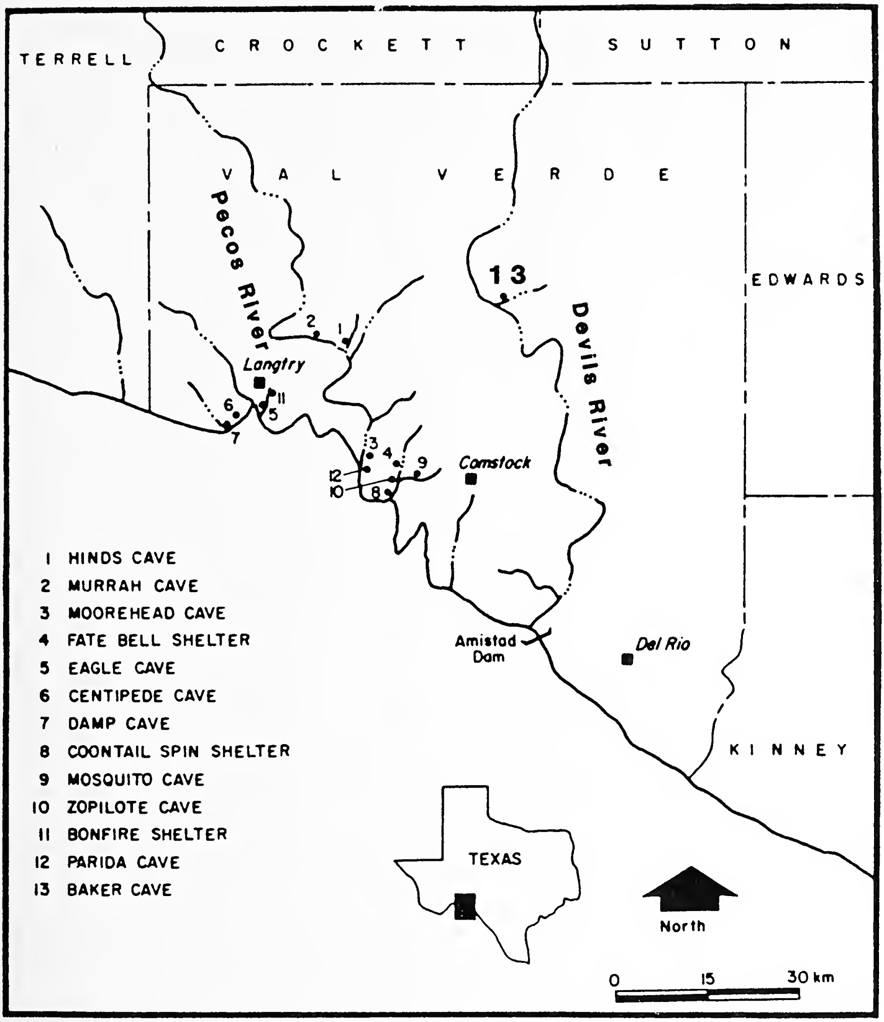

FIGURE 1. Location of Baker Cave in Val Verde County, Texas (from Lord, 1984).

Due to the status of the prehistoric occupants of Baker Cave as hunter-gatherers and their longevity in the area, it has been assumed that these people were healthy, nutritionally prosperous, and physically strong. Osteological data analyzed by Marks et al. (1985) and reviewed by Reinhard et al. (1990), however, indicate problems of iron and other nutrient deficiencies, caries, enamel hypoplasia, and extreme dental wear. This information suggests times of stress and malnutrition in the seasonal rounds and overall lifestyle of the lower Pecos population. The nutritional analysis of the coprolite constituents will test these studies.

COPROLITE CONSTITUENTS

The Baker Cave coprolites were studied using both micro- and macroremains (Sobolik, 1988*a*). Microremains included pollen and parasites, whereas macroremains included bone, hair, fiber, seeds, charcoal, and insects. Macroremains were divided into those associated with plants and those associated with animals. The major constituents of the coprolites are listed in Table 1. This table shows the percentage of the 38 coprolites that contained each constituent. Animal remains from coprolites were identified using bone, fur, feathers, and scales.

TABLE 1. The main constituents of the Baker Cave coprolites. Values represent the percent of the total number of coprolites in which a constituent was observed.

Constituent	Percentage of coprolites
Fiber	100
Onion Bulbs	29
Prickly Pear Seeds	16
Mustard Seeds	8
Juniper Seed Hulls	5
Mesquite Pods	3
Goosefoot Seeds	3
Bone	53
Fish	37
Rodent	34
Bird	18
Lizard	5
Rabbit	3

The pollen types most easily recognized as intentionally ingested items (Sobolik, 1988*b*) include Brassicaceae (mustard family) pollen, *Artemisia* (sagebrush) pollen, and Poaceae (grass family) pollen. Eight coprolite samples from the Baker Cave latrine area contained extremely high frequencies of Brassicaceae pollen. Many of the samples contained aggregates of this pollen type, suggesting that anthers were eaten. *Artemisia* pollen also was observed at high frequencies, and aggregates of this pollen type were observed as well. Poaceae (grass) pollen was found at high frequencies in many of the coprolites analyzed, indicating intentional ingestion of grass inflorescences or seeds.

HUMAN DIETARY REQUIREMENTS

The recommended dietary allowances of the committee on Dietary Allowances (1980) will be used to illustrate the essential dietary constituents needed by humans. Dietary requirements include carbohydrates, protein, and lipids (for energy), and fiber, vitamins,

TABLE 2. Human nutritional requirements.

- Carbohydrates
- Fiber
- Protein

- Amino acids
  - Alanine
  - Histidine
  - Isoleucine
  - Leucine
  - Lysine
  - Methionine
  - Phenylalanine
  - Threonine
  - Tryptophan
  - Valine

- Water-soluble vitamins
  - Vitamin C
  - Thiamin
  - Riboflavin
  - Niacin
  - Vitamin B_6
  - Vitamin B_{12}
  - Folacin
  - Biotin
  - Pantothenic Acid

- Trace elements
  - Manganese
  - Iron
  - Copper
  - Iodine
  - Zine
  - Flourine
  - Selenium
  - Chromium
  - Molybdenum

- Lipids
  - Linoleic acid
  - Linolenic acid

- Fat-soluble vitamins
  - Vitamin A
  - Vitamin D
  - Vitamin E
  - Vitamin K

- Minerals
  - Calcium
  - Magnesium
  - Sodium
  - Potassium
  - Phosphorous
  - Chlorine
  - Sulfur

minerals, and water (Table 2). These substances are directly converted to energy in order to maintain or rebuild body structures, or are stored for later use. The requirements that will be discussed reflect the average of the actual needs of a population (FAO/WHO, 1973). Some individuals need more and some less of the specific nutrients; therefore, only the group population is considered.

Recommended nutritional intakes have not been estimated for other populations. However, some studies (Srinivasan, 1981; Seckler, 1982) maintain that recommended dietary allowances should not be used to compare and analyze "populations that have adapted to different physical and socioeconomic environments" (Messer, 1986:57). Populations may adapt and survive on lower nutritional intakes than those deemed adequate for western societies (Stini, 1975), mainly by reducing energy expenditure with a decreased level of work and physical activity (Messer, 1986). Individuals also may "adapt to lower levels of energy and protein intake at no function cost" (Messer, 1986:58).

Energy is the essential outcome from use by the body of dietary constituents. Carbohydrates, lipids, and protein are the sources of energy for the human body (Committee on Dietary Allowances, 1980; FAO/WHO, 1973). Energy needs are dependent on physical activity, body size, age, and climate (Committee on Dietary Allowances, 1980; FAO/WHO 1973). Additional energy (kilocalories) also is needed for pregnant (+300 kcal) and lactating (+500 kcal) females. If energy intake is deficient, then part of the dietary protein is needed to provide that energy (FAO/WHO, 1973). Physical activity is the main factor determining differences in energy requirements, and is variable within a population, especially delineated along gender lines and roles. The more active a person the more energy that person expends and needs replaced. Body size is also important in determining how much energy an individual needs. A person of large size requires "more total energy per unit of time for activities" (FAO/WHO, 1973) than one of smaller size. The energy used in moving a larger body mass is higher (Committee on Dietary Allowances, 1980).

Age is also a significant determining factor in the amount of energy needed and expended by an individual. As a person grows older, basal metabolic rate and activity gradually decline. The resting metabolic rate has been estimated to decline two percent per decade (Durnin and Passmore, 1967), but the decline in physical activity varies for each individual (Committee on Dietary Allowances, 1980). Age also affects energy requirements due to changes in body composition and weight, and a possible increase in disease and disability (FAO/WHO, 1973). More energy also is required for growth and metabolism. During childhood, proper energy intake is essential to fulfill the needs of an expanding and ever active body.

Climate also may influence the amount of energy expended. When performing activities in a colder temperature, energy requirements are increased, along with overall body temperature and metabolic rate (Johnson, 1963). Johnson (1963) also provided evidence that in temperate environments energy expenditure is greater than in warm environments, with the cold inducing the production of heat through shivering (FAO/WHO, 1973). Differential human behaviors and adaptations to climate are great, however, and climate has been determined to be an unquantifiable energy correction by the FAO/WHO (1973) and the Committee on Dietary Allowances (1980).

Nutritional Content of the Coprolite Food Items

Analysis of the nutritional aspect of a diet that is approximately 1000 years old has many obstacles. The main problem is that what was considered edible and "good eating" at that time is not necessarily viewed in that context today. Many of the Baker Cave dietary items are not recorded in modern day nutrition books and lists. Substitutions of the closest approximate item had to be made for some of the dietary constituents, such as frog (*Rana*) in place of lizard and pigeon in place of small birds.

Energy

In estimating efficiency of the diet of Baker Cave inhabitants, it must be realized that they were shorter in stature and lighter in weight than modern populations, which have been used to estimate recommended energy intake. Consequently, it is probably safe to assume that the Baker Cave occupants required a lower energy intake. However, the activity of the Baker Cave inhabitants would be much higher than that observed in a modern day population, due to their status as nomadic hunter-gatherers. In order to evaluate the amount of energy a population receives, carbohydrate, lipid, and protein intake must be considered. The main energy sources of the prehistoric population under analysis are those foods with the highest kilocaloric (kcal) value per 100 grams of edible portion, and with the highest lipid, carbohydrate, and protein content.

Food items recovered from the coprolites with the highest caloric values (Table 3) are prickly pear seeds (289 kcal), after they have been ground to a pulp in what is called "queso de tuna" (Winkler, 1982), goosefoot seeds (195 kcal), mustard seeds (469 kcal), birds (294 kcal), and rabbits (166 kcal). Foods with high protein and fat contents are similar and include birds, mustard seeds, rabbits, fish, and goosefoot seeds. Protein from meat would be underrepresented in the coprolites because meat is entirely digested, and bone remains from larger animals would not be observed in the coprolite specimens. Carbohydrate content cannot be determined due to the lack of data.

A "meal" of onion bulbs (35 kcal), a small fish (96 kcal), a bird (294 kcal), and mustard seeds (469 kcal) (Table 3), will provide at least 894 kcal and 49.72 grams of fat. With the addition of goosefoot seeds (195 kcal), another bird, and "queso de tuna" (289 kcal) the lowest energy intake is 1672 kcal. This amount of energy is probably sufficient for females and children, with the fat content more than sufficient for the daily requirements for both males and females (15 to 25 grams). With the addition of a few more staples, such as *Opuntia* fruits and especially nutritious seeds and meat, the daily energy intake would be sufficient to sustain males in the population.

Thus, mainly due to the higher caloric values, protein content, and fat content of birds, rabbits, mustard seeds, goosefoot seeds, and larger meat products not observed in the coprolites, along with the supplement of other less energy-sufficient dietetic items, the inhabitants of Baker Cave probably received sufficient energy.

Fiber

The main bulk of the diet of the prehistoric occupants of Baker Cave was that of fiber from many different sources. The main effect of fiber is to provide bulk to the diet, increase fecal output (Cummings, 1986), allow for easier food passage, and possible prevention of disease. Hunter-gatherers (prehistorically and historically) typically have had a diet that revolved around the consumption of fiber in bulk (Burkitt and Spiller, 1986). High fiber diets also have been observed for other prehistoric occupants in the Baker Cave area (Williams-Dean, 1978; Stock, 1983). Specific fiber content of foods usually have not been analyzed, but due to the high-fiber diet of Baker Cave occupants, their fiber intake was most likely nutritionally sufficient.

Protein and Amino Acids

Due to the problems in amino acid content conversion, the overall amino acids found in foods cannot be directly compared to the required amount. Infants require much more protein by weight than other age groups due to their continual expansion of tissue and bone. This protein requirement usually is met with the intake of human breast milk. An adult 70-kilogram male requires 56 grams of protein daily and an adult (55 kilograms) female requires 44 grams of protein daily (Committee on Dietary Allowances, 1980).

Foods high in protein are mainly the same foods high in energy content—goosefoot seeds, mustard seeds, lizards, rodents, rabbits, and birds. In my sample "meal," the approximate protein content is 68.63 grams. This provides the necessary protein for the average adult male and female. Goosefoot seeds, fish, and rabbit are three food items found in the coprolites that have the highest protein content. It must be realized, however, that the protein content of larger game, not represented in the coprolites, would produce a much higher intake than what is represented here in the sample meal. Meat is one of the best and most efficient sources of protein in the diet.

Vitamins

Vitamins are divided into fat soluble (vitamins A, D, E, and K) and water soluble (vitamins C, B_6, B_{12}, thiamin, riboflavin, niacin, folacin, biotin, and pantothenic acid). There is an overall lack of information on

Table 3. Nutritional content of food items from the Baker Cave coprolites (values given in 100 grams of edible portion).

Item	Energy (kcal)	Fat (g)	Protein (g)	Vitamin C (g)	Thiamin (mg)	Riboflavin (mg)	Niacin (mg)	Calcium (mg)	Phosphorus (mg)	
Onion bulbs	35.0	0.14	0.09	25.0	0.03	0.05	0.02	140.0	24.0	A
Goosefoot seeds	195.0	3.6	19.1	363.0	0.70	2.0	5.5	1402.0	327.0	B
Mustard seeds	469.0	28.76	24.94	—	0.54	0.38	7.9	521.0	841.0	C
Prickly pear fruit w/ seeds	38.0	0.1	0.3	31.0	0.01	0.02	0.3	63.0	—	B
Prickly pear “queso de tuna”	289.0	—	1.3	88.0	0.20	0.20	1.5	51.0	—	B
Catfish	96.0	7.62	15.8	—	0.20	0.06	2.4	20.0	179.0	D
Lizard	73.0	0.3	16.4	—	0.14	0.25	1.2	18.0	147.0	E
Rabbit	166.0	7.62	20.8	3.0	0.11	0.066	8.6	14.0	224.0	D
Pigeon	294.0	13.2	27.8	—	—	—	6.86	—	—	F

A (Paul and Southgate, 1978)
B (Winkler, 1982)
C (Marsh et al., 1977)
D (Souci et al., 1981)
E (Fraps and Cory, 1940)
F (Posati, 1979)

fat soluble vitamin requirements, as well as the requirements of vitamins B_6, B_{12}, folacin, biotin, and pantothenic acid. This deficiency must be resolved before the complete nutritional status of the Baker Cave occupants can be determined.

Sixty milligrams of vitamin C daily is the recommended allowance for adults. This requirement could be met by eating two prickly pear fruits with the seeds, onions, or a few goosefoot seeds. Due to the high frequency of prickly pear seeds and onions in the Baker Cave diet, vitamin C probably was not a problem for the inhabitants.

Thiamin, vitamin B_1, is required at an average of 1.0 to 1.5 milligrams per day for adults. This requirement can be easily met with the ingestion of my "meal," as well as through eating mustard seeds and catfish. Due to the availability of these foods, thiamin probably was present in the diet at the appropriate level to maintain health.

Riboflavin is needed in the diet in slightly higher amounts than thiamin (average of 1.2 to 1.7 milligrams recommended daily), and the same foods that contain high amounts of thiamin also contain high amounts of riboflavin. Thus the same food combinations that provided a nutritionally sufficient supply of thiamin also supplied that of riboflavin.

Niacin is required in amounts averaging 13 to 16 milligrams daily. Foods high in niacin include mustard seeds, chenopod seeds, and rabbit. All of these items were observed in the coprolites, and would provide an individual with a sufficient supply of niacin.

Minerals

The essential mineral content of food is fairly well represented, especially for calcium and phosphorous. The highest calcium content in the food array is goosefoot seeds (1402 milligrams), showing that 100 grams of this food item will provide the daily recommended calcium for all ages. Mustard seeds (521 milligrams) and onions (140) are also high in calcium. The requirements for phosphorus are the same as those for calcium (800 to 1000 milligrams daily). Mustard seeds are also high in phosphorus (841 milligrams) as are chenopod seeds (327) and rabbit (224). These food items thus could have supplied the daily requirements of calcium and phosphorus for the Baker Cave population.

Data on the human requirements of electrolytes—sodium, potassium, and chlorine, as well as magnesium, iron, copper, zinc, and sulfur—are scarce. Sodium, required in amounts from 1100 to 3300 milligrams for adults, is found only in relatively low amounts in the food items studied. Thus, a huge amount of these foods would need to be consumed in order to fulfill the recommended daily allowance for sodium. However, it is quite probable that a food item (or items) not studied contains higher amounts of sodium than that already observed. This is also the case for potassium and chloride, although not enough information on chloride has been obtained to make even a generalized statement.

Drinking water contains a high number of these electrolytes, which are obtained from the soil. The content of the drinking water in the Baker Cave area has not been analyzed, but until further research can be conducted it can be assumed tentatively that the occupants of Baker Cave most likely were not deficient in sodium, potassium, or chlorine.

Trace Elements

As with other nutritionally important elements, not enough information is available on trace elements of food items. The trace element requirments for the inhabitants of Baker Cave, however, probably were met with the large amounts of dirt and sand that were consumed, and in drinking water. Soil contains the majority of the trace elements and in quantities that probably would not reach toxicity levels for humans. Dirt and sand were found in 91 percent of the coprolites, indicating that the Baker Cave occupants probably ingested enough trace elements.

Conclusions

Determination of the health of the Baker Cave occupants has been attempted through a nutritional analysis of the contents of latrine coprolites. It must be realized that contents of coprolites do not reflect the entire dietary intake, and other dietary remains must be analyzed before a complete nutritional statement can be made. Remains of coprolites are the parts of foods that have not been digested. Energy and nutrients that have been digested must be estimated from the remaining portion. The nutritional analysis also is biased toward the season in which the coprolites were deposited. In order to determine what the nutrition of the prehistoric population was like year-round, analysis of a larger sample size, as well as other dietary indicators, must be available.

It has been suggested that the lower Pecos populations had a nutritionally sound diet and an overall healthy existence, due to their stable occupation of the lower Pecos area for more than 9000 years (Shafer, 1986). The preliminary nutritional analysis conducted indicates that the Baker Cave occupants at approximately A.D. 900, as reflected through their coprolites, were generally healthy. Skeletal information, summarized by Steele and Olive (1990), and Reinhard et al. (1990) suggests that there was nutritional stress in the lower Pecos population. This "stress," however, was mainly observed in the dentition, and most likely resulted from the rough, fiberous diet inherent in the lower Pecos area, and to the high sugar and carbohydrate content of many of the food items, such as prickly pear and mesquite.

The nutritional status of the occupants of Baker Cave, as indicated in this analysis, appears to have been generally good, although a much more rigorous study needs to be conducted. Such a study should include an analysis of the archaeological faunal, floral, and human remains from the area. More information on the nutritional contents of food items in the lower Pecos region is also essential. Additional information is especially needed on trace mineral and electrolyte content, fat soluble vitamin content, and a few water soluble vitamin contents. With the addition of this information, a nutritional analysis would provide an extensive study and would greatly facilitate the knowledge that can be gained archaeologically about the lower Pecos prehistoric population, and about other similar groups.

Acknowledgments

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ABNORMAL TERMINAL CRETACEOUS FORAMINIFERA OF EAST-CENTRAL TEXAS

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Abstract.—Morphologically abnormal planktic foraminifera are present in the uppermost meter of the upper Maestrichtian Kemp Clay in east-central Texas. Morphologically abnormal foraminifera have been well described from Recent sediments, but not from fossil populations. Abnormal specimens are heavily concentrated in biserial genera *Heterohelix, Pseudoguembelina,* and *Planoguembelina.* Abnormal specimens are assigned to several categories based upon common abnormal morphological characteristics. The most unusual specimens are "twinned." The majority of the deformities probably were associated with ecological deterioration or predation. *Key words:* foraminifera; Cretaceous-Tertiary boundary; Brazos River.

Upper Cretaceous rocks of the Kemp Clay containing abnormal foraminiferal faunas are present at Cretaceous-Tertiary boundary sections along the Brazos River in Falls County, Texas (Fig. 1). Section B2 contains abundant, well-preserved, planktic foraminifera. The planktic populations are neither diverse nor completely morphologically "normal." Grossly abnormal specimens comprise approximately 0.5 percent of the complete study sample of 20,000, ranging up to five percent in individual samples. With the exception of foraminifera from other Kemp Clay localities and smaller concentrations of abnormal specimens recovered from Texas Turonian, Cenomanian, and Paleocene rocks, abnormal foraminifera from the Brazos Kemp Clay are found in a much greater percentage than I have encountered in other Cretaceous and Tertiary faunas in Texas. The Brazos percentages are low in comparison with other reported, Recent, deformed populations. The highest percentage of "abnormals" I am familiar with is a population of deformed *Globorotalia menardii*, which constituted up to 67 percent of the total observed specimens (Aktürk, 1976).

Little is known concerning the causes of abnormal morphologies in fossil foraminifera. Abnormal test morphologies in extant species have been attributed to: 1) stressful ecological conditions produced by detrimental water quality (Arnal, 1955; Watkins, 1961; Seiglie, 1974); 2) predation and wound healing (Aktürk, 1976), and selective mechanical damage imitating predation (Bé and Spero, 1981; Bé, 1982). Under stressful environmental conditions (low oxygen and overly abundant organic matter), foraminifera were found to be smaller and had thicker tests than normal individuals (Seiglie, 1974). Abnormal test shape and unusual ornamentation was attributed to polluted environments (Watkins, 1961). Aberrant *Globorotalia menardii* were attributed to high water temperature (Lidz, 1966). Crushed shells resulted in "bizarre"

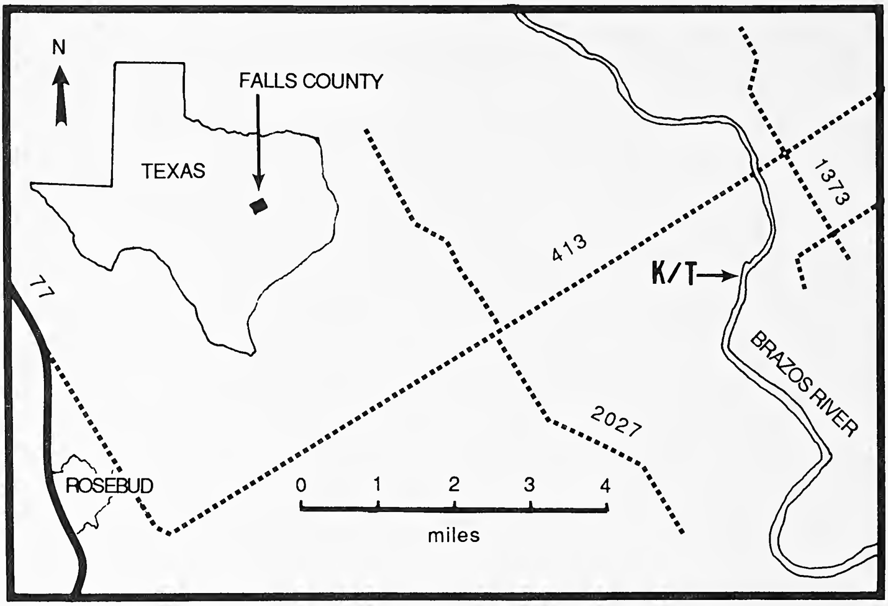

Figure 1. Location of the Cretaceous-Tertiary boundary sections.

specimens, whereas amputated individuals regenerated normally (Bé and Spero, 1981). Test distortion and abnormal expansion of ultimate chambers were attributed to the effects of parasites or mechanical, traumatic damage (Aktürk, 1976).

Biostratigraphy

The Cretaceous-Tertiary boundary is placed between samples 4 and 5 based on the initial appearance of the Tertiary forms *Globoconusa daubjergensis* and *Globorotalia pseudobulloides* (Fig. 2). *Guembelitria cretacea* persists undiminished at least 50 centimeters above the appearance of *G. daubjergensis*. Several heterohelicids, especially *Heterohelix striata*, are present in association with *G. daubjergensis*. The Paleocene foraminiferan *Chiloguembelina* sp. increases in abundance inversely to *H. striata*. *Rugoglobigerina rugosa* also is found in the basal Paleocene. *Globotruncana aegyptiaca* and *Globotruncana duwi* persist into uppermost Cretaceous strata. Planktic to benthic ratios vary considerably from 2.7 in the lowest part of section B2 to 1.0 just below the first occurrence of Paleocene foraminifera (Hansen et al., 1984, 1987). The planktic to benthic ratio in the basal Paleocene is no greater than 0.4. Bioturbation is probably responsible for some of the more obvious reworking of Cretaceous fossils into Paleocene strata. No general homogenation of sediment has occurred as only the foraminifera listed

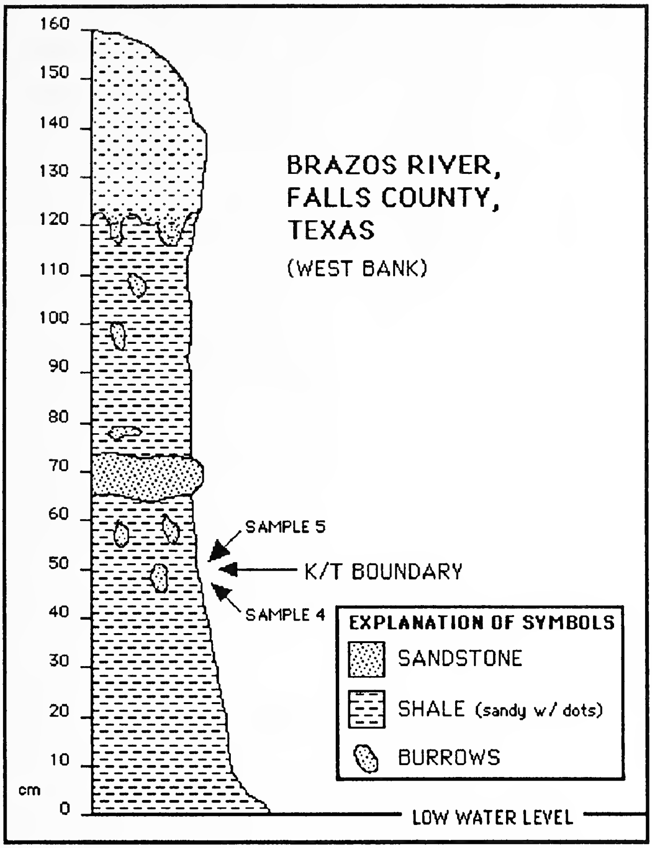

FIGURE 2. Outcrop profile showing samples locations and Cretaceous-Tertiary boundary.

above are found associated with Tertiary foraminifera, whereas coextant Cretaceous taxa are not.

The fauna suggests an incomplete boundary interval in spite of the uninterrupted appearance in outcrop. *Abathomphalus mayaroensis* and *Pseudotextularia intermedia* are not present, indicating probable absence of the terminal Cretaceous section. The Paleocene is missing the lowest Danian primitive globigerinids. The possibility of facies or paleogeographic control, or both, of these taxa is not impossible, but remains unproven.

ABNORMAL MORPHOLOGIES

Foraminiferal abnormalities at the Brazos locality are concentrated heavily in the biserial *Heterohelix* group, which underwent a bewildering combination of torsion, extreme chamber shape, and number modifications, as well as growth of various special structures such as

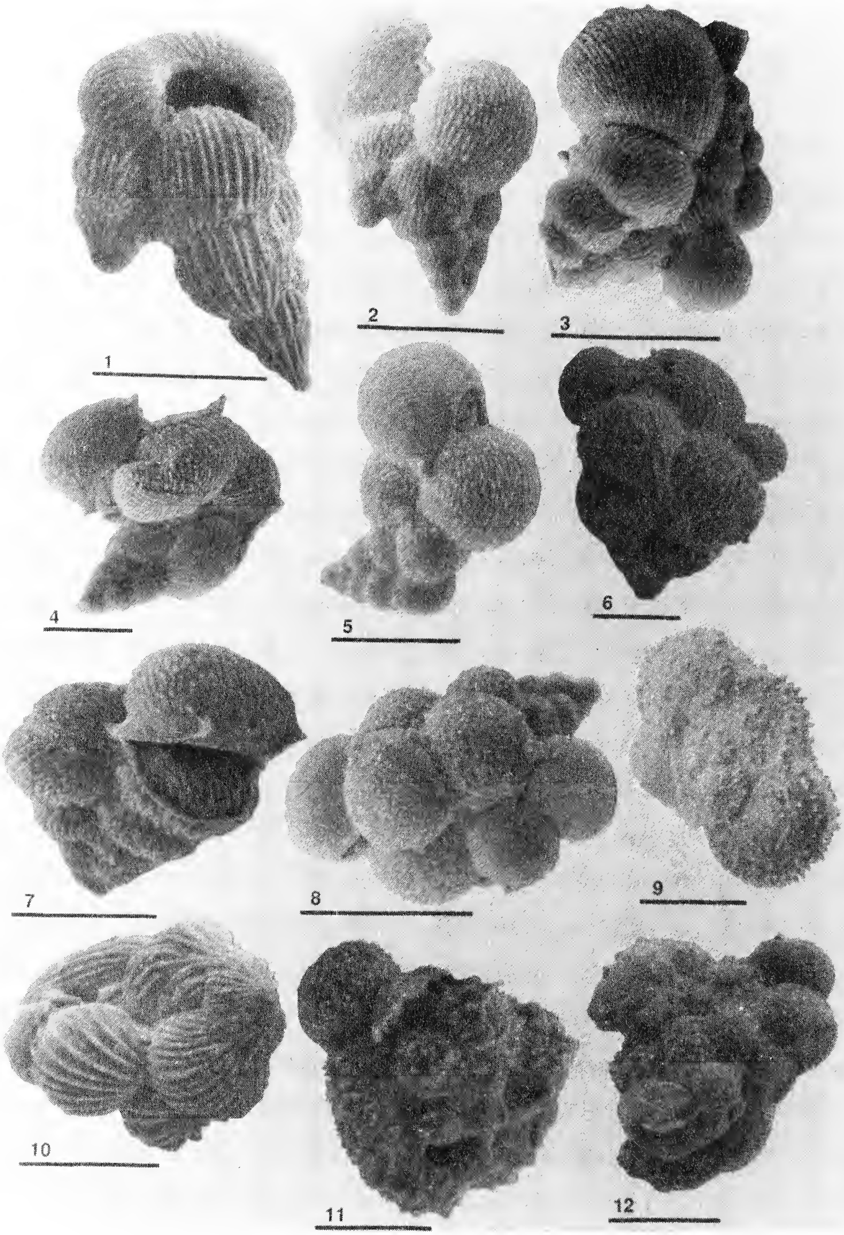

FIGURE 3. Abnormal foraminiferans of the Brazos River, Texas. Bar is one millimeter.

bulla or uncharacteristically overlapping chambers. Abnormal Paleocene foraminifera are concentrated in the globular trochospiral group, whereas biserial forms are mostly affected in the middle Cretaceous. Abnormalities can be divided into categories based on easily recognized aberrant morphologies. The categories below are presented in relative order of abundance from greatest to least.

Attached twins.—Attached twins most often appear as two foraminifera sharing the last few chambers (Fig. 3, 1-2). A much smaller proportion of twins have a common proloculus. Other specimens are composed of three or four complete but fused tests (Fig. 3, 3). The twin deformity is apparently only present in biserial species such at *Heterohelix striata, Pseudoguembelina costulata, P. palpebra,* and *Gublerina robusta.* Twins join one another most commonly at 30 to 60 degree angles, but tests may lie in the same plane or at 90 degrees.

Exaggerated expansion of final chamber.—Exaggerated ultimate chamber expansion is especially extreme in biserial taxa (Fig. 3, 4). Ultimate chamber volumes of two or three times that of normal specimens is not uncommon. Abnormal chamber size frequently is associated with increase in aperture size. An associated decrease in ultimate chamber ornamentation is common, but chamber perforation does not seem to vary.

Kinking.—Other foraminifera, especially *Planoglobulina* sp., are kinked or bent at an angle reflecting a change in growth direction (Fig. 3, 5). The kink is an offset in direction of chamber growth, not just an offset due to a missing chamber. Kinked individuals frequently posses chambers of radically expanded volume in post-kink position.

Bulla overgrowths.—Various bulla and unusual apertural coverings are present in many taxa severely complicating identification. *Globotruncana* is the dominant group involved. Bulla frequently partially cover apertures or wrap around the test, usually extending from the apertural area (Fig. 3, 6). Eccentric bulla appear not only in the Kemp Clay, but also upsection in *Globorotalia pseudobulloides* of the Paleocene Wills Point Formation.

Gaping or multiple apertures.—Racemiguembelina powelli, Pseudoguembelina costulata, P. palpebra, Planoglobulina carseyae and *P. acervulinoides* possess gaping or unusual multiple apertures (Fig. 3, 7). Apertures extend completely across the test with openings approaching 25 percent of the chamber area.

Multiple ultimate chambers.—Multiple ultimate chambers are present mostly in biserial species, but also are found in *Globotruncana* sp. Biserial foraminifera have up to six chambers arranged radially around the ultimate chamber (Fig. 3, 8). One specimen of *Globotruncana* had two complete and identical ultimate chambers (Fig. 3, 9).

General monstrosities.—In the monstrosity category are various *Globotruncana, Rugoglobigerina,* and *Heterohelix* (Fig. 3, 10-12). Many monstrosities resemble the experimentally crushed specimens of Bé and Spero (1981) in which one or more chambers were broken or collapsed

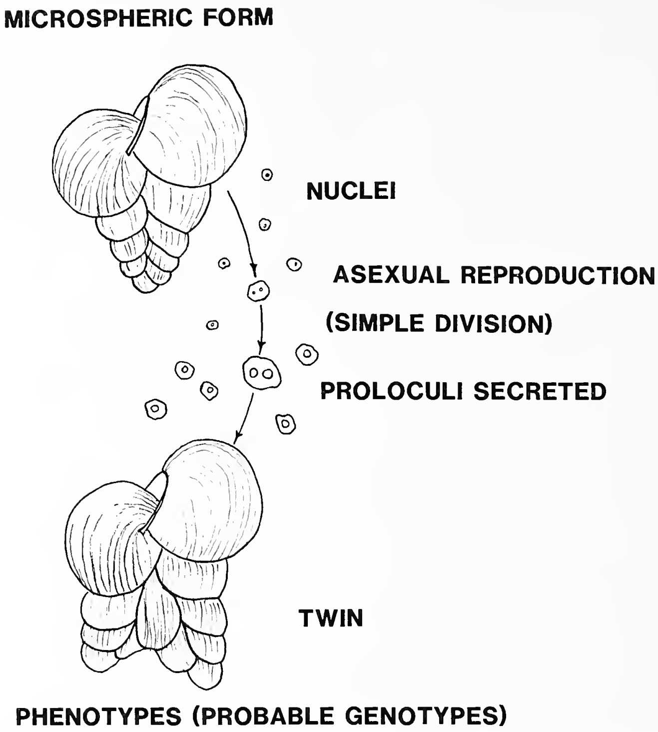

Figure 4. Illustration of proposed origin of twinned specimens through reproductive complications.

and subsequently repaired. Fragments of crushed chambers have been retained, and the tests appear substantially thickened overall.

Discussion

Attributing the various deformities in planktic specimens to a single cause is not easily accomplished. Rather, specific deformation mechanisms are indicated at least at the generic level. This scenario does not preclude comprehensive pressures such as environmental or predatory stress.

Twined specimens with two proloculi and one ultimate chamber may have resulted from reproductive complications. Upon separation of nuclei of the microspheric form (with each gathering protoplasm) two nuclei (genotypically identical) remained in one mass of protoplasm (Fig. 4). Two proloculi formed. The protoplasm divided normally yielding two megalospheric individuals that remained adjacent each other. The individuals fused after secretion of one or more chambers. This process was apparently repeated with three and four proloculi.

The cause for radical ultimate chamber expansion along with an increase in apertural size or number (or both) remains difficult to explain. Olsson (1973) argued that kummerform (diminutive ultimate chamber) foraminifera are the norm, and that normal form (equal or slightly expanded ultimate chamber) may result from environmental stress. If this is the case, then by extrapolation the Brazos foraminifera suffered extreme stress. Hecht and Savin (1972) presented the opposite argument that kummerforms are stress related and associated with colder water temperatures.

Test kinking may represent incipient coiling except that the test remains relatively linear after kinking rather than continuing to coil. The recognized gerontic trend is uncoiling, thus the Brazos forminifera would not be a gerontic population. More probably kinking is a response to stress rather than incipient coiling.

Bulla placement may have functioned as apertural covering, possibly for protection. Bulla covering apertures would be a counter strategy to the biserial foraminifera with gaping apertures. Bulla development appears abnormal, and could attributed to stressful conditions. The normal growth cycle in these specimens appears complete. I believe bulla developed on unusually long-lived specimens. Hecht and Savin (1972) presented limited evidence that bulla are more common in warmer waters.

Foraminifera with two or more ultimate chambers are perhaps some sort of gerontic kummerforms. Multiple ultimate chambers tend to be downsized and of similar shape. If this is a sort of ultimate kummerform, then long life certainly is indicated.

Conclusions

The Brazos River foraminiferal monstrosities probably resulted from different mechanisms stimulated by stressful shifts in their environment. Twinned specimens indicate reproductive difficulties. Crushed and repaired specimens reflect increased predation by organisms such as copepods. Other abnormalities, including incipient coiling, development of bullae, and extreme ornamentation, may be directed toward defense. Rapid test expansion and the addition of oddly placed chambers reduce surface area in relation to greatly increased protoplasm volume—again a possible defense mechanism. Cretaceous planktic foraminifera definitely underwent size increase and complex structural development (keels, bullae, tegilla, and so forth). The Brazos monstrosities mimiced this trend with occasionally extreme results.

The next step in studying abnormal foraminifera is to better document their occurrence in other parts of the Cretaceous and Tertiary as well as in other areas of clearly different paleogeographic setting. Thin sectioning of specimens will better determine causal factors. For example, crushed and repaired foraminifera tend to have retained fragments and abnormally thickened tests. Examination of the common sutures in twinned tests should be intriguing.

The geological significance of the bizarre Brazos River foraminiferal populations remains unclear. Essentially instantaneous extinction scenarios at the end of the Cretaceous are prominant in the literature (especially Alvarez et al., 1980), and are not uncommonly inconsistent with much of the boundary data (Keller, 1989) or are based solely on speculation. Morphological monstrosities extant just below the notorious Cretaceous-Tertiary boundary would indicate preboundary stress rather than an instantaneous boundary extinction "event."

Acknowledgments

I would like to thank the University of Texas at Austin for use of their scanning electron microscope as well as Ingrid Carré of the University of Puerto Rico for photographic work. Field assistance and advice from R. Farrand and H. Billman were invaluable.

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SYNTHESES OF 2-(2-PYRIDYL)CYCLOHEXANONE AND RELATED CYCLOHEXANONES

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Abstract.—Five 4-alkyl-2-(2-pyridyl)cyclohexanones were synthesized by the condensation of morpholine enamine of the appropriate cyclohexanone with pyridine-1-oxide in the presence of benzoyl chloride. In addition to cyclohexanone, 4-methyl, 4-ethyl, 4-isopropyl, and 4-*tert*-butylcyclohexanone were utilized. Hydantoin derivatives were prepared and the enol/keto ratios determined. *Key words:* enol/keto; tautomerization; hydantoin; cyclohexanone.

Our interest in enolizable ketones (Sund and Strickland, 1988) led us to a paper that discussed the synthesis of 2-(2-pyridyl)cyclohexanone (Fig. 1) and its enolization (Hamana and Noda, 1965). We synthesized a series of 4-alkyl-2-(2-pyridyl)cyclohexanones using their method, which consisted of condensing morpholine enamine of the appropriate 4-alkylcyclohexanone with pyridine-1-oxide in the presence of benzoyl chloride. The enamines were prepared from the requisite 4-alkylcyclohexanones and morpholine by a standard method and used without further characterization (Hünig et al., 1973). These 4-alkyl-2-(2-pyridyl)cyclohexanones were yellow to orange oils and were characterized by conversion into hydantoin (Fig. 1) derivatives (Henze and Speer, 1942).

Table 1 lists the 4-alkyl-2-(2-pyridyl)cyclohexanones prepared as well as their boiling points, yields, enol/keto ratios and melting points, and yields of the hydantoin derivatives.

Experimental Section

All chemicals were purchased commercially, except 4-ethylcyclohexanone, which was prepared by the standard oxidation of 4-ethylcyclohexanol. Elemental analyses were performed by Huffman Microanalytical Laboratories, Golden, Colorado 80403. We determined melting points on a Thomas-Hoover melting point apparatus and they

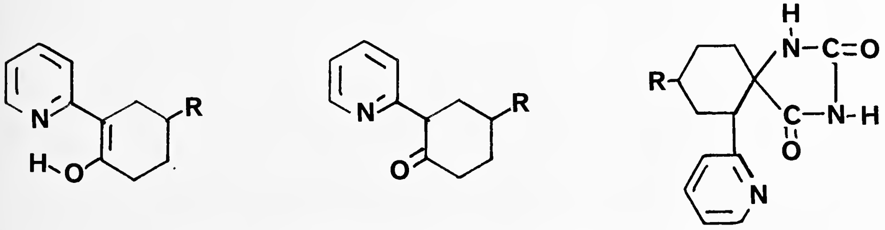

Figure 1. Enol (left), keto (center), and hydantoin (right).

TABLE 1. 4-alkyl-2-(2-Pyridyl)cyclohexanones and 8-alkyl-6-pyridyl-1,3-diaza-2,4-dioxospiro [4.5] decanes (Fig. 1).

R	Yield %	Bp °C/mm	enol/keto ratio	mp, °C	Yield %
H	46	135/0.9[a]	2.3	258-259	45
CH_3	32	125/2	1.5	295-297	87
C_2H_5	46	152/6	1.8	288-290	45
iso-C_3H_7	38	137/2	1.8	274-276	65
tert-C_4H_9	48	142/3	1.5	302-304	73

(a) reported bp 99-100/0.01 mm (Funke and Rissi, 1954); bp 138-140/0.13 mm (Hamana and Noda, 1965).

were corrected. Only one preparation was done for each ketone and thus the yields represent single preparations and could in all probability be improved. The following example illustrates the synthesis of 4-alkyl-2-(2-pyridyl)cyclohexanones.

4-ethyl-2-(2-pyridyl)cyclohexanone.—Fifty milliliters of chloroform and 5.7 grams (0.06 mol) pyridine-1-oxide were placed in a stirred flask. The enamine, 2-ethyl-1-morpholino-1-cyclohexane, 23.4 grams (0.11 mol), was added, the reaction mixture cooled in an ice bath, and 9.9 grams (0.07 mol) benzoyl chloride added dropwise. The reaction mixture stood for three days at room temperature. The Japanese literature suggests that some pyridine-1-benzoate forms during this period of time. The benzoate is a facile leaving group, thus facilitating the acylation of the pyridine by the enamine. At the end of this time, the reaction mixture was acidified with 20 percent HCl to a pH of 1 and the solvents removed under reduced pressure using a water aspirator. The residue was redissolved in five percent HCl and the solution extracted with a toluene-ether mixture. The aqueous layer was made alkaline with solid K_2CO_3, extracted with methylene chloride, and after evaporating the methylene chloride, distilled under reduced pressure, collecting the fraction distilling at 152°C/(6 mm Hg). We obtained 5.6 grams (46 percent yield) of 4-ethyl-2-(2-pyridyl)cyclohexanone. A hydantoin was prepared, mp 286-288°C. The NMR spectrum was obtained with a Perkin-Elmer 9O MHz R-32 spectrometer. The NMR spectrum in $DCCl_3$ showed the following characteristics: we assigned a complex series of signals at one to four parts per million to the various aliphatic protons, the number of peaks being doubled because both enol and keto tautomers were present in approximately equal amounts, a multiplet at 6.9-7.7 ppm for the aromatic protons, with two sharp doublets at 8.5 ppm and 8.2 ppm due to the protons in the 6 position of the pyridine ring of the enol form and the keto form, respectively. Tetramethylsilane was used as an internal standard; the chemical shifts are reported in ppm relative to it all cases.

TABLE 2. Analytical data for review. 8-alkyl-6-pyridyl-1,3-diaza-2,4-dioxospiro [4.5] decanes analysis.

	Calculated			Found		
	%C	%H	%N	%C	%H	%N
H	63.66	6.16	17.13	63.85	6.31	16.99
CH_3	64.85	6.61	16.20	64.59	6.69	15.92
C_2H_5	65.91	7.01	15.37	65.61	7.08	15.07
iso-C_3H_7	66.88	7.37	14.62	66.85	7.46	14.93
tert-C_4H_9	67.75	7.69	13.99	67.54	7.75	14.15

The relative area of the enol proton at 8.5 ppm and the keto proton at 8.2 ppm were determined by integrating the peak areas. Several integrations were performed and the enol/keto ratio was determined to be approximately 1.8. Elemental analysis for C, H, and N in agreement with theoretical values were obtained and submitted for review (Table 2).

ACKNOWLEDGEMENT

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AN EFFICIENT RETRACTABLE MOBILE ANTENNA TOWER FOR RADIO-TELEMETRY STUDIES

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Abstract.—The design and construction of a retractable mobile antenna tower for use with null radio-telemetry receiving systems are described. We discuss the advantages it offers for radio-telemetry studies on large areas, study sites with rough roads, and localities where overhanging vegetation poses a problem for travel with a permanently erected mobile unit. The integrity of the antenna was maintained throughout the study because of the retractable design and its durability. *Key words:* antenna; mobile; retractable; storage; telemetry.

Various mobile telemetry antennas have been described for tracking radio-collared animals. A retractable, directional tower antenna was used with ruffed grouse, *Bonasa umbellus* (Marshall and Kupa, 1963). A directional loop antenna, mounted to a vehicle roof-top and rotated from within, was used to track striped skunks, *Mephitis mephitis* (Verts, 1963). Other vehicle-mounted antennas (Andelt, 1985; Balkenbush and Hallett, 1988) and antenna elevating devices (Kolz and Johnson, 1975) also have been described to aid in the collection of telemetry data.

Mobile antenna towers offer several benefits over land-based antennas. Areas devoid of permanent land-based antenna towers can be "explored" until the proper station (or stations) can be identified. Mobile antennas are particularly beneficial when animals move out of the receiving range for land-based antenna towers. Increased mobility allows the observer to reduce the distance to the animal (Hegdal and Colvin, 1986), thereby decreasing error polygons and overall error potential. Elevated antennas also improve signal strength and minimize antenna interference from motor vehicles (Kenward, 1987).

Mobile antenna towers do have some limitations associated with them. A permanently erected mobile antenna tower cannot be driven in areas with overhanging vegetation or under electric power lines. When using permanently erected mobile units, roads may have to be cleared of overhanging branches (Hegdal and Colvin, 1986), especially for a null system consisting of two yagis spaced one wavelength apart (183 centimeters). Additionally, supports for the antenna array may not protect the elements on rough roads, which may affect accuracy.

A completely retractable mobile tower alleviates problems of overhanging vegetation and rough roads. Furthermore, an antenna capable of total retraction provides a safe means for storage during travel and maintenance of the receiving system. Marshall and Kupa (1963) developed a retractable mobile directional antenna that was designed for

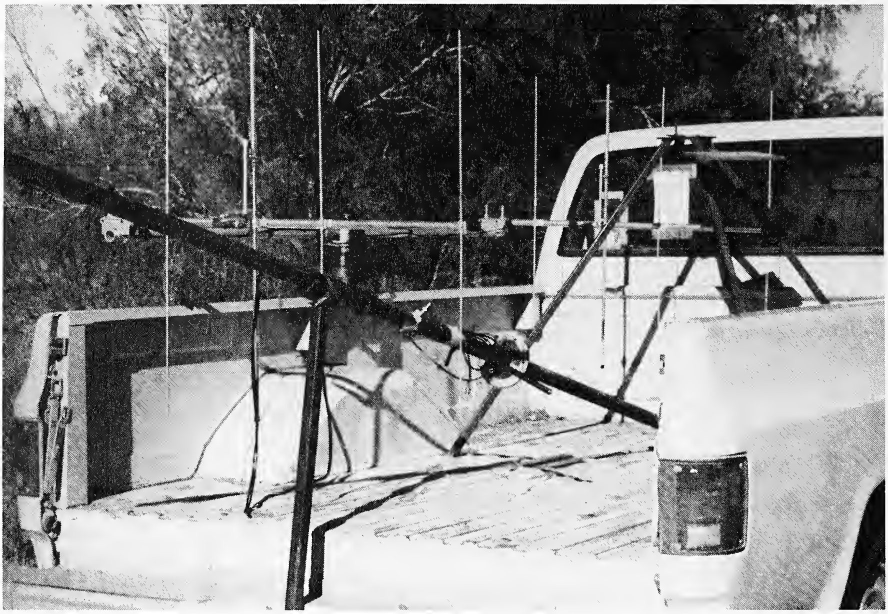

FIGURE 1. Photograph of the mobile antenna tower in the fully retracted position ready for travel.

storage of a single yagi. Balkenbush and Hallett (1988) used a retractable antenna but did not describe the way in which the single yagi antenna was stored for protection. The present report describes the construction of an efficient, retractable null mobile antenna tower (hereafter referred to as the mobile unit), which includes storage of a dual yagi array.

STUDY AREA AND METHODS

A study of white-tailed deer (*Odocoileus virginianus*) habitat utilization was conducted on the 42,510-hectare Piloncillo Ranch in Dimmit, Webb, and LaSalle counties, Texas. The ranch has a good network of roads, primarily of sandy loams, which frequently erode during storms. In addition, many of them are found in areas possessing overhanging woody vegetation.

Project objectives required two simultaneous readings upon the radio-collared animals with error polygons less than two hectares. To avoid purchasing and erecting more permanent land-based towers, we developed the mobile unit for use in conjunction with our existing land-based towers. The mobile unit had to withstand travel at moderate speed over rough, sandy roads with overhanging vegetation and electric power lines. Our mobile unit consisted of five parts: a null antenna array, a mast, an antenna holder, a vertical tripod mast support, and a horizontal mast support.

The null antenna array consisted of two, four-element, directional yagi antennas (Advanced Telemetry Systems, Inc., Isanti, Minnesota), separated by a cross boom 183 centimeters wide, and fastened with T-clamps. Coaxial cables extended from the respective yagis, along the cross boom, and down the mast.

The function of the mast was to elevate the antenna 1.5 transmitter wavelengths (2.74 meters) above the pickup truck cab, thereby maximizing signal strength and minimizing

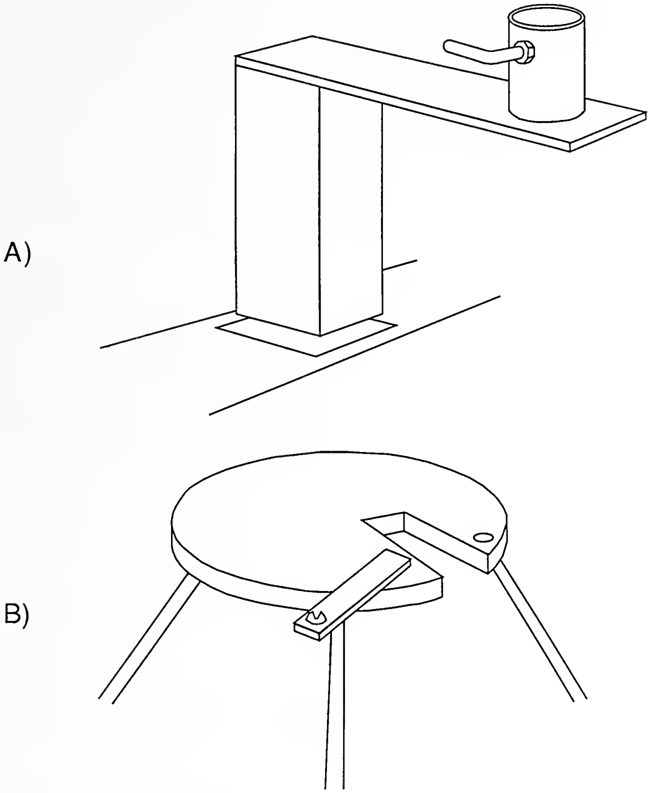

FIGURE 2. Line drawing showing the antenna holder (A) in its proper orientation and the vertical tripod mast support (B) for use during data collection periods.

potential interference. A four-meter pipe, composed of one- and three-meter sections, functioned as the antenna mast. The smaller section was connected to the bed of the truck by a pivoting bracket, which allowed the mast to be erected to a vertical orientation and retracted to a near-horizontal orientation (Fig. 1). A steel rod fit securely into the bottom section and extended from it 30 centimeters. This allowed the three-meter section to be slipped over the steel rod and rotated in a full 360° circle. An adjustable compass rosette, attached to the bottom portion, was used to orient the antenna to true-north and to quantify animal locations. Upon erection of the tower, the mast slid securely into the vertical tripod mast support.

The holder held the array in the bed of the truck, protecting the antenna elements during travel. The antenna holder consisted of two 0.64-centimeters (0.25-inch) angle irons measuring 20.3 centimeters in length, a 7.6-centimeters section of 3.2-centimeters (1.25-inch) pipe, a sheet metal plate (eight by 20 centimeters), and a nut-and-bolt assembly. Two pieces of angle iron were welded together (Fig. 2A), and placed into the vehicle's accessory mount. The sheet metal plate (eight by 20 centimeters) was welded to the angle irons so the plate extended over the inside of the truck bed by 10.2 centimeters. The pipe, welded vertically onto the sheet metal plate, held the antenna array during travel (Fig. 2A). A nut-and-bolt assembly on the side of the pipe allowed for tightening of the antenna array into the holder.

The vertical tripod support served to maintain the mast in an upright position during periods of telemetry data collection. It consisted of three sections of four-sided pipe (one meter long), an oval-shaped sheet metal plate (25.4 centimeters in diameter), and a latch for securing the mast in a vertical position (Fig. 2B). The tripod legs were secured to the bed of the truck by a bolt that passed through the surface of the bed. The oval-shaped sheet metal plate was welded to the top of the tripod legs. A U-shaped cut was made into the plate which permitted the mast to be placed in an upright position.

During transport of the mobile unit, the antenna mast was positioned horizontally on a support located on the truck bumper, similar to Marshall and Kupa's (1963) design. The support consisted of a pipe, welded to a steel plate bolted to the bumper. A 13-centimeters section of 0.64-centimeters (0.25-inch) angle iron, welded to the top of the support, prevented the mast from falling sideways and into the bed. A hose clamp was moved down the mast over the angle iron during travel to hold the mast firmly in place.

Results and Discussion

Field tests were conducted to assess the error and utility of the antenna. Known and calculated bearings were compared for 15 beacons placed throughout the study area (Springer, 1979). Observations from 23 stations produced a mean standard deviation of 1.86° (range 0.24 to 5.60°). Travel at speeds up to 40 miles per hour did not affect the integrity of the antenna according to subsequent accuracy tests. Furthermore, set-up of this design required only 20 seconds and was not fatiguing to the operator. The ease of construction, maintenance, and set-up made this an efficient antenna design. The design permitted easy travel through areas with dense overhanging brush because antenna elements were shielded by the truck.

Approximately 12 hours were required for the construction of the mobile unit and the cost of the materials was inexpensive. The sheet metal, pipe, and angle iron used in construction, cost approximately $60. The antenna array was purchased commercially for about $257, making the total cost some $317.

In summary, our retractable mobile unit was a cost-effective product that offered flexibility for collecting telemetry data under the conditions described. A thorough coverage of our large study area was obtained without building many permanent land-based towers, clearing overhanging vegetation, or avoiding travel under electric power wires. Furthermore, accuracy tests proved that this design was an efficient one in which the integrity of the antenna was maintained.

Acknowledgments

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ORIGIN OF COLOR OF AMERICAN INDIAN BLACK AND RED CERAMICS

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Abstract.—Results of studies on the chemical cause of the black coloration imparted to ferruginous clay ceramics that are fired under reducing conditions, and of the red color of these ceramics when fired under oxidizing conditions, are presented. Carbon and carbonaceous matter are ruled out as the principal blackening agent, as are iron and iron-oxide species of sizes greater than 300 nm, in the pottery studied here. The iron and iron-oxide system is likely responsible nonetheless, but if it is, the particle sizes of any such species must be less than 300 nm. In a red pottery sample studied, the principal coloring agent was hematite.

Early in this century, Hewett (1909*a*, 1909*b*) excavated archaeological sites on the Pajarito Plateau in New Mexico (an area that later became widely known with the establishment of the Manhattan project and then the Los Alamos National Laboratory). During excavations, Dr. Hewett was intrigued by pottery found at the sites, which was matte black with shiny polished black designs. In order to more nearly establish the technical aspects of its production, Hewett requested the aid of Maria Martinez, a native American potter, to attempt to duplicate this pottery. Maria, along with her husband Julian, who had been a laborer on Hewett's dig, were not successful, however, until shortly after the end of the First World War. After their rediscovery of the technique, this type of pottery became, and has remained, a popular style of "traditional" pottery in the San Ildefonso and Santa Clara Pueblo Indian settlements.

Although the necessity for reducing conditions is well known, the specific chemical cause of the black coloration of ancient ceramics has only recently began to be well understood (Hofmann, 1962, 1966; Hegde, 1966, 1975; Shepard, 1971; Hedges, 1975; Longworth and Warren, 1975; Noll et al., 1975; Longworth and Tite, 1979; Rogers, 1979; Maggetti et al., 1981; Maggetti and Schwab, 1982; Gilles and Urch, 1983; Chazan and McGovern, 1984; Makundi et al., 1989). Gilles and Urch (1983) summarized and expanded on the usual attributions in potteries from other countries:

"Iron oxide and hydroxides present in ferruginous clays, or added in the form of ocherous earths, for example will, on firing under reducing conditions, form spinel phases which are predominantly black in colour. The most common of these are hercynite ($FeOAl_2O_3$) and its solid solution series, and magnetite (Fe_3O_4) (Hofmann 1962, 1966, Longworth and Tite 1979, Longworth and Warren 1975, Maggetti et al., 1981). Iron-rich silicates containing a high percentage of ferrous ions occur naturally in some clays and are another possible cause of black colouration provided that they are not oxidised or destroyed during firing. In ceramics in which vitrification has occurred, a black colour could be produced by ferrous ions in a glassy matrix (Hegde 1975).

"Clays rich in organic material, or to which carbonaceous material has been added, will fire black in colour under reducing conditions, owing to the formation of carbon. Alternatively, carbon can be deposited in the surface of wares by firing in a smoky atmosphere (Noll 1977) or by application of a 'carbon' paint (Shepard 1971) or possibly bitumin (Rahtz and Greenfield 1977)."

Almost all of the above references dealt with the black paints used on ancient ceramics from various regions. Most of these styles differ considerably in detail from the American Indian potteries studied in this work; we restricted our study to pottery that is black (or red) throughout. Black coloration of ancient and modern American Indian ceramics is generally attributed to the presence of carbon (or carbonaceous matter), or to manganese oxide, or to one of the several iron oxide compounds. A critical examination of reported studies reveals little unambiguous or even strong evidence supporting these conclusions when the discussion is limited to ceramics with both black surface and fabric.

We will discuss these possibilities below as we describe our own studies attempting to understand the coloration in modern, "black on black" (B/B) pottery of the San Ildefonso and Santa Clara Pueblos in northern New Mexico, and by implication, ancient American Indian ceramics, and other archaeological ceramics throughout the world with black color occurring throughout the pottery. We are not considering the surface blackening of ceramics with nonblack fabric, which occurs during use over fires, or by painting with the various agents mentioned above, although the cause of the black coloration may be closely related in some cases; studies referenced above are almost all of this situation. We took broken, modern American Indian pottery, a red on red pot and a black on black pot from the Santa Clara, New Mexico, Pueblo as our objects of study and supplemented those with pottery samples prepared from local clay and fired to produce both red and black colored ceramic samples.

EXPERIMENTAL METHODS

Two broken modern American Indian ceramic pots were purchased for study. One was a carved, polished black on matte black Santa Clara Indian pot. Upon breaking the pot into smaller samples for study, the black coloration was seen to extend throughout the pot. It was uniformly black with no red or paler coloration being observed. For comparison, a polished red on red Santa Clara pot also was purchased for study.

We also prepared a series of both red and black ceramic samples from a local clay for comparative studies. For these, a sample of dry clay was sifted through an Allen-Bradley no. 35, 500-micron screen and mixed well to ensure homogeneity. The sifted dry clay then was mixed with water to create a wet, moldable clay that was rolled out into a rope of approximately one centimeter in diameter, cut into buttons two to three mm thick, and allowed to dry in a desiccator for two weeks. Twenty-eight such buttons were made and adjacent buttons were selected to be fired alternately black and red, that is, under reducing and oxidizing conditions, respectively. A few interspersed buttons were saved unfired.

For firing the pottery, a homemade kiln fueled with propane was used. The samples to be fired under oxidizing conditions were simply laid on the kiln floor and heated. The samples to be fired under reducing conditions were placed in layers of sawdust and charcoal in a two-inch diameter steel pipe. These remained in the pipe throughout the firing and subsequent cooling processes. A charcoal-sawdust mixture was added to the pipe as it burned away during firing. The firing temperature of 840° C was reached approximately 30 minutes after the kiln was lit and was held for one hour to ensure equilibration of the samples within the pipe. After cooling, we removed the red pieces, still too hot to touch, which were at that time black, but which turned red as they cooled and oxidized in air. Most of these red buttons had broken during firing and cooling as we had not added temper. We allowed the black pieces to cool overnight inside the pipe. Removal of the black buttons the next day confirmed that they were indeed black and none of these had broken during either the firing or the cooling process. Subsequently, we broke open some red buttons and some black buttons to confirm that the surface coloration occurred throughout the samples.

Results and Discussion

We utilized a number of analytical methods in an attempt to elucidate the chemical origin for production of the black color arising from a red clay, which is fired under reducing conditions, including chemical analysis of carbon and manganese, thermomagnetic analysis, x-ray diffraction, and low-temperature/low-pressure oxygen and hydrogen plasma reactions. Each of these techniques was chosen because of its utility in examining various possibilities. Nonetheless we cannot yet say unequivocally in a detailed way what precise chemical reaction(s) are responsible for the color transformation. We will discuss below each of the techniques we used and the information indicated by each. In large measure, we were only able to eliminate some of the possibilities often ascribed as the reason for the production of the black coloration.

Carbon and Manganese Analyses

Our first experiment was designed to test the suggestion that firing clays in environments rich in organic material, as in the American Indian technique of smothering a fire with dried horse manure, will cause the incorporation of carbon into the ceramic matrix and, therefore, lead to black coloration. This was the explanation given to us by several archaeologists in the Santa Fe, New Mexico, area when we initially enquired whether the cause for this transformation in color was known. However, the elemental carbon analyses we conducted indicated that the carbon content of both the red and the black potteries were too low to cause significant blackening. Values of less than 0.4 percent carbon were found in all samples with no significant difference found between red and the black ceramics. In some analyses, the red had slightly higher carbon content and in some carbon was higher in the black samples. To establish the degree of blackening that might be expected by the presence of elemental carbon, we added 1 percent carbon black to a white (kaolinite) clay; only slight darkening compared to the color of the black pottery samples was observed. The white clay became off-white, not even darkening to a notable gray color. We conclude that formation or implantation of elemental carbon is not a factor in determining black coloration in potteries of the sort studied here. This conclusion confirms that of Makundi et al. (1989). We will include more about this in our discussion of the plasma reactions, where this conclusion is strengthened and extended to include carbonaceous matter in general.

Although we have measured the manganese contents of several varieties of Etruscan ceramics from Murlo, Italy, in our laboratory (Tobey et al., 1986), it is not clear that elemental analyses of manganese will shed much light on the suggestion that reduction of manganese oxides causes black coloration in some ceramics. It is likely that both the oxides and metallic manganese will be black in the finely divided state encountered in the pottery samples. We see no reason to suspect that metallic manganese will color ceramic fabric significantly darker than will oxides. Our analyses showed no significant enrichment of manganese of Etruscan ceramics. Manganese and its oxides do not play a significant role in the coloration of the ceramics of the type considered here.

Thermomagnetic Analysis

We previously had utilized thermomagnetic analysis of carbonaceous chondrites to establish the presence of magnetite (Fe_3O_4) in those black colored meteorites similar, at least superficially, to the color of the black pottery and used saturation magnetization to measure percent of magnetite in those samples (Larson et al., 1972; Watson et al., 1973; Herndon et al., 1974; Hyman and Rowe, 1983, 1986). The presence of metallic iron also can be established by the same technique. For instance, a clear indication of the presence of both metallic iron and magnetite in the carbonaceous meteorite, Novo-Urei, is demonstrated in Figure 1. Magnetite is indicated in Figure 1 with a Curie temperature of approximately, 590° C; that is, the magnetization curve drops rapidly near 590° C as the magnetic magnetite is rendered nonmagnetic by the thermal agitation. Metallic iron also is illustrated in Figure 1 by the presence of a second Curie temperature near 790° C, that is, the point at which the magnetization shown by the second plateau disappears. Hematite (Fe_2O_3), which is less magnetic than either the magnetite or metallic iron, is characterized by a Curie temperature at 675° C; as

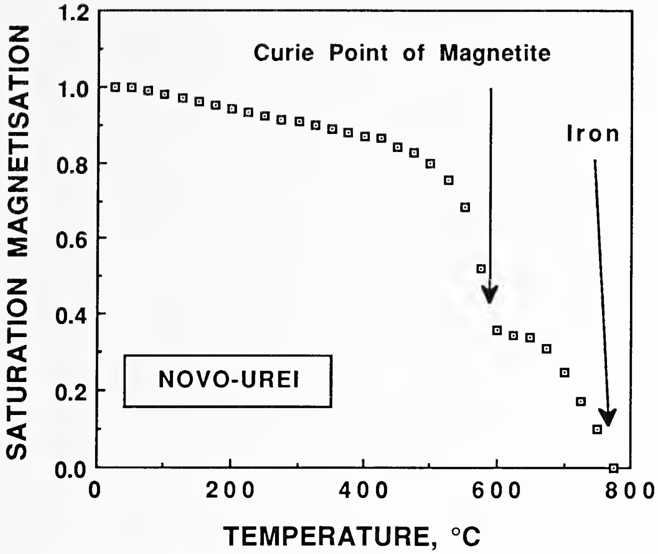

FIGURE 1. Saturation magnetisation versus temperature curve for the Novo-Urei carbonaceous meteorite. Thermal analysis clearly shows both the presence of magnetite (Curie temperature causing an inflection at approximately 590° C) and metallilc iron (Curie temperature at 790° C) in this sample.

indicated by the thermomagnetic curve for Novo-Urei pictured in Figure 1, no hematite is present.

Because the partial reduction of the red iron oxide, hematite, to the black oxide, magnetite, has been suggested as producing the black coloration in ceramics fired under reducing conditions, we decided to subject various red and black pottery samples to thermomagnetic analysis. Buddington and Lindsley (1964) have shown that hematite will not reduce to magnetite at 500° C unless the oxygen fugacity is less than 10^{-18} atmospheres. However, Kobayashi and Schwartz (1966) found hematite converting to magnetite in a red sandstone in a thermomagnetic run in air. It thus is probable that, under conditions used by native American Indian potters, magnetite (and even metallic iron in some cases) will form. In the simplest possible case, that is, if pure hematite were the cause of the red coloration on red pottery, the samples should lose their magnetization near 675° C. The black pottery, on the other hand, if blackened by the conversion of hematite to magnetite, should lose its magnetization near 590° C. A typical sample of the red Indian pottery showed a Curie temperature of approximately 675° C, as seen in Figure 2B, indicating the probable presence of hematite. Results on black Indian pottery did not show the presence of magnetite (or metallic iron), however. For example, a black Indian pottery sample studied showed a Curie temperature of 525° C, as set forth in Figure 2A. In none of the

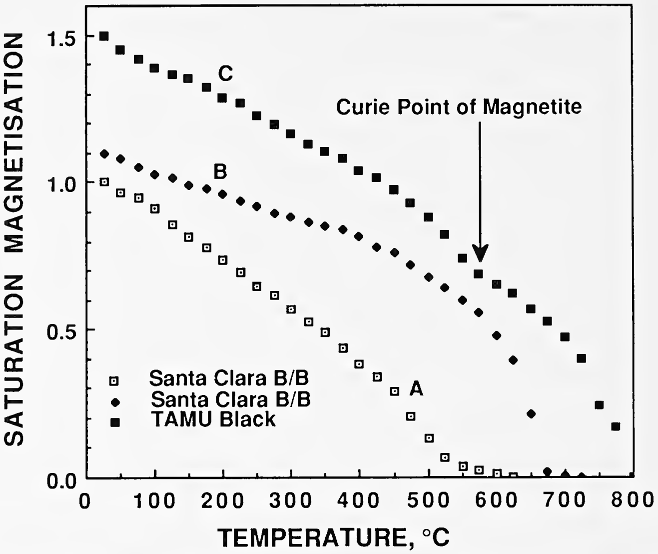

FIGURE 2. Saturation magnetisation versus magnetisation curves for a sample of black Indian ceramic (A), a sample of red Indian ceramic (B), and a homemade black pottery button, (C) (see text). Whatever causes the curve for the black sample of Indian pottery, it is not predominantly magnetite nor metallic iron. The curve C for the homemade black button was suggestive of a small component of magnetite (minor inflection at 590° C) and metallic iron (Curie temperature at 790° C). See Figure 1 for comparison, where both magnetite and metallic iron are clearly indicated.

samples of black Indian pottery selected for thermomagnetic analysis did we see a Curie temperature that would suggest that either magnetite or metallic iron was responsible for the thermomagnetic curve observed. A thermomagnetic curve (2C) of a homemade black pottery button (TAMU Black) did show a hint of an inflection at 590° C, which most probably was caused by the presence of a slight amount of magnetite, as well as a pronounced Curie point at approximately 780° C, which was almost certainly due to metallilc iron. It seems that the reductions we carried out using the charcoal-sawdust mixture were at a lower oxygen fugacity, that is, a more highly reducing environment, than the Indian pottery samples we investigated. Oddly, after sitting in the open, these black buttons slowly reoxidized to red. Apparently, the iron metal we produced was more easily oxidized in the atmosphere back to hematite than is the blackening agent in the Indian ceramics, which do not redden under the same conditions even after 70 years or more.

We conclude that reduction of hematite, which is present in the red pottery, to relatively pure magnetite does not play a dominant, if significant at all, role in producing the black coloration, in ferruginous clays fired under the conditions typically used by the modern American Pueblo Indians. Our thermomagnetic evidence does not preclude formation of another, nonmagnetic, iron oxide, for instance wüstite (FeO), which may have a strong effect on the black color. Wüstite was ruled out by x-ray diffraction, however (see next section). There is a critically important caveat that we must place on the conclusion that magnetite (or other iron oxides and other spinels) plays only a minor role in causing black color. Thermomagnetic analysis will not detect magnetite particles that are superparamagnetic, that is, particles below approximately 300 nm in diameter. It is conceivable, even likely, that reduction of the hematite in ceramics results in the formation of magnetite particles less than 300 nm in size, which may nonetheless contribute to the black color. A scanning electron microscope survey of the black American Indian pottery indicated that fine magnetite was feasible because of the fine-grained nature of the pottery fabric. Magnetite grains that were greater than one micrometer would have been visible with the scanning electron microscope.

The possibility of superparamagnetic magnetite in the black ceramics could be investigated through use of low-temperature (liquid nitrogen) Mössbauer spectroscopy, a technique not available to us at this time. Other workers (Hedges, 1975; Longworth and Tite, 1979; Longworth and Warren, 1979), using Mössbauer spectroscopy on black potteries of a different sort, found that magnetite played a significant role in determining the color of black glazes in Chinese, Greek, and East Indian, and finally in Etruscan ceramics. A recent report by Makundi et al. (1989) using Mössbauer spectroscopy concluded that black coloration in early Cypriote and Nubian C-group black-topped potteries, coloration that seemed to have been achieved by the firing process as is the case for the Indian potteries studied in our work, "is due to Fe^{2+} ions in nonmagnetic compounds. . . . The refiring experiments confirmed that the presence of carbon is not necessary for the black color."

X-Ray Diffraction

X-ray diffraction is another technique that is informative concerning the presence of crystalline materials, and that exhibits characteristic peaks for magnetite and other iron oxides. We began with x-ray diffraction spectrometry of a sample of red Santa Clara pottery. The major peaks were, as expected, due to quartz and hematite as is shown in Figure 3. This was followed by an x-ray diffractometry spectrum taken on a sample of black Santa Clara pottery that gave quite unexpected results. Only one small unidentified peak, except for those of quartz, was seen above background. In a further attempt to investigate this puzzling situation, we ground a piece of the black pottery, subjected it to a magnetic separation, and then ran an x-ray diffraction spectrum on the magnetic fraction. The results are shown in Figure 4. Even after the magnetic separation, there is only weak indication for the presence of

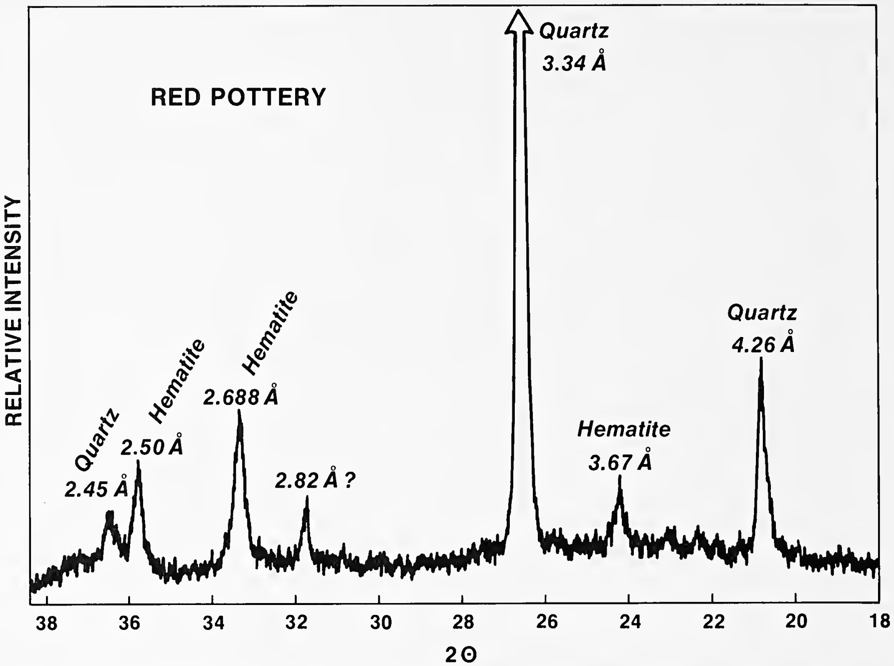

FIGURE 3. X-ray diffractometry spectrum of a sample of red Santa Clara Indian pottery. Major peaks are seen due to quartz and hematite, as expected.

magnetite, Fe_3O_4, and also for maghemite, a different form of Fe_3O_4. The large peak at 2.88 A is unidentified and did not appear in the run before the magnetic separation. No FeO peaks were observed in the x-ray diffraction spectra. As in thermomagnetic analysis, the presence of extremely minute particles of magnetite or maghemite, or both, would not be detected by x-ray diffraction. Again with the critical caveat, that is, that magnetite or maghemite, or both, may be present as fine particles of less than 300 nm, we conclude that neither magnetite nor maghemite are responsible for the black coloration in the Indian ceramics studied here. The lack of distinctive x-ray peaks in the black pottery remains a mystery, unless the compounds responsible for the color are present as extremely small particles, a situation that seems likely when all the evidence presented in this paper is considered. An additional x-ray diffraction spectrum showed minor peaks due to hercynite, $FeOAl_2O_3$. Unless the iron oxides are present as particles less than 300 nm, we are left with a quandary. In what chemical form are the iron oxides after reduction in the black pottery that were demonstrated before reduction to be present in red pottery as hematite?

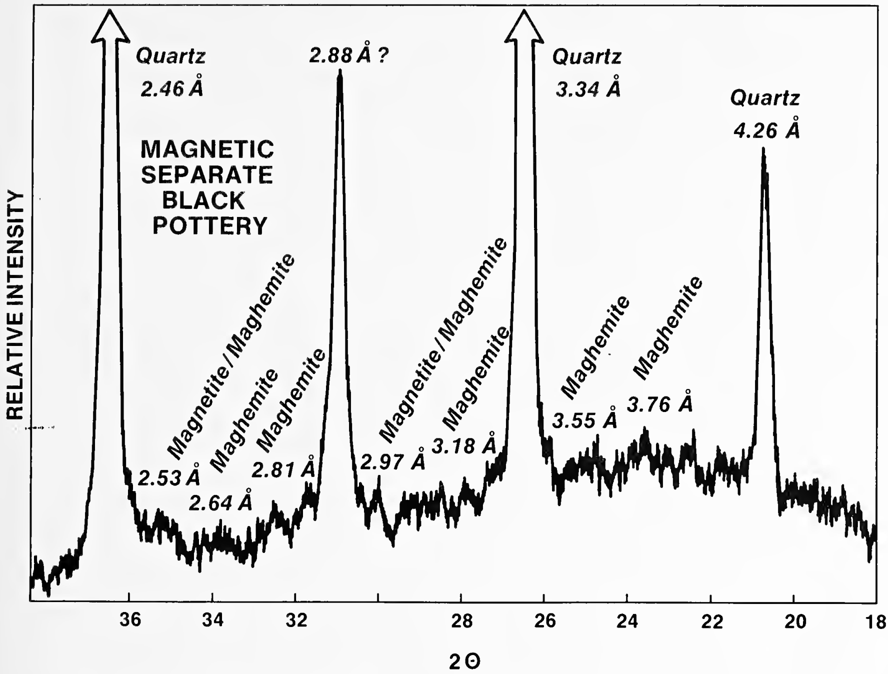

Figure 4. X-ray diffractometry spectrum of a magnetic separate from a sample of black Santa Clara Indian pottery. Even in the magnetic fraction, there is only a weak indication of magnetite and maghemite.

Low-Temperature/Low-Pressure Plasmas

We have subjected pottery samples to repeated reductions and oxidations in low-temperature/low-pressure oxygen and hydrogen plasmas in a reaction chamber similar to that shown, schematically in Figure 5. We produced an oxygen plasma for reaction of a black ceramic sample. In the conditions we used, the primary reactive species was atomic oxygen, present as approximately 10 to 20 percent of the particles in the reaction gas chamber. A majority of the particles remained as molecular oxygen, O_2. Only a small percent of the oxygen species were ionized (for example, $O^{2+,2-}$, $O^{+,-}$, and so forth), and the ceramic sample was far enough removed from the external plasma electrodes so that ionic recombination was expected to be virtually complete at the sample. The primary reaction of interest that we expected, therefore, was of atomic oxygen with iron oxides. After reaction with an oxygen plasma, the initially black pottery was rendered reddish-brown in color. A similar situation existed for the hydrogen plasma; there, of course, the expected reaction is the reduction of the hematite to the black oxides of magnetite/maghemite or wüstite, or both. The initially red-brown pottery

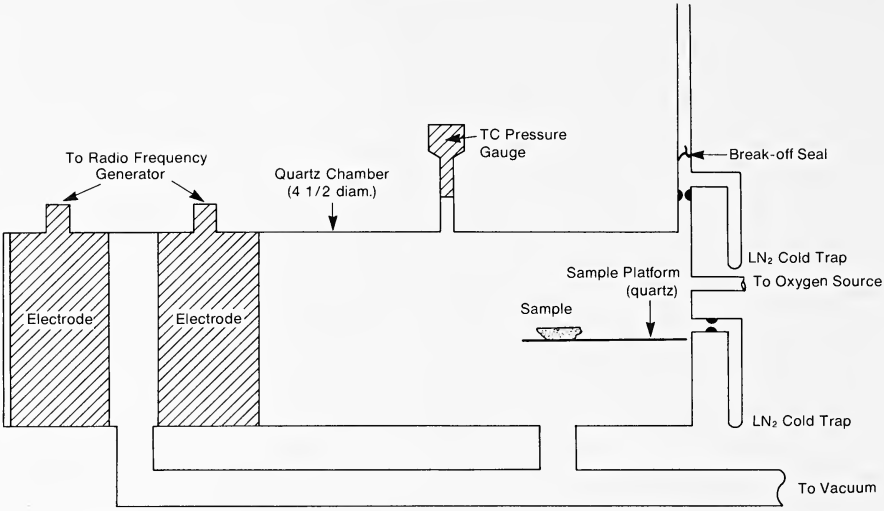

FIGURE 5. Schematic diagram of the low-temperature/low-pressure oxygen plasma chamber. The gas could easily be switched to hydrogen and back to oxygen to yield reactive alternating oxidizing and reducing conditions within the chamber.

turned black in hydrogen plasma. Such samples could be repeatedly recycled from black to red and back.

One of the properties of an oxygen plasma, and one of interest here, is that it is quite reactive with virtually all varieties of carbonaceous materials. If the black coloration of these ceramics were due to carbon or even to the carbonaceous furfurans, as suggested by Rodgers (1979) for black smudges on pottery used over open fires, then it would be expected that the oxygen plasma would react with the carbonaceous matter to form CO_2, CO and H_2O. However, the samples were recycled from black to red to black to red, and so on, by subjecting the sample first to an oxidizing oxygen plasma, then to a reducing hydrogen plasma, back to an oxygen plasma, and so on. Inasmuch as the black color reappeared each time upon reduction, it was not due to carbon or other carbonaceous matter that would have been converted to gaseous CO_2, CO, and H_2O during the course of this oxidation-reduction cycling. Rather it was more likely due to a metal oxide system as that of iron, possibly including other spinels such as hercynite, in which the changes between the various coloring agents (for example, red hematite contrasted with black magnetite, or maghemite, or wüstite, or some combination thereof) are reversible. We reaffirm, however, that if magnetite, or maghemite, or wüstite are really involved, they are present as particles smaller than the sizes that would respond to thermomagnetic analysis and x-ray diffraction.

CONCLUSIONS

Our work, like that before us, has not been totally successful in pointing to the precise chemical reactions most responsible for producing the black coloration in ferruginous clay ceramics, fired under reducing conditions, such as those used, for example, by modern American Indian potters. It is probable that the various reactions are complicated enough that, in fact, the precise reactions will depend critically on the exact extent of the reducing conditions to which the particular ceramic was exposed. We have, however, been able to rule out carbon and other carbonaceous material as the principal blackening agent in cases where the black coloration extends throughout the fabric of the ceramic material. Our evidence does not preclude that the iron and iron-oxide system may be responsible; if it is, however, the particle size of the black-reduced metallic iron or iron oxides must be less than 300 nm in diameter. Considering the present evidence, we think that this is likely the case. It appears to us that the definitive experiments are the low (liquid nitrogen) temperature Mössbauer spectroscopy experiments, which can detect and differentiate the iron-iron oxide species of interest even at extremely small particle sizes. Both of the Mössbauer studies on black and red surface paints on Chinese, Greek, and East Indian ceramics have in fact concluded that magnetite was important in causing black coloration and that the magnetite particles were quite small (Hedges, 1975; Longworth and Tite, 1979). In a third study, one involving Etruscan ceramics, the same conclusion was reached (Longworth and Warren, 1979). More germane to our studies here, however, was the Mössbauer study by Makundi et al. (1989), who found that the black coloration in the Cypriote and Nubian C-group ceramics, a product of the firing conditions, not paints, was due to the formation of ferrous ions in nonmagnetic compounds. Our thermomagnetic analyses are consistent with their Mössbauer results.

NOTE ADDED IN PRESS

In a report of a Mössbauer study on red-black pottery from Early Bronze Age Cyprus just received from Waern-Sperber (1988), the same conclusions were reached as stated in our summary. She concluded: "To sum up, the results of the analyses indicate that the black colour of the EC II Red Polished black-topped bowl is not entirely due to carbon as suggested. Neither is it mainly due to manganese. Furthermore, positive evidence of magnetite in the black slip could not be obtained. The investigation indicates that the red part contains haematite and has been subjected to strongly oxidizing firing. The black part, though resembling haematite [in the Mössbauer spectrum] is different in that it also contains Fe^{2+} and has, it seems, been affected by more reducing conditions."

Obviously, further investigations are necessary for a complete understanding of the chemical cause for the black coloration in American Indian ceramics and in others worldwide.

ACKNOWLEDGMENTS

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OBSERVATIONS ON OBTAINING WHITE-TAILED DEER FAWNS FOR EXPERIMENTAL PURPOSES

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Abstract.—In an attempt to obtain fawns for experimental purposes, 26 adult female white-tailed deer were captured using a drive net at the Welder Wildlife Refuge, San Patricio Co., Texas, on 12 March 1986. Deer were held in a 1.6-hectare enclosure until the end of the fawning season. Twenty-two does survived and at least 15 produced fawns. Thirty fawns (11 females, 19 males) were born alive between the dates 24 May and 23 June 1986. These results suggest that obtaining fawns from wild-trapped does held temporarily is feasible. Further, the stress of trapping, handling, close confinement, and daily disturbance apparently did not adversely affect birth rates. *Key words:* white-tailed deer; *Odocoileus virginianus;* Texas; captives; does; fawns.

Tame white-tailed deer (*Odocoileus virginianus*) are used to study physiology, nutrition, growth rates, and behavior or food habits (Robbins and Moen, 1975; Bryant et al., 1981). Fawns generally are removed from their does shortly after birth to facilitate the taming process. Techniques used include capturing fawns in large enclosures where does are maintained throughout their lifetimes (Downing and McGinnes, 1969) or catching them in the wild by observing the behavior of wild does (White et al., 1972).

This paper describes the results of obtaining fawns from wild-trapped females held temporarily in an enclosure and then released back into the wild soon after birth of their young. The purpose of the project was to obtain fawns that were sufficiently tamed at one year of age to obtain data on food habits through direct observation.

Methods

Twenty-six adult female white-tailed deer were captured using a drive net (Beasom et al., 1980) at the Welder Wildlife Refuge, Sinton, Texas, on 12 March 1986. No attempt was made to determine if does were pregnant. Each animal was injected with one milliliter of acepromazine maleate (10 milligrams per milliliter) at the time of capture. Deer were transported two to nine kilometers by trailer to a 1.6-hectare enclosure within one to five hrs after capture. When the effect of the tranquilizer wore off, the deer often became excited and ran into enclosure fences, resulting in some minor injuries (lacerations and bruises). In mid-April, two semi-tame does were baited-in, captured and placed with the rest of the does.

The enclosure consisted of four interconnected pens (64 by 32 meters each, Fig. 1 A). By keeping the internal gates open, deer were allowed access to the entire 1.6-hectare enclosure. Outside fences were V-mesh net wire, 2.5 meters high. Inside fences were common net wire

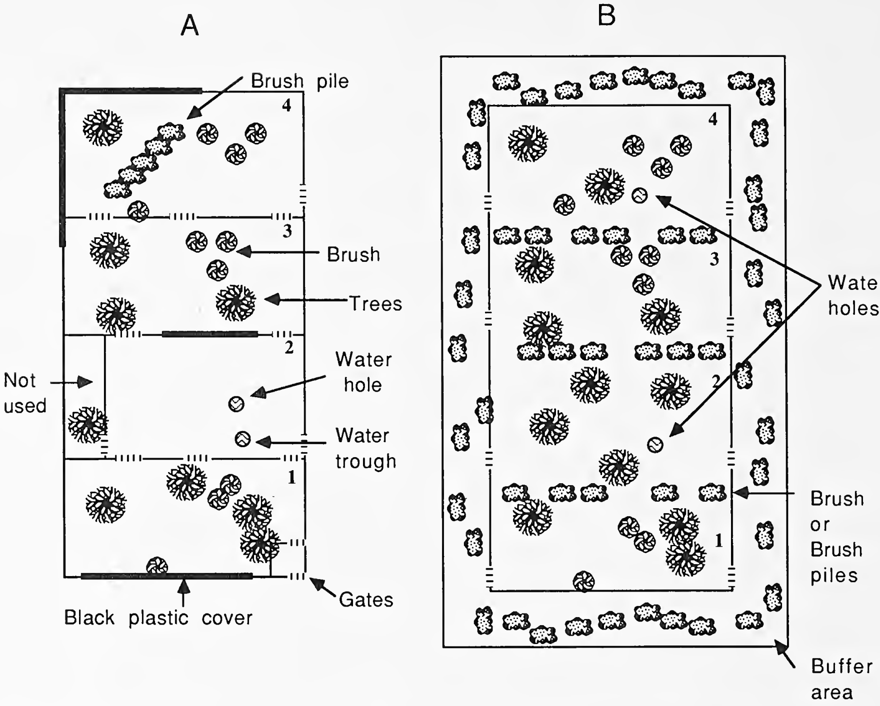

FIGURE 1. Pen used this study (A) and that suggested for similar studies (B).

(15 by 15 centimeter mesh). To minimize human interference and disturbance by free-ranging cattle, portions of the exterior fence were covered with black plastic sheeting to create visual obstruction. We also covered some internal fences with black plastic to provide a visual obstruction between the deer and people setting out feed or working in the pens. The holding pens were cleared of understory brush and mowed one week prior to capture of does to facilitate searching for fawns. A 30-meter line of brush was piled two-meters high in the fourth pen to provide screening cover.

Because deer are not fed supplements on the refuge, wild-trapped does had no experience eating pelleted feeds. Whole corn was offered ad libitum for 14 days but deer refused this feed. For the next eight days, two-centimeter pellets of cottonseed cake (35 percent crude protein) and 0.6-centimeter pelleted deer food were offered ad libitum. Deer did not feed regularly until alfalfa (*Medicago sativa*) hay was offered on 3 April. Once deer began eating alfalfa hay, they also began eating the pelleted deer food. The captured deer refused to drink from a trough that was 0.5 meters high as evidenced by the lack of deer tracks at the trough. When deer tracks were observed at a small puddle formed by a leaking water hose, we buried a pan at ground level and allowed a water hose to drip into it. The watering hole was used the same day it was installed and every day thereafter.

Five does died during the first three weeks of captivity. A sixth doe escaped by jumping the 2.5-meter-high fence. The remaining 22 does survived and produced fawns. Some does showed a loss of weight during their captivity but had regained normal body condition at the time of their release back into the wild.

Daily searches for fawns were begun in mid-May. Newborn fawns were tagged with numbered aluminum poultry tags. Males were tagged in both ears and females in one ear. Male fawns were left with does, whereas female fawns were removed 48 to 72 hours after birth. All were bottle-raised in concrete-floor cages until weaning following the guidelines of Kirkpatrick and Scanlon (1984). Female fawns were moved to a 0.5-hectare pen at 14 weeks of age, and fed alfalfa and horse-mule feed or deer pellets (16 percent crude protein) until one year of age.

RESULTS AND RECOMMENDATIONS

Thirty fawns (11 females, 19 males) were born alive in captivity. One set of twins was aborted early in May. However, at least 15 of 22 (68 percent) does gave birth to normal fawns.

Two of the 11 female fawns were born with hind leg abnormalities (abnormal tarsus). This may have been caused by physical damage to the fetus when handling wild-trapped does at capture. The fate of one abnormal fawn released with its dam at approximately one month of age is unknown. The second abnormal fawn was bottle raised but died at six months of age. At death, this fawn weighed the same as a fawn raised under confinement that was two to three months old.

Apparently confinement of the dams for three to four months prior to parturition did not affect birth weights of normal fawns. Fawn birth weight averaged 2472 grams and is comparable to the birth weights mentioned by Haugen and Davenport (1950) and Rue (1978).

These results suggest that obtaining fawns from wild-trapped does held temporarily is feasible. They also suggest that trapping and transporting deer in late gestation did not markedly affect birth rates.

The following are suggestions for maintaining captive, pregnant does.

1. The pen where does are enclosed should be at least 1.5-hectare in size and should include brush or other visual obstructions (1.5 meters high by 15 to 20 meters long) placed in at least one location to provide screening cover for the deer (see Fig. 1B).
2. The enclosure should be located away from areas of human disturbance, and at least 100 meters from the nearest roadway.
3. A buffer area at least 50 meters wide should separate the pen from grazing livestock. The buffer area should contain enough brush or tall vegetation to minimize outside interference.
4. The pen should be fenced with V-mesh net wire at least 2.5 meters high. This wire should be buried 30 centimeters to protect the does and fawns against predators. The pen should be divided for separation of the deer.
5. The pen should be cleared of brush and tall grass before capture of does to facilitate location of fawns.
6. A water source should be installed at ground level.
7. The pen should contain tall trees to provide shelter against weather. The does in this study avoided man-made structures such as a three-meter high roof over feeding areas.
8. Although native foods are best, obtaining them may be labor intensive. If native forage is not provided, alfalfa hay should be provided

as soon as the does are placed in the pens. Pelleted feed should be provided to insure a balanced diet.

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A NOTE ON SOME ASPECTS OF PITMAN NEARNESS

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Abstract.—Peddada (1985, 1986) and Berry (1986) have given sufficient conditions for an estimator that has smaller mean squared error or smaller mean absolute error than a competing estimator to be Pitman nearer. This note corrects a technical error and improves Peddada's and Berry's results through the use of the Cantelli-Fréchet-Uspensky inequality. Finally, we note some variations on the definition of Pitman nearer that have appeared in the literature and the consequences of the differences in these definitions. *Key words:* mean square error; mean absolute error; Cantelli-Fréchet-Uspensky inequality; Gauss inequalities; unimodality.

Peddada (1985) discussed the relationship among minimum mean square error, minimum absolute error, and Pitman nearness. For a given loss function $L(T,\theta)$, he defined an estimator T_1 to be closer to θ than an estimator T_2 in the Pitman nearer (PN) sense if $P[L(T_1,\theta) < L(T_2,\theta)] > 1/2$. In his Theorem 2.2, Peddada provided sufficient conditions on the difference $U = L(T_1,\theta) - L(T_2,\theta)$ to imply that T_1 is closer to θ than T_2 in the PN sense. These included the following moment conditions: $E(U) = u_o < -2.67$ and $E(U - u_o)^j < j!$ for $j = 1,2,\ldots$.

Berry (1986) used the Bienaymé-Chebyshev inequality to prove that weaker conditions on the moments suffice in Peddada's Theorem 2.2. Specifically, Berry's conditions were that $u_o < -2.67$ and $\sigma^2 = \mathrm{Var}(U) < \frac{1}{2}(2.67)^2$.

We point out a slight technical flaw in the arguments of both Berry and Peddada and provide a new, less restrictive, sufficient condition for the PN criterion to hold based on the Cantelli-Fréchet-Uspensky inequality. We also discuss a potential further improvement via the assumption of unimodality and a Gauss-type inequality. Finally, we consider variations on the definition of PN that have appeared in the literature and some consequences of these variations.

A New Sufficient Condition for Pitman Nearness

Berry's proof relied on the following implication: $P(\,|\,U - u_0\,| < 2^{1/2}\sigma) \geq 1/2 => P(U < u_0 + 2^{1/2}\sigma) > 1/2$. This implication need not hold. For example, suppose $U - u_0$ has an absolutely continuous distribution function with support $[-2^{1/2}\sigma, +\infty)$ and that $P(\,|\,U - u_0\,| < 2^{1/2}\sigma) = 1/2$. Then we must have $P(U - u_0 < 2^{1/2}\sigma) = 1/2$ as well and the implication above does not hold. Of course, this problem can be alleviated by placing conditions on the distribution of U or by modifying the PN criterion by requiring only $P(U < 0) \geq 1/2$. This version of the PN criterion may be found, for example, in Mood et al. (1974), where L is taken to be absolute value loss. Indeed, in Peddada and Khattree (1986), the criterion is taken to be $P(U \leq 0) \geq 1/2$. We discuss variations of the definition of PN in a following section.

Peddada (1986) established an even weaker condition on the moments of U as he showed that the moments need only satisfy $(u_0/\sigma) < -2^{1/2}$. However, again, we must either assume that $P(U < -2^{1/2}\sigma) > 0$ or suitably modify the PN criterion.

We now establish a sufficient condition on the moments in Peddada's Theorem 2.2, which are weaker than those presented by Berry and Peddada. We shall use the PN criterion in the sense of Mood et al. (1974) mentioned above, but under general loss. The condition follows from the Cantelli-Fréchet-Uspensky (CFU) inequality (Fréchet, 1950:137; Uspensky, 1937:198). For a random variable X with mean and variance μ and τ^2, respectively, and a constant k, the CFU inequality is $P(X - \mu \geq k\tau) \leq 1/(1 + k^2)$.

Theorem.—Let T_1 and T_2 be estimators of θ. Let L be a loss function, $U = L(T_1,\theta) - L(T_2,\theta)$, $E(U) = u_0$, and $Var(U) = \sigma^2$. If $(u_0/\sigma) < -1$, then T_1 is closer to θ than T_2 in the PN sense.

Proof: By the CFU inequality, $P(U < u_0 + \sigma) \geq 1/2$. If $(u_0/\sigma) \leq -1$, then $P(U < 0) \geq 1/2$ and the theorem is proved.

Note that the condition $(u_0/\sigma) < -1$ is a considerable relaxation of the condition $(u_0/\sigma) < -2^{1/2}$, which was the best previous sufficient condition. Lee (1990) obtained a similar result.

A Sufficient Condition for Pitman Nearness Based on Unimodality

Berry's improvement on Peddada's sufficient condition was derived using Chebyshev's inequality. Our improvement on Berry's result has been obtained via a tighter probability inequality. We now consider what improvement may be had by assuming that U is unimodal, and employing a version of Gauss's inequality.

Under the assumption of unimodality, Chebyshev's inequality may be sharpened (though not uniformly). Probability inequalities that incorporate the assumption of unimodality are known as Gauss inequalities. We shall use the following Gauss inequality, which has been formulated by Vysochanskii and Petunin (1979). Let X be a unimodal random variable with mean μ and variance τ^2. Then for all $k > 0$,

$$P(\,|X - \mu| > k\tau) \leq \max\left\{\frac{4 - k^2}{3k^2},\ \frac{4}{9k^2}\right\}.$$

Now, let U be defined as before and suppose that it is unimodal. Set k

$= d\sigma$, for $d > 0$. In order that $P(U < u_0 + d_0\sigma) \geq 1/2$, we must have d_0 such that

$$\max\left\{\frac{4 - k^2}{3k^2}, \frac{4}{9k^2}\right\} \leq 1/2.$$

Unfortunately, this inequality implies $d_0 \geq (8/5)^{1/2} > 1$. Thus, we obtain no improvement over the result obtained using the CFU inequality.

Variations on the Definition of Pitman Nearness

Let T_1 and T_2 be estimators of θ. Pitman's original criterion, established in his 1937 paper, is that T_1 is closer to θ than T_2 if $P(\,|T_1 - \theta| < |T_2 - \theta|\,) > 1/2$ for all θ.

Peddada (1985) and Rao et al. (1986), among others, used a generalized version of the PN criterion in which a general loss function is allowed. For a loss function L, the generalized PN criterion is that, for all θ, $P[L(T_1,\theta) < L(T_2,\theta)] > 1/2$. This generalization affords the treatment of multiparameter estimation problems.

The generalized criterion may be further modified by changing one or both of the inequalities to allow equality. The four possible variations are listed below:

PN1: $P[L(T_1,\theta) < L(T_2,\theta)] > 1/2$
PN2: $P[L(T_1,\theta) \leq L(T_2,\theta)] > 1/2$
PN3: $P[L(T_1,\theta) \leq L(T_2,\theta)] \geq 1/2$
PN4: $P[L(T_1,\theta) < L(T_2,\theta)] \geq 1/2$.

A cursory search of the literature reveals that PN1, PN3, and PN4 have been employed. In some cases, the same author used different versions in different papers. For example, Peddada and Khattree (1986) used PN3, whereas Khattree (1987) used PN4. Mood et al. (1974) used PN4 in their widely read text on mathematical statistics.

Our purpose in this section is to note that different results may be obtained using different versions of the PN criterion. We illustrate this fact with an example.

Let X be a unimodal random variable with support [a, b] and variance σ^2. Upper bounds on the variance of such random variables have been established by several authors; see Seaman and Odell (1988) for an overview. Seaman et al. (1987) considered the use of such bounds in small sample variance estimation. For example, when sampling from a distribution that is known to be symmetric unimodal, it can be shown that $\sigma^2 \leq (b - a)^2/12$. The U-statistic for estimating variance in this case is the usual unbiased sample variance, S^2. By truncating S^2 at the upper bound, the mean square error (MSE) may be reduced for small ($n < 10$)

sample sizes. If the criterion is minimum MSE, then the truncated estimator is superior. One may ask whether the truncated estimator, call it S_T^2, is Pitman nearer to σ^2 than S^2. The answer depends on which version of the PN criterion is employed.

Consider the following illustration. We have simulated 1000 samples of size 4 from a beta distribution with shape parameters three and three. This distribution is symmetric unimodal and therefore has variance not exceeding 1/12. We find that the ratio of the MSE for S_T^2 to the MSE of S^2 is approximately .910. However, using PN1 or PN4, we have $P(|S_T^2 - \sigma^2| < |S^2 - \sigma^2|) \approx .047$, so that S^2 is PN to σ^2 than S_T^2. By contrast, using PN2 or PN3, we have $P(|S_T^2 - \sigma^2| \leq |S^2 - \sigma^2|) = 1$, so that one concludes that S_T^2 is PN to σ^2 than S^2. The two versions of the PN criterion, therefore, lead to opposite conclusions.

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PHYLLODONT (PARALBULINAE) FISH TOOTHPLATES FROM THE LOWER CRETACEOUS GLEN ROSE FORMATION OF CENTRAL TEXAS

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Abstract.—Seven partial phyllodont toothplates from the Lower Cretaceous (Comanchean) Glen Rose Formation of Erath County, Texas, represent the largest collection of phyllodont toothplates known from a single locality in the state. Both parasphenoid and basibranchial toothplates, referrable to the Paralbulinae, are known from the site. The specimens compare favorably with *Casierius heckelii*. *Key words:* phyllodont; *Casierius*; fish; Lower Cretaceous.

Collections of vertebrate fossils made by the author and by field crews from Southern Methodist University and Tarleton State University have been reported from fossil localities on the Huggins Ranch, 5 mi. (8.6 km.) NW Hico, in Erath Co., Texas. These localities have been referred to as the Huggins Localities or SMU nos. 108-1 and 108-2 (Winkler et al., 1990). Vertebrate fossils reported from the fossil localities include sharks, *Hybodus* sp., *Pseudohypolophus mcnultyi, Rhinobatos* sp., and *Leptostyrax bicuspidatus*, and an amphibian, *Prosiren elinorae*, as well as other Caudata and Anura (Winkler et al., 1990). Most of these collections are from the locality designated as SMU no. 108-2. Seven toothplates (described here) were collected earlier from the site by the author and Chester Huggins.

Toothplates were found at the contact between the Glen Rose and the overlying Paluxy Formation or within a three-meter interval immediately above the contact. As the collection comes primarily from sediments turned up during the excavation of a stock pond, the precise stratigraphic horizon could not be determined. The Glen Rose Formation here is a dense, fossiliferous limestone that represents the Upper Member (Boone 1968; Perkins 1987). The Paluxy Formation immediately above the contact consists of poorly consolidated quartz sandstone.

Casierius has been reported from brackish-water, freshwater, and marine environments. The locality reported herein was an estuarine or transitional marine-terrestrial environment (Winkler et al., 1990), thus supporting the supposition that *Casierius* was diadromous.

General Description

Seven fossil toothplates were discovered at the site that show a phyllodont type of tooth replacement, with superposed sets of replacement teeth (Estes 1969*a*). All seven toothplates are believed to belong to the phyllodont subfamily Paralbulinae, although there are minor differences in the morphologies of the plates. Three of the toothplates represent major portions of toothplates, the other four are fragmentary.

The teeth are irregularly stacked and are subcircular to oblong in occlusal view. In lateral view, they appear flattened or shallowly cupped, with the concave surface toward the attachment surface. There is no evidence of sculpturing on the surfaces of the teeth, although some show wear due to trituration. Wear on these teeth probably is due to predation on molluscs and crustaceans by these fishes (Estes 1969*a*). The teeth vary in size from 0.7 to 2.1 mm. The larger teeth are typically in the center of the plate and the smaller teeth toward the edges. In lateral view, the toothplates taper anteriorly. No sigmoid curvature of the occlusal surface of the toothplates is present, as seen from both occlusal and lateral views, thus differentiating them from members of the Phyllodontinae.

Of the seven toothplates, six have a convex occlusal surface whereas the seventh is concave. The concave plate (SMU 72340; Figs. 1A, 1B, and 1C) differs from the other toothplates in many respects. In particular, it has six layers of irregularly stacked teeth, whereas the other specimens have only three or four. Occlusal view of the specimen reveals moderate tooth wear. The lateral edges of the plate are raised, with parallel grooves perpendicular to the occlusal surface, which may represent the symphyseal attachment surface, as seen in Figure 1B. On the dorsal portion of the plate, a pair of raised facets may be for articulation with other bones of the skull. The bulbous dorsal attachment surfaces, raised lateral edges, and concave occlusal surface indicate that this is a parasphenoid toothplate (Estes 1969*a*). The concave occlusal surface would have fit around a smaller basibranchial plate in the frontal mandibular area. Thurmond (1974) referred to a fragmentary concave phyllodont plate from the Garvin Church local fauna in the lower Paluxy Formation of Wise County, Texas, as a pterygoid plate from *Casierius heckelii*. Although one of the characters used to define the Phyllodontidae is the presumed lack of pterygoids (Estes 1969*b*), this is only a superficial definition and cannot be supported due to a lack of other cranial and skeletal bones.

Convex basibranchial tooth patches, which lack sigmoid curvature of the occlusal surface, are also characteristic of the more primitive genera of the subfamily Paralbulinae (Estes 1969*a*). The other six specimens (SMU 772341, 72342, 72343, 72344, 72345, 72346) are consistent with this morphology and are, therefore, also believed to be referrable to the Paralbulinae. These plates are similar in regard to tooth size, shape, the irregular stacking of the replacement teeth, and the mode and extent of tooth wear. The specimens have convex occlusal surfaces and, where present, flattened ventral attachment areas.

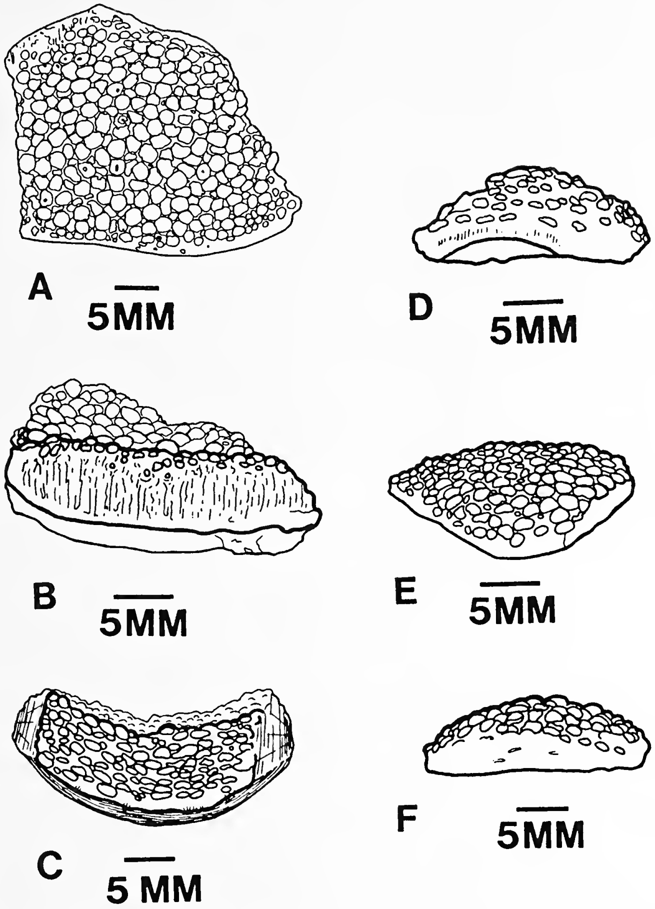

Figure 1. A. *Casierius heckelii* (anterior to left), occlusal view of fragmentary parasphenoid, showing trituration of tooth surfaces (SMU 72340).

B. *C. heckelii*, (anterior to left), right lateral view of SMU 72340 showing parallel grooves of lateral edges, presumed symphyseal attachment surface.

C. *C. heckelii*, medial view of broken anterior end, showing multiple sets of replacement teeth and concave structure (SMU 72340).

D. SMU 72341, medial view of broken anterior end of basibranchial toothplate showing high-domed occlusal surface, *C. heckelii*.

E. SMU 72342 (anterior to left), lateral view of basibranchial toothplate showing flattened occlusal surface and smaller teeth toward edge, *C. heckelii*.

F. SMU 72342, medial view of broken anterior end.

Specimen SMU 72341 represents the posterior portion of a toothplate. It has a high-domed dorsal surface (see Fig. 1D). The posterior edge of the specimen is three millimeters thick, and the central portion of the toothplate thickens to seven millimeters. The larger teeth are found in the middle two-thirds of the plate.

Specimen SMU 72342 has a much flatter occlusal surface than in specimen SMU 72341 (see Figs. 1E, 1F). Also, teeth are smaller in comparison (1.0 to 2.1 mm in 72341 as opposed to 0.7 to 1.8 mm in 72342). Both SMU 72341 and 72342 have approximately four layers of teeth. Inasmuch as the toothplates are approximately the same size, it cannot be determined whether these represent different taxa, different toothplate series, or differences in preservation. However, the ventral surface of SMU 72342 is flattened, whereas the ventral surface of SMU 72341 is slightly concave, also revealing significant differences between these plates of similar size.

Specimens SMU 72343, 72344, 72345, and 72346 consist of poorly preserved fragments with convex occlusal surfaces. However, tooth morphology and replacement indicates placement within the paralbulines.

Discussion

The extinct phyllodont fishes may be divided into the subfamilies Phyllodontinae and Paralbulinae. There are clear distinctions between the two subfamilies. The Phyllodontinae are characterized by toothplates with sigmoid curvature and in having multiple sets of teeth that are directly successional in stacks on the main portion of the plate. Conversely, the Paralbulinae are phyllodont fishes with basibranchial and parasphenoid plates that lack a sigmoid curvature. Other characteristics of the subfamily include the presence of abundant interstitial matrix between the teeth, which is composed of a calci-phosphatic replacement material. The assumed presence of interstitial matrix is due to the irregular stacking of the toothplates in the Paralbulinae (Estes 1969*a*).

All specimens described herein possess characteristics of the Paralbulinae. Of the genera described from the subfamily, the SMU specimens most closely resemble those described as *Casierius* sp. A single basibranchial plate of *C. heckelii* has been described from the Glen Rose Formation of northern Bosque County, Texas (Johnson, 1972). The curvature of the toothplate and the irregularity of tooth stacking is identical between Johnson's plate and those reported here. In addition, tooth shape, size, and basic morphology are comparable. The Huggins toothplates differ in size from the specimen described by Johnson, although this is not necessarily a constraining factor. SMU 72340 represents the first parasphenoid plate described and figured from the Lower Cretaceous of Texas.

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IMPORTANCE OF CANOPY POSITION FOR GROWTH OF *CELTIS LAEVIGATA* SEEDLINGS

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Abstract.—Seedlings of *Celtis laevigata* (Willd.), Texas sugarberry, were planted in the field to determine affects of canopy position, root competition, nutrient addition and herbivory on their growth. Growth was greatest under a mature *Acacia smallii* (Isley), huisache, canopy and least in open grassland between the mature *Acacia* trees. Mortality was highest in the open grassland compared to below the *Acacia* canopy. Other factors examined had no significant effect on *C. laevigata* seedling growth. *Celtis laevigata* is a mature community species that is shade tolerant and requires high levels of soil nitrogen. As such, growth should be limited in areas typical of early successional communities and promoted by conditions typical of mature communities. *Key words:* competition; herbivory; light levels; nutrients; shade; Texas sugarberry; trenching.

Secondary succssion in parts of southern Texas may begin with abandonment of farmland. If farming is stopped, colonization by various annual species occurs quickly, followed by establishment of woody plants like *Acacia smallii* (Isely), huisache, within five years (Van Auken and Bush, 1985). *Acacia smallii* dominates the savanna-woodland for the next 25 to 35 years, after which it declines. It is shade intolerant (Bush and Van Auken, 1986*a*) and grows poorly below its own canopy (Lohstroh and Van Auken, 1987). During this time period, *Celtis laevigata* (Willd.), Texas sugarberry, becomes established and then dominates the mature community (Bush and Van Auken, 1984). *Celtis laevigata* is shade tolerant as might be expected for mature community species (Bush and Van Auken, 1986*a*).

Although *C. laevigata* is tolerant of low light levels in the greenhouse, we have not identified any reports of its ability to grow in the field or its site requirements for establishment. Late successional species are usually tolerant of low levels of light (Grime, 1965; Loach, 1967, 1970), but may require higher levels of nutrients (Bormann, 1953; Tilman, 1982; Van Auken et al., 1985). Additional factors that could be important in determining plant establishment and dominance are herbivory and ability to compete for resources below ground (Weaver and Clements, 1966; Harper, 1977; Smith, 1980).

This study was designed to determine the importance of canopy position, nutrient addition, herbivory, and root competition on the growth of seedlings of *C. laevigata* in the field.

METHODS

Fruits of *Celtis laevigata* were collected in February 1985 from trees located along the San Antonio River, Bexar County, Texas. Seeds were soaked in giberellic acid for 3.5 hours to break dormancy (Kahn, 1968) and then rinsed thoroughly with distilled water. Three seeds were sown in each 15-centimeter diameter by 15-centimeter deep plastic pot containing 1400-gram sieved, Frio clay-loam soil (Taylor et al., 1966) from an early successional site. The soil was a Mollisol, classified as a fine, mixed, thermic, Cumulic Haplustoll, low in carbon (1.29 ± 0.45 percent, by weight), nitrogen (0.14 ± 0.03 percent), and phosphorous (8 ± 2 milligrams per kilogram). Calcium was high (2400 ± 800 milligrams per kilogram) and magnesium and potassium were at intermediate levels (30 ± 11 milligrams per kilogram, 11 ± 5 milligrams per kilogram, respectively) (Bush and Van Auken, 1986*b*). Rainfall data were taken from the NOAA local climatological data summary (NOAA, 1985).

Seven weeks after sowing, plants were sized according to height and vigor and thinned to one per pot. One-hundred-nineteen plants were used in the experiment. Seven randomly selected plants were kept in the greenhouse and the remaining plants were transplanted to a field site along the San Antonio River. Seven randomly selected plants were placed into each of the 16 treatments. All plants were given 300 milliliters of distilled water every third day for 10 days (equilibration) before initial measurements. Greenhouse plants were harvested for initial measurements by cutting at the cotyledon scars and drying (70°C) to a constant weight.

The experimental design was 2^4 factorial with canopy position (under an *Acacia smallii* canopy or in the open), nutrients (added or not added), root competition (roots present or trenching, no woody plant roots), and herbivory (herbivores present or insecticide treatment, no herbivores) as factors. With all combinations, there were 16 treatments. The canopy position was beneath five mature *A. smallii* trees and the open area was adjacent. Mean light levels were 515 ± 153 $\mu M \cdot m^{-2} \cdot sec^{-1}$ under the canopy and 2173 ± 174 $\mu M \cdot m^{-2} \cdot sec^{-1}$ in the open. Light levels were measured with a Li-cor® LI-188 integrating quantum sensor. Nutrient treatment consisted of 250 milliliters of a complete nutrient solution (Van Auken and Kapley, 1979) once per week starting at zero time for 12 weeks. No nutrient-treatment plants were given 250 milliliters of distilled water at the same time intervals. Root competition was reduced (no competition treatment) by trenching a one square meter perimeter around the plants, to a depth of 20 centimeters. Root competition treatments were untrenched. No herbivory plants were sprayed with malathion (2.95 milliliters per liter) once each week for the duration of the experiment. A four-sided cardboard box prevented the insecticide from being blown onto other test plants. Herbivory treatment plants were sprayed with an equal amount of distilled water at the same time intervals.

The experiment was terminated 12 weeks after initial measurements were taken (1 November 1985). Plants were cut at the cotyledon scars and dry weights were measured. Data were statistically analyzed by an analysis of variance (ANOVA) procedure and means were separated using the Least Significant Difference test. Mortality data was analyzed with a X^2 test (Steel and Torrie, 1980; SAS Institute, 1982).

RESULTS

Position was the only main factor tested that was significant (ANOVA, $F = 64.03$, $P < 0.0001$, Fig. 1). Herbivory, competition, or nutrient additions were not significant (ANOVA, $F = 0.00\text{-}3.59$, $P > 0.05$). Of the 10 two-way and three-way interactions, only the herbivory-nutrient interaction was significant (ANOVA, $F = 4.37$, $P = 0.0397$). Mean aboveground dry weight of *Celtis laevigata* seedlings grown in the open (grassland, full sunlight) was 0.25 ± 0.21 grams, whereas mean aboveground dry weight of plants grown below the *Acacia* canopy (shade) was 0.96 ± 0.45 grams. Mean aboveground dry weight of the plants harvested at the start of the experiment was 0.14 ± 0.08 grams.

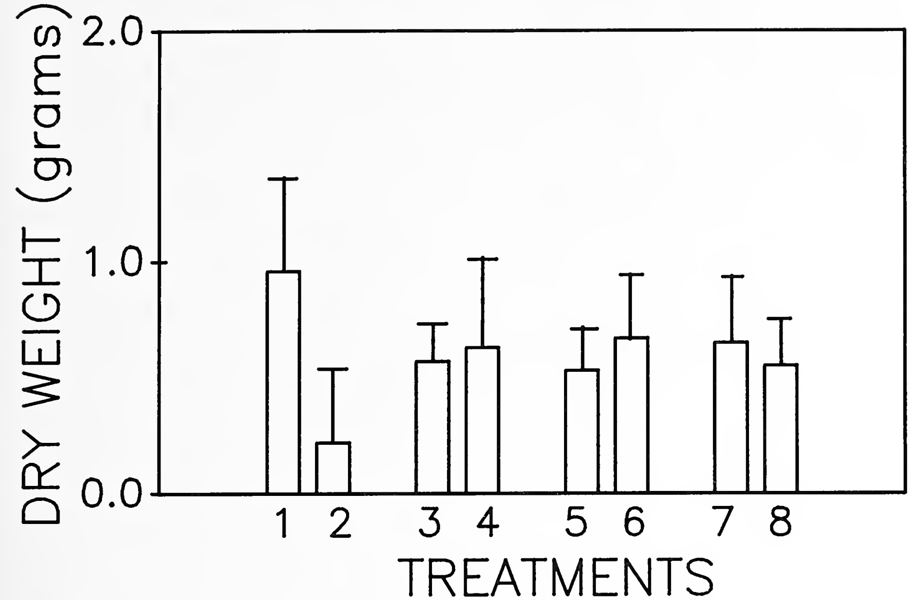

FIGURE 1. Bar graph presenting mean aboveground dry weight (± SD) of *Celtis laevigata* seedlings grown for 12 weeks under various field conditions. Treatments included the following: 1, under canopy; 2, open; 3, herbivory; 4, no herbivory; 5, competition; 6, no competition; 7, nutrient supplemented; 8, no nutrients added. Mean Dry weight of plants in treatment 1 was significantly different from those in treatment 2 (ANOVA, LSD, $P < 0.05$). There were no significant differences between the other treatments.

Thus, plants in the open (grassland) increased in dry weight 1.79 times, while those in the shade below the *Acacia* canopy increased 6.86 times.

Means of all treatments were separated using the least significant difference test (Table 1). The main differences were in canopy position. Mean values for all plants in treatments in the open were lower than means for plants in treatments below the *Acacia* canopy. Other differences are slight and should not be considered because other main effects were not significant when tested with ANOVA.

Overall seedling mortality in the field was 36 percent, and 98 percent of these mortalities occured in the open (grassland, full sunlight), which was highly significant ($X^2 = 36.1$, $P < 0.005$). Rainfall during August 1985 was only 0.45″, which was 83 percent below normal, and this was the time when almost all of the *Celtis* mortalities occured (Fig. 2). Rainfall during September and October was 28 percent and 36 percent above normal, and only one mortality occurred during this time.

DISCUSSION

Many abiotic and biotic factors affect the establishment and growth of woody plants (Harper, 1977). However, the present field study identified

TABLE 1. Mean aboveground dry weight (± SD) for *Celtis laevigata* grown in 16 treatments and initial measurements. Mean values followed by the same letter are not significantly different (ANOVA, LSD $P > 0.05$).

Treatments	Dry-weight (grams)
Zero time	0.14 ± 0.08A
Open, herbivory, competition, nutrients	0.18 ± 0.31A
Open, herbivory, competition, no nutrients	0.08 ± 0.03A
Open, herbivory, no competition, nutrients	0.23 ± 0.28AB
Open, herbivory, no competition, no nutrients	0.35 ± 0.36ABC
Open, no herbivory, competition, nutrients	0.23 ± 0.42AB
Open, no herbivory, competition, no nutrients	0.17 ± 0.19A
Open, no herbivory, no competition, nutrients	0.40 ± 0.35ABC
Open, no herbivory, no competition, no nutrients	0.28 ± 0.45AB
Under canopy, herbivory, competition, nutrients	1.00 ± 0.55DE
Under canopy, herbivory, competition, no nutrients	0.91 ± 0.29CDE
Under canopy, herbivory, no competition, nutrients	0.85 ± 0.36CDE
Under canopy, herbivory, no competition, no nutrients	0.93 ± 0.19CDE
Under canopy, no herbivory, competition, nutrients	0.88 ± 0.49CDE
Under canopy, no herbivory, competition, no nutrients	0.79 ± 0.41BCD
Under canopy, no herbivory, no competition, nutrients	1.41 ± 0.93E
Under canopy, no herbivory, no competition, no nutrients	0.90 ± 0.42CDE

C. laevigata seedling position relative to an *Acacia smallii* canopy as the major factor. Growth of *C. laevigata* seedlings below the *Acacia* canopy was 3.84 times higher than that of seedlings in open grassland. Reciproically, mortality of *C. laevigata* seedlings in the open grassland was 39 times higher compared to those below the *Acacia* canopy.

Light intensity, an obvious variable influenced by the presence of a woody plant canopy, may be reduced by more than 90 percent by the *A. smallii* overstory (Bush and Van Auken, 1986*a*). But, low light levels should reduce, not stimulate, *C. laevigata* growth. Apparently, the stimulation of *C. laevigata* seedling growth is mediated by another factor associated with the *A. smallii* canopy. Soil temperature, soil nutrients, and soil water content all have been shown to change below the canopies of certain woody species (Tiedemann and Klemmedson, 1973*a*, 1973*b*, 1986; Bush and Van Auken, 1986*b*). Higher levels of soil nutrients may be a factor involved in stimulating the growth of *C. laevigata*. However, we did not find a nutrient stimulation in the present experiment. Soil nutrients, especially nitrogen, have been shown to increase during successional events (Gorham et al., 1979), and total soil nitrogen has been demonstrated to increase during secondary succession in this area (to 2.5 ± 0.7 $g{\cdot}kg^{-1}$, Bush and Van Auken, 1986b). In addition, total soil nitrogen is almost twice as high under a 15-year-old *Acacia smallii* canopy compared to open grassland. Low light levels occur below the canopy, but higher soil nitrogen levels also are found. Added nitrogen,

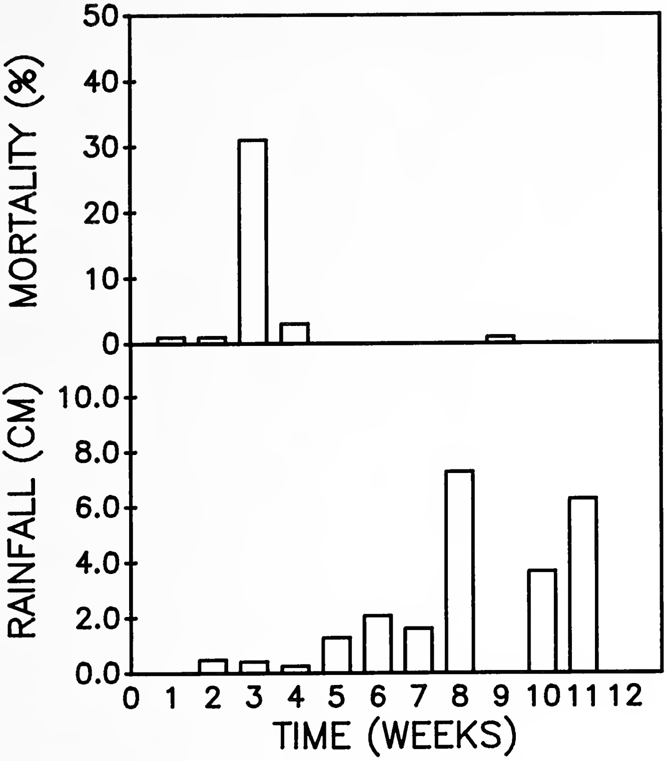

FIGURE 2. Bar graph presenting weekly rainfall and weekly mortality of *Celtis laevigata* seedlings during the experiment.

rather than other nutrients, has been shown to stimulate *C. laevigata* growth in the same Frio soil in greenhouse experiments (Van Auken et al., 1985). Thus, soil nitrogen seems to be a major candidate for causing the increased growth observed.

Other factors examined, including competition, nutrient supplements, and herbivory, did not cause significant changes in *C. laevigata* growth. Competition for soil-borne resources, mainly water and nutrients, can play a significant role in establishment and subsequent growth of woody species (Harper, 1977). Trenching effectively eliminates root competition (Ehrenfeld, 1980; Horn, 1985). But, we did not see a difference in *C. laevigata* growth between trenched and nontrenched plots and concluded that competition between adult and seedling plants was unimportant. Competition with woody plant roots may have been masked by competition with herbaceous plants that were not removed from the study plots (both canopy and open plots). Competition between woody plant seedlings and herbaceous plants can cause significant growth reduction in woody plants (Glendening and Paulsen, 1955; Van Auken and Bush, 1989).

Nutrient additions were expected to have stimulatory effects on the growth of *C. laevigata* as seen in previous studies (Van Auken et al., 1985). However, additional nitrogen in the canopy soil could have masked that effect. The lack of stimulation of growth of *C. laevigata* in the open when nutrients were added was probably the result of the early drought and later stimulation of associated herbaceous species by the removal of a nutrient limitation. With the growth limitation removed, the herbaceous species may have used up a nutrient required for *C. laevigata* growth.

Herbivores can have drastic effects on plant populations and change successional sequences (Harper, 1977; Gilbert, 1985), although not shown in the present study. This study was completed in the autumn and was of limited duration. A study completed over a longer time and including both the spring and autumn growing seasons might show significant growth reduction due to herbivory, if herbivores are present.

Celtis laevigata appears to be a late successional species, requiring high soil nitrogen and capable of growth in canopy shade. Although it can grow in disturbed areas or grasslands, it would do so at reduced rates, depending on the presence of competition and soil nitrogen levels. A more favored site would be in the reduced light and higher soil nitrogen environment below the canopy of *A. smallii.*

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SOLAR POND FEASIBILITY FOR LOW COST ENERGY AND WATER PRODUCTION

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Abstract.—The High Plains region in Texas and New Mexico seems to be a favorite site for salt-gradient solar ponds due to its potential for overcoming the major drawbacks in cost effectiveness of these ponds. Strong points for this region are the availability of a 1) naturally level ground with pre-existing large alkaline lake basins, 2) high insolation almost year round at a height of one kilometer above sea level, 3) salt from alkaline lake basins and oil-brine emulsion from oil fields, 4) soils with good impervious and insulating properties, and 5) demand of low to moderate temperature heat and fresh water in the area. The feasibility of production of electricity from low-temperature heat also is discussed. *Key words:* solar pond; energy cost; High Plains; energy sources.

In a recent paper published in a previous issue of Texas Journal of Science, the principle and potential of salt-gradient solar-pond (SGSP) were discussed with reference to the High Plains region of western Texas and New Mexico (Lodhi, 1989). Laboratory research and field tests around the world have shown that there are three main drawbacks in the cost effectiveness of SGSP. They are costs of 1) pond construction, 2) salt, and 3) generating electric power from moderate-temperature energy available from solar ponds (despite their well proven efficiency in collecting and storing solar energy). Nevertheless, when certain local parameters are favorable, and are stratgically exploited, they can, in principle, lead to the cost effectiveness of SGSP. In offsetting the drawbacks of SGSP in a local geographic area, the following parameters are identified: 1) naturally level ground, with a type of soil possessing impervious and insulating properties, preferably having some pre-existing lakes or ponds, 2) endemic availability of abundant amounts of salt, and 3) demand for a large quantity of heat energy at a moderate temperature range. Texas and adjacent New Mexico thus become strong candidates in overcoming the main drawbacks of SGSP in that all of these parameters are present in the High Plains region.

The groundwater resources of the Ogallala Aquifer of the Southern High Plains of western Texas and eastern New Mexico have been extensively used for agriculture since the 1930s. Today, about six million acres of irrigated land, approximately 70 percent of the total irrigated area in Texas, are watered by about 78,000 wells in western Texas. Coupled with the increase in both civil and industrial usage, groundwater resources have been dwindling, and the water table has been dropping to lower and lower levels, particularly since the intensification of irrigation (Gazdar, 1981). Consequently, this has produced higher irrigation costs. It obviously requires more energy to draw water from the lower levels in the aquifer. With rising energy costs (electricity, gasoline, gas, diesel), a sustainable agriculture may become uneconomical, with an adverse cost-benefit ratio of crops grown, if no measures are taken to offset energy costs. This challenge could be met in a variety of ways, for example: 1) conserving and economizing the existing water and energy resources, 2) looking for new and alternative sources, and 3) exploiting unused sources existing in the area. It is this third option on which attention is focused here.

On the Southern High Plains, there is a great natural potential for converting solar energy into a reliable source of useable energy by means of salt gradient solar ponds. There are a large number of small and medium-sized natural depressions, locally termed "playas," scattered over this region. Many of them seem to satisfy the physical, chemical, and geological conditions needed for constructing and operating solar ponds economically (Lodhi, 1989). On the Southern High Plains, a lake modified on the principle of the salt-gradient solar pond design can provide a simple, economical, and reliable source of thermal or electrical energy or both, suitable for applications such as: 1) direct heating and cooling of space; 2) low-temperature industrial process heating, or preheating for industrial processes in oil fields, cotton ginning, and other agribusiness operations; 3) draft power for water holes for grazing livestock, farm irrigation operations, heating of livestock barns, and crop drying; 4) biomass processing for methane generation; 5) domestic uses, and so on. In the United States, a five-megawatt solar pond facility at Salton Sea, California (Lin, 1982), and a 1.2-megawatt facility at Truscott Lake, Childress, Texas (SERI, 1981), are under development. These facilities will use natural salt resources and drainage water of inland basins, similar to the playa lake basins of the Southern High Plains.

The agricultural and related economy of the area can be benefited significantly with the application of solar technology to the natural lakes or playas. Agriculture and oil-based industry such as described by Lambert (1983) would be beneficiaries of solar pond power in the region. This paper specifically aims at the naturally occurring potential of the region by suggesting utilization of these lakes and their brine waters for salt gradient solar ponds.

Alkaline Lake Basins

An unmodified salty basin is an economic drag on farm resources as it requires extra time and effort of a farmer to control unwanted weeds or to level land around the basin. Additionally, the farmer must pay taxes on all land, whether productive or not. If the farmer brings this basin under cultivation, he may run a risk of losing the crops due to rainfall runoff before harvest time.

An alkaline lake may be developed into an asset rather than remaining a liability by converting it into a salt-gradient solar pond through simple technology (with added tax incentives for solar energy conversion). By appropriately modifying the lake basin, a portion of it can be used for salt-brine concentration and for water storage and supply. As such, this natural resource of water and salt can be utilized for economic benefit.

A cursory survey of literature (Reeves, 1970) shows that in Terry, Lynn, Gaines, Lamb, and Bailey counties of western Texas alkaline lake basins having playas with stagnant water at depth may offer promising sites for the salt-gradient solar ponds. These alkaline lake basins are randomly scattered on the flat, plateaulike topography of the High Plains.

Surface water resources such as rivers and streams are lacking on the High Plains although the region has tens of thousands of small natural depressions in the form of playa lakes. Most of the smaller playas, when intermittently filled with water, are fresh water lakes. There also exist about 40 larger alkaline basins covering 1.5 to 125 square kilometers, which usually contain one or more saline lakes. Most of these lakes serve as drainage outlets for surface runoff from rains. Their commercial, recreational, and other uses are limited or wanting. Several of the larger alkaline lake basins could be utilized for energy production for adjacent farm operations, and particularly for the power needed for lifting groundwater from the Ogallala Aquifer.

CLIMATE

The climate of the High Palins area is semiarid with high ambient surface and air temperatures. The mean temperature in summer is 25 degrees C, and in winter, 10 degrees C. Mean annual precipitation ranges from 350 to 575 millimeters with the rainy season from 15 September to 15 April. Most heavy rainfall is in the form of thunderstorms. Floods are of rare occurrence. In winter months, snowfall is the major source of moisture. Annually, the area has about 200 frost-free days on the average, and 275 to 350 cloud-free days with at least 75 percent mean annual sunshine. The amount of average yearly solar insulation is about 1200 Watts per square meter (450 to 500 langley gram-calories per square centimeter). Evaporation and transpiration is about three and a half to four times average annual precipitation, ranging from 1500 to 2760 millimeters yearly. Low humidity is characteristic of the region.

Maximum winds across the area are associated with intense thunderstorms and are of short duration. Winds in excess of 40 kilometers per hour, which occur occasionally for periods of 12 hours or longer, are associated with late winter and spring low pressure troughs that develop in front of massive, colder, high pressure ridges. The intensity of duststorms, which are invariably produced by strong southwesterly to westerly winds, depends on current precipitation that of the preceding year, and local agricultural profile. The eco-climatological parameters of the area are favorable for operation of salt-gradient solar ponds and for concentrating the water supplies.

The Southern High Plains have a low surface gradient and a plateau-like topographic configuration. The elevation ranges between 900 to 1000 meters above mean sea level. Playa basins, ranging in size from less than 10 meters to more than 5000 meters in diameter, and from less than one meter to more than 15 meters deep, are not evenly distributed. For example, the larger basins, which tend to occur in the northern part of the region, are found at a density of approximately one per 1250 square kilometers, whereas smaller basins exhibit a density of approximately one per 2.6 square kilometers in many counties.

The playa lake basins account for almost all the total storage capacity of surface water resources in the region. Each basin forms a micro-drainage network of its own, independent of the adjacent watershed and catchment area, ranging from a few square kilometers to more than 25 square kilometers. Most surface and thunderstorm runoff collects in these natural depressions, forming wet-weather lakes. Generally, areas of fine-textured soils have a greater number of large lakes, and the lakes have larger volume per unit surface size than lakes in areas of medium-textured soils. Some of the larger playas are on loessic-type soils. Drainage from local watershed areas contributes to flow in the playas during the rainfall period. Sediments of the playas consist of thick smectitic and other expanding clays that permit minimal infiltration into the underlying horizons of caliche and other strata (Reeves, 1970)

Besides the natural playa lakes, the area has many man-made depressions termed "caliche pits." Cliche has been used for road-surfaces, crushed stone, and in other ways. Many abandoned pits, in which caliche has been exhausted, offer ready-made sites for solar ponds.

The envionmental and geological setting of the alkaline lakes is ideally suited for solar pond applications because: 1) favorable mineralogical composition of impervious beds at the bottom of the playas, and good insulating properties of the materials flanking their sides; 2) absence of water-table recharge or discharge into the lake basins; 3) ground water lying 50 meters and deeper below the lake bottoms; 4) geochemical distribution of sediment-salt offering easily available water and salt resources; and 5) accessibility of playas and ease of modifications to them. These characteristics will result in excellent heat insulation on the sides of a pond, and little seepage and infiltration below it. Consequently, infrastructure costs could be reduced with minimal use of liners, insulating materials, and excavations, which contribute to the major expenditures in construction and operation of solar ponds.

Playas constitute the major surface water resource on the Southern High Plains (Reeves, 1972). Annual surface runoff contributes an average of 33 million cubic meters of water to the playa lake basins; 90 percent is lost to the atmosphere through evaporation. The Water Resources Center, Texas Tech University, has been carrying out studies to utilize playa lake basins for artificial recharge of the ground water into the Ogallala Aquifer (L. V. Urban and R. M. Sweazy, personal communication).

SALT RESOURCES

The Southern High Plains have salt deposits of Permian and Triassic age in salt lake basins and springs. Brine water produced in gas and oil drilling operations in the area is available in abundance. Springs within the lake basins are alkaline. Salinity ranges from a half to more than 10 percent at many locations within the lake basins (Reeves, 1970; Lodhi, 1989). The saline water of these lakes and basins mostly is unutilized on the High Plains. Some insignificant amounts of salt are currently extracted in Texas (C. C. Reeves, personal communication). Use of runoff water, with a different approach than that proposed in this study, was suggested in the report of a project study for a 1.2-megawatt power station by a SERI Task Force (1981). In order not to pollute potable water in Red River, the brine waters are diverted to a dammed natural basin in the southeast part of Truscot Brine Lake. It is planned for brine to be concentrated by natural evaporation to these salinities required for solar ponds. The electricity produced from the ponds is intended to serve the pumping needs of the chloride control project for the Red River, brine from the natural source to evaporation ponds, and concentrated brine from evaporation ponds to solar ponds for maintenance of the solar ponds. The naturally occurring brine on the High Plains, along with thousands of oil and gas wells, is in geological formations of Permian and Triassic age associated with the oil and gas field operations (see Fig. 1).

The amount and concentration of brine differs from field to field with an approximate content of sodium chloride from less than two to 30 percent by weight (Hager, 1951). For example, a well producing 150 barrels per day of crude oil may have as much as 50 barrels brine water associated with it. The crude oil-brine emulsion requires heat treatment to separate the oil from the salt. Usually, fossil fuel (gas and oil) is used in this heating process (Manning et al., 1983; Lambert, 1983). The disposal of brine involves both an environmental hazard and an economic drain. Disposal is regulated by the Texas Railroad Commission (1982). Brine is disposed of in an injection well or at a salt depository where fees are paid by oil well operators. A playa lake facility could be used to serve as a salt (brine) depository from which brine could be used for a solar pond,

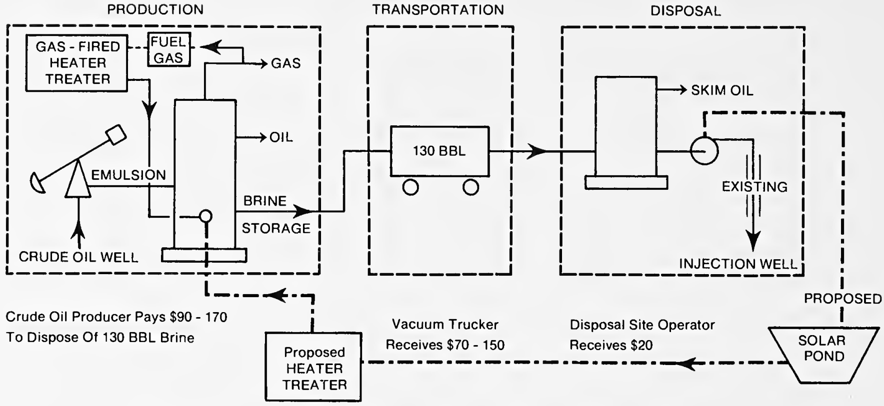

FIGURE 1. Existing and proposed waste brine disposal process.

which in turn could provide heat for the separation of crude oil-brine emulsion. Playa lake development for a depository can be tailored to adjacent crude oil operations. A crude oil producer can maximize benefits from such a waste product, like brine, in terms of process heat procurement by replacing the natural gas used in separating the crude oil from brine. A feasibility study of this concept was carried out for the Double U Oil Company well operation near Big Wells, Dimmit Co., Texas (Manning et al., 1983).

Many of the lake basins can meet the Texas Railroad Commission's guidelines for becoming "salt-brine depositories." Such brine dumping from oil field operations would provide a major source of salts. The salt depository can collect disposal fees. Revenues generated from the brine dumping would offset the capital cost of construction of a solar pond and, to some extent, its operation. Some of the alkaline lake basin sites in western Texas have been used for dumping brine from the oil fields, and some lake deposits are being commercially mined for their salts.

A major step in the U. S. Department of Energy (DOE) process of selecting a site for a high-level nuclear waste repository is detailed site characterization. The purpose of this process is to determine suitability of the site for a repository. During site characterization, shallow boreholes and wells are drilled to study rock characteristics and ground water. It is estimated that 140,000 tons of salt would be excavated during the site characterization process only. When the work is completed for the repository, some several million tons of salt will be excavated out of which DOE plans to store three to four million tons. A large portion of the salt excavated for the repository would be used for backfill after the repository is filled to capacity. The DOE concern is the nuclear waste disposal as well as salt disposal and storage.

The excavated salt and brine could be utilized as intermediary substance for SGSP in a nearby playa lake basin. This would save on expenditures in storing, moving, and disposing of salt and brine. Utilization of this salt and brine, either from the site characterization or for the repository, would be best utilized in SGSP in which all salt used could remain preserved and precipitated for backfill at a designated, distant future.

The High Plains region has abundant salt resources. Accordingly, the cost of procurement of salts would be marginal. Salt is a major cost item in developing a solar pond. Moreover, the revenue generated from a salt depository site of alkaline lake basins would make it feasible to operate a salt-gradient solar pond to produce heat or electrical energy, which could be sold to adjacent users and utility grids.

Potential For Energy

The alkaline lake basins of the High Plains are ideally suited for development of their solar pond potential in terms of land, material, and labor costs. Most saline playas in the alkaline lake basins have formed on impervious clays, which prevent leakage; thus, any adjacent water tables are not recharged by saline lake water. Salt concentration gradients increase in depth in an ideal meromicitic lake.

By registering a suitable playa lake basin as a brine disposal site with the Texas Railroad Commission, it is possible to acquire the necessary brine for development of a solar pond at minimal or even negative cost. A systematic cost-effective study of sites with respect to locations of oil producing wells and playa basins can be made. Other issues related to this method of brine procurement include consideration of 1) the availability of the required quantity of the brine, 2) salt concentration, and 3) the receiving and treating facilities for brine as it arrives on the site. There is no detailed record available for brine production in this area, nor is salt concentration well documented. A cursory survey of cost benefit provides a net gain to the solar pond by using the brine depository as a service pond to the solar pond as seen in Figure 1.

This study has been intended for feasibility and cost effectiveness of solar ponds on the High Plains or in a similar environment. The main thrust has been directed toward site selection of a playa lake with respect to the essential factors, namely the availability of sunshine, land, water, and salts. Location factors such as climatic parameters, soil conditions, groundwater, waterflow, and intended application of economic and environmental aspects also are important in site selection.

Projected Available Energy and Costs

Extraction of energy by means of a heat exchanger in an alkaline lake basin could be a means of offsetting the high cost of the presently available energy. Moreover, alkaline lake basins, as solar ponds, become an integral part of the envionmental system. Certainly, any energy

TABLE 1. Small solar pond (one acre by five meters deep) cost estimate.

Item	Cost in $\$10^3$	
	California[a]	This work
Land	5	1
Excavation and diking	120	25
Salt	120	−7
Liner	45	10
Equipment and Instrumentation	25	25
Total pond construction	305	54
Unit pond construction (dollars per square meter)	75	13

[a] Lin (1982).

produced by salt-gradient solar ponds would contribute to efforts of sustaining agriculture, oil production, and related industry in the region by providing heat power for animal housing, drying crops, tractors, and pumps. Energy production for daily or seasonal use could stored or sold by putting in a utility grid.

The estimated cost of a functional solar pond based on the factors discussed here and in a recent article by the author (Lodhi, 1989) is given in Table 1. A comparison of the cost and energy of the proposed pond with those of others also was made. The estimate is preliminary and highly tentative because a conceptual, rather than a formal, design is treated in this paper. All costs given are gross, installed, costs including labor and supervision. The primary factors bringing down cost of the pond and that of the energy are: 1) labor costs of excavation would be reduced considerably by use of already existing playa lakes; 2) salt and brine would be available from alkaline lakes and oil wells; and 3) negative cost of salt could come from dumping a charge for brine from oil fields and disposal charge for salt and brine from a nearby repository site for radioactive waste material.

The electricity production units, when coupled with solar ponds, could produce electric energy at a reasonable cost. High-efficiency units have been suggested and used with flat plate collectors and solar ponds.

The economics of solar ponds depend primarily on factors like the price of land, water, salt, liners, and so on. However, other factors such as location, soil properties, or type of applications also may affect the cost. I have taken into account possible sources that could lower cost of the pond. A large pond would be expected to cost less per unit area than a small one on the basis of simple economics. For a small-sized pond of one acre and five meters deep, the predicted cost is $13 per square meter in comparison to the same 1979 figure of $13 per square meter of SOLMAT Company of Israel, excluding heat exchangers (Tabor, 1981). Thermal and electrical energy costs are, respectively, 2.6 cents and 11 cents per kilowatt hour. Eddesses (1982) estimated the cost as ranging from $7 to $28 per square meter. The Miamisburg pond was estimated at $35 per square meter in 1977, about the same as the estimation in 1988 for a copper refinery in Townsville, Queensland, Australia (Lin, 1982; Ortabasi and Gurgenci, 1983). For a pond of a similar size, (Table 1) one acre and 3.5 meters deep, Lin (1982) estimated $75 per square meter.

Electric energy via large solar ponds of capacity 600 megawatts was estimated 8.5 cents per kilowatt hours and 25.9 per kilowatt hours for the southwestern and northeastern regions of the United States, respectively (Ortabasi and Gurgenci, 1983). Lambert et al. (1983) discussed four examples and estimated the cost of electric energy as 20.6 cents per unit for a 100-kilowatt plant, 6.4 cents to 18 cents for a one-megawatt unit, and 7.2 cents for a 400-megawatt unit. They concluded that perhaps the most important single parameter that affects the overall economic feasibility of solar ponds for electric energy production is the cost per square meter of the pond. In the case of my proposed pond, the economics are quite competitive and bring the cost down for both thermal as well as electrical energy.

Conclusions

Salt-gradient solar ponds have been built all around the world because of their distinct advantage over other solar systems. Experience totals 20 to 25 pond-years in the United States, 10 to 15 pond-years in Israel, and about 10 pond-years in the rest of the world (Tabor, 1981). It is an irony that there are none on the High Plains region of Texas and New Mexico where parameters for the construction and operation of SGSP are most favorable. SGSP is a device for collecting and storing solar energy. Daily and weekly storage is no problem for a solar pond. Solar ponds can continue providing energy even for months during long cloudy spells, which no other solar system can do. With sufficient depth of water, even seasonal storage is easy to attain in a SGSP.

The viability of solar ponds to produce low-cost thermal energy is well proven. It is five to six times cheaper than oil heating. The solar pond does not have such a clear cut edge over competing electrical power production. In the High Plains region, even this may not be true for parameters fortuitously in favor of SGSP. The cheap, flat land at an elevation of more than one kilometer, receiving clear solar energy for 275 to 305 cloud-free days, alkaline lake basins and oil field brine, providing a negative cost for salt, less excavation costs, and soil characteristics that cut the cost of the liner, are some of the features making the SGSP competitive with conventional electricity production.

When these resources are harnessed, the High Plains region will be benefited. If these resources are not utilized, they become a drag on it's economy. The SGSP's mid-termperature thermal energy can be used for many areas of application. A solar pond can provide heat for space heating pool below the current cost of using oil fuel. As for the generation of electricity, some large-scale solar pond power plants, like Salton Sea (Peelgen, 1982) are quite economically feasible. On the High Plains, however, even smaller-sized ponds of one acre or more are likely to become quite competitive. SGSP could produce salt commercially, if desired, twice as much as a usual open evaporation pan would produce for the same acreage. SGSP also would provide the necessary temperature for a multiple-stage distillation desalination plant. This would increase the supply of fresh water to the local area.

Some of the features of the High Plains region discussed here are especially characteristic to this area, and make solar pond technology application greatly favorable. Once SGSP technology has been developed on these lines on the High Plains, it can be transferred to other locations where similar features exist. In this way, Texas could lead in this technology development and application.

Acknowledgments

I wish to acknowledge, gratefully, the help of Dr. M. N. Gazdar, in supplying the relevant information and library search during the preparation of this article. I am also appreciative of a review of the manuscript by Professor C. C. Reeves, who made invaluable suggestions.

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GENERAL NOTES

DISTRIBUTIONAL RECORDS OF THE YELLOW-NOSED COTTON RAT, *SIGMODON OCHROGNATHUS* BAILEY, IN TEXAS

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The yellow-nosed cotton rat, *Sigmodon ochrognathus*, occurs in Texas only in some isolated mountain ranges of the Trans-Pecos region (Fig. 1). It has been reported from the Chisos Mountains in southern Brewster County, the Sierra Vieja of western Presidio County, and the Davis Mountains of Jeff Davis and northern Brewster counties (Schmidly, 1977; Hall, 1981).

On 19 June 1986, a field party from Sul Ross State University (SRSU) obtained an adult male cotton rat (SRSU 2404) from the Ligon Ranch, 3 mi. NE Guadalupe Mountains National Park Headquarters, Culberson County, Texas. This locality is a northerly extension of the known range of this species in Texas of approximately 80 miles. Also of note is the occurrence of *S. ochrognathus* in the Del Norte Mountains of north-central Brewster County. On 11 February 1989, an adult male (SRSU 2669) was trapped on Mt. Ord, 10 mi. S Alpine, Brewster County. This locality is within the shaded area of the distribution maps of both Schmidly and Hall (*loc. cit.*) but is from a mountain range on which *S. ochrognathus* was not previously known to occur (Fig. 1). These two records are also the first for this species from areas of nonigneous rocks.

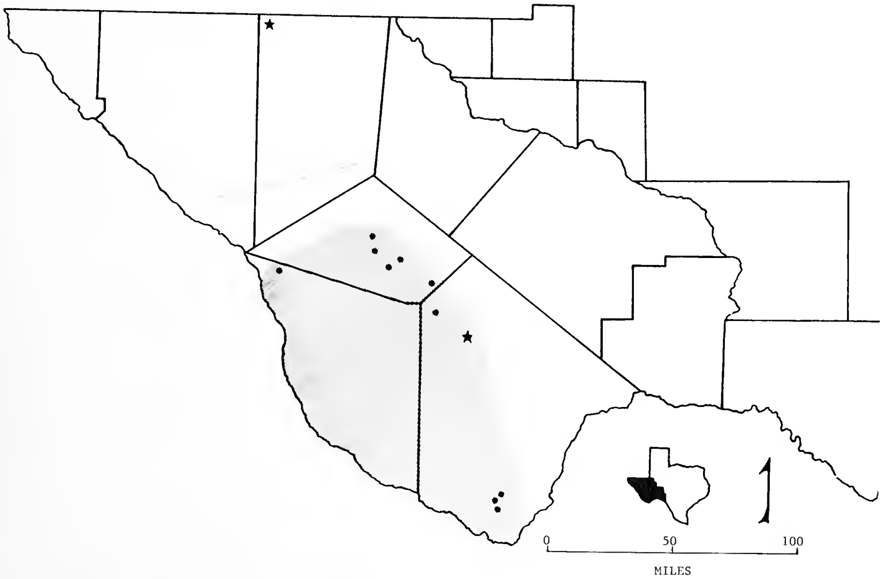

Figure 1. Map showing the previously reported distribution of *Sigmodon ochrognathus* (shaded area) with the specific localities marked with dots (modified from Schmidly, 1977). The new localities reported herein from Texas are marked with stars.

Rose and Birney (1985) pointed out that *Sigmodon* and *Microtus* were ecological competitors and generally mutually exclusive. Dalquest and Stangl (1984) made the same point when analyzing Pleistocene fossil remains from Fowlkes Cave in southern Culberson County. Their contention was that the montane rodents, *Microtus mexicanus* and *S. ochrognathus*, were ecological vicars, with the former occurring in the Guadalupe Mountains to the north and the latter occupying the Davis Mountains to the south of Fowlkes Cave. All *Sigmodon* remains from the cave were tentatively identified by Dalquest and Stangl as *S. hispidus* because no specimens of *S. ochrognathus* had been reported from north of the Davis Mountains at that time. The occurrence of this species in the Guadalupe Mountains as reported herein leads to several important ecological and historical biogeographic questions. Do yellow-nosed cotton rats and Mexican voles truly occur sympatrically in the Guadalupe's, or do they maintain some level of ecological distinctness there? Did they occur together in the past? Are the current distribution patterns the results of factors other than interspecific competition? Additional research on these species will be necessary to answer any of these questions.

Schmidly (1977) listed one specimen each of *S. ochrognathus* and *S. hispidus* from Black Gap Wildlife Management Area of southeastern Brewster County but did not discuss their occurrence there in text. Both specimens are housed in the mammal collection of The Museum, Texas Tech University. Upon our request, Dr. J. K. Jones, Jr., examined these specimens and concluded that both were *S. hispidus*, thus invalidating Schmidly's report of *S. ochrognathus* from Black Gap.

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MANATEE STRANDING ON THE COAST OF TEXAS

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The sporadic occurrence of the West Indian manatee, *Trichechus manatus*, in Texas waters has been noted by some authors. Gunter (1941) reported records of nine manatees obtained from 1853 to 1937. Two were carcasses: one washed ashore in Copano Bay, near Bayside; the other was seen floating in Cow Bayou, which connects to Sabine Lake, near the Louisiana border. The remaining animals were captured alive on the lower coast (Laguna Madre and Río Grande) except for a skull that was recovered from Brazos Island. Powell and Rathbun (1984) mentioned a 1979 sighting near Corpus Christi. These authors and Lowery (1974) suspected that some, if not all, of these manatees were seasonal visitors from Mexican waters.

On 4 February 1986, a manatee stranding was reported to the Texas Marine Mammal Stranding Network (TMMSN), Galveston Region. A local fisherman found the carcass of a male, in an advanced state of decomposition, rolling in the surf *ca.* 1 mi. W Caplen, Bolivar Peninsula (29°29′8″N, 94°32′7″W). Parts of the anterior portion of the skull, the flipper bones, and sternum were exposed. The total length of this manatee, measured from the tip of the exposed rostrum to the fluke tip, was 274 centimeters. Along the right side of the abdomen were 10 golfball-sized holes, which penetrated, but did not pass through, the blubber. Seven holes formed a V-shaped figure, with the other three forming a straight line immediately beneath it. The cause of these holes (as well as the precise origin of the animal) is unknown. A recent rope mark was visible around the tail stock. These wounds showed up well in a photograph.

No gross anatomical abnormalities were detected during a field necropsy. A mass of semidigested vegetal matter was found in the posterior section of the large intestine and a small sample was preserved for future analysis. The rest of the digestive tract was empty.

The carcass was buried, subsequently excavated, and the skeleton cleaned at Texas A&M University at Galveston. The skeleton is stored in the Texas Cooperative Wildlife Collection at Texas A&M University, College Station (catalog no. C271). This manatee stranding is the first to be recorded by TMMSN since its inception in 1980.

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OCCURRENCE OF HOUSE DUST MITES IN CENTRAL TEXAS

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House dust mites have received considerable attention because of their allergic effect on humans. Allergens derived from cultures and feces of *Dermatophagoides pteronyssinus, D. farinae, Euroglyphus maynei,* and *E. longior* have been linked with perennial rhinitis, atopic dermatitis, and asthma (Platts-Mills and Chapman, 1987). It has also been suggested that there may be an association between the sudden infant death syndrome and exposure to house dust mites (Mulvey, 1972).

D. pteronyssinus has been found in house dust samples from California, Colorado, and Ohio (Arlian et al., 1982; Moyer et al., 1985; Mulla et al., 1975). *D. farinae* has been identified in house dust samples from California, Colorado, Ohio, Tennessee, and Texas (Arlian et al., 1982; Hall et al., 1971; Moyer et al., 1985; Mulla et al., 1975; Shamiyeh et al., 1971). Although both *D. pteronyssinus* and *D. farinae* have been reported in the United States, the former is usually more common in Europe and South America (Cunnington et al., 1987). The Entomological Society of America has approved the names "European house dust mite" for *D. pteronyssinus* and "American house dust mite" for *D. farinae* (Wharton, 1976).

In an earlier study, Hall et al. (1971) found *D. farinae* in dust samples from the Fort Worth-Dallas area in Texas. Although it is probable that house dust mites occur throughout the state, this assumption has not been confirmed by actual collection in the field. The purpose of this study was to determine if *Dermatophagoides* occurs in central Texas.

Dust samples were collected between 9 June and 28 June 1989 in Bell and Coryell counties using a hand-held rechargeable vacuum (Black and Decker Dustbuster, model 9330) with the internal filter removed. Samples from residential and public buildings were collected by vacuuming an area encompassing half a square yard for two and one-half minutes. Dust was collected in a coffee filter held over the rectangular nozzle of the vacuum by a rubber band. Dust samples were preserved in a solution of 50 percent ethyl alcohol and stored until they could be examined for mites.

Mites were separated from the dust using the method of Furumizo (1973). Each sample was mixed with alcohol, teased apart, seived, and allowed to settle in a graduated cylinder for 24 hours so that the volume of dust could be measured in milliliters. The original sample sizes ranged from 0.2-3.6 milliliters of dust. If the original sample size exceeded one milliliter, it was divided to reduce the amount of time spent searching for mites. Division was accomplished by stirring the sample to suspend the particles and quickly pouring it into a splitter-funnel to minimize bias in obtaining equal fractions. All of the mite counts were reported with respect to one milliliter of dust.

Number of individuals, stage of life-cycle, and species of house dust mite were noted for each sample. Stages in the life cycle of *Dermatophagoides* include egg, larva, protonymph, tritonymph, and adult. In this study, mites were identified as larva, nymph (including both protonymphs and tritonymphs), adult male and female, or as "unknown" when only a fragment of the exoskeleton was found. Because identification is based on sexually mature mites, the species could be determined only when adults were found. *D. farinae* was distinguished from *D. pteronyssinus* by the shape of the distal portion of the bursa copulatrix in the female and the enlarged second pair of legs and length of the hysteronotal shield in the male.

Thirteen (72 percent) of 18 dust samples examined were positive for house dust mites (Table 1). Most mites were found in samples taken from carpets. No trend was apparent

Table 1. Occurrence of house dust mites.

Origin of dust	Species found	Lifestages					Total no. of mites	No. mites per ml/dust
		L	N	M	F	U		
House[2]	*D. farinae*	0	2	0	3	2	7	12
House[2]	*D. pteronyssinus*	0	8	5	12	0	25	36
House[2]	*D. farinae*	10	14	3	2	0	29	32
House[3]	*D. farinae* (25 percent) *D. pteronyssinus* (75 percent)	0	3	5	4	0	12	15
House[3]	None			0			0	0
House[4]	*D. pteronyssinus*	0	0	1	0	1	2	3
Office[2]	None			0			0	0
Office[2]	*D. farinae*	0	0	1	0	0	1	5
Office[3]	*D. farinae* (50 percent) *D. pteronyssinus* (50 percent)	0	2	5	1	0	8	10
Office hall[2]	None			0			0	0
Office hall[2]	None			0			0	0
Church sanctuary[2]	*D. farinae* (50 percent) *D. pteronyssinus* (50 percent)	0	4	3	3	1	11	28
Church class[2]	*D. farinae*	0	3	0	2	2	7	9
Church class[2]	*D. farinae*	12	57	42	49	0	160	160
School class[2]	*D. farinae* (91 percent) *D. pteronyssinus* (9 percent)	6	29	12	10	1	58	97
Library[3]	Unidentified	0	1	0	0	0	1	1
Library[3]	None			0			0	0
Weight room[2]	*D. farinae* (62 percent) *D. pteronyssinus* (39 percent)	2	6	9	4	0	21	26

[1] Number of mites of each stage: L, larvae; N, Nymph; M, Male; F, Female; U, Unknown.

[2] Carpeted floor.

[3] Hardwood floor.

[4] Upholstered furniture.

between the number of mites found and the use of the location as a private residence or a public facility. The sample with the most mites (160 mites per milliliter) was from a church classroom with short weave carpet. The room was used only one or two times a week by approximately 10 persons. However, for most samples, an association seemed to exist between the number of mites and the extent of human use. Five (38 percent) of the 13 locations where mites were obtained were infested only with *D. farinae*, five (38 percent) with both species, and two (15 percent) contained *D. pteronyssinus* alone. One sample (eight percent) contained only a single nymph, thus preventing identification of the species present. Other mites found in this study included unidentified species of Oribatidae, Cunaxidae, Raphignathidae, Acaridae, and Bdellidae.

The findings in this study demonstrate that house dust mites occur in a variety of locations in central Texas. In a previous study of house dust mites in the Forth Worth-Dallas area, only *D. farinae* was found to be present (Hall et al., 1971). The occurrence of *D. pteronyssinus* in central Texas represents a new locality record for this species. *D.*

pteronyssinus originally may have become established in this area due to the movement of infested furniture, carpets, and bedding materials between Europe and the Fort Hood military installation in Bell County.

We thank Dr. Dennis Dillin for his help in acquiring special equipment.

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A BIGHORN SHEEP, *OVIS CANADENSIS*, FROM THE LATE PLEISTOCENE OF MESA DEL ORO, CIBOLA COUNTY, NEW MEXICO

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In August 1985, the partial skeletal remains of a bighorn sheep were found in Witch Cave (NW1/4, NW1/4, sec. 14, T6N, R5W) on the northern end of Mesa del Oro, Cibola County, New Mexico. Witch Cave is one of many caves of the Pronoun Cave Complex containing late Pleistocene fossil-bearing fill. The mesa consists of early Pleistocene travertine deposits (Jicha, 1956), and most of the caves are partially closed fissures formed by settling of the travertine blocks. Surface openings of the fissures act as pitfall traps and account for the richness of fossil material. The remains of the bighorn sheep were recovered from within the cave on the underside of a clogged fissure approximately 15 meters below the surface and on the cave floor directly beneath it.

The material recovered includes a left partial horn core (Fig. 1), fragments of the right horn core, the complete occipital and right temporal with part of the parietal attached, both

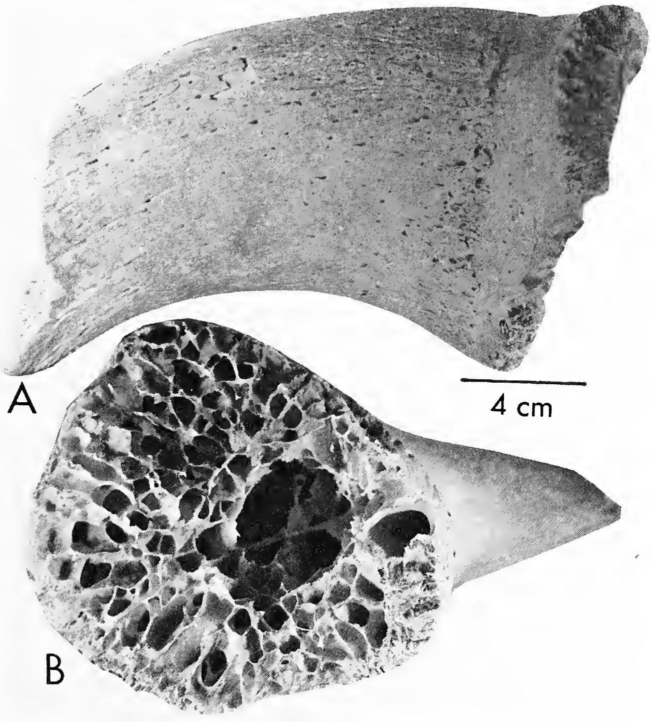

Figure 1. *Ovis canadensis catclawensis* from Witch Cave, Cibola Co., New Mexico: A) lateral view of left horn core; B) basal view of left horn core.

TABLE 1. Comparisons of cranial and tooth measurements (mm) for Pleistocene and Holocene *Ovis canadensis*. WIC = Witch Cave, New Mexico; DYC = Dry Cave, New Mexico (Harris and Mundel, 1974); LIT = Littleton, Colorado (Wang and Neas, 1987); BLF = Bloomfield, New Mexico (Stovall, 1946); GBA = Great Basin (Stokes and Condie, 1961); UTA = modern specimen from the University of Utah (Stokes and Condie, 1961).

Character	WIC	DYC	LIT	BLF	GBA	UTA
Maximum diameter at base of horn core	124	139	143	118.5	101-127 (N=12)	120
Circumference of horn core at base	349	428	410	346	330-385 (N=12)	335
Maximum diameter of occipital condyle	76	76		62.8	55-83 (N=7)	68
Minimum basioccipital width	40	35	40		29-33 (N=5)	
Anterior-Posterior length of M1	20.7				17.5-18 (N=2)	17 (N=1)
Anterior-Posterior length of M2	24.8				22 (N=2)	21 (N=1)
Anterior-Posterior length of M3	30	27			28-30 (N=2)	22 (N=1)
Transverse width M1	15				14 (N=2)	13 (N=1)
Transverse width M2	17				14.5-15 (N=2)	14 (N=1)
Transverse width M3	16.5				13.5-14 (N=2)	15 (N=1)

M3s, right M2, right M1 and a nearly complete left scapula. The material is deposited in the paleontological collection of the New Mexico Museum of Natural History (NMMNH P-3693).

Selected skull and tooth measurements of this specimen are compared with those of other late Pleistocene and Holocene *Ovis canadensis* from the western United States in Table 1. The Witch Cave specimen is larger in all measurements than modern *Ovis canadensis* measured by Stokes and Condie (1961) and is similar in size to Great Basin Pleistocene bighorn sheep (Stokes and Condie, 1961) except for its generally larger molars (Table 1). Specimens from Dry Cave, New Mexico (Harris and Mundel, 1974), and Littleton, Colorado (Wang and Neas, 1987), have significantly larger horn core measurements than does the Witch Cave bighorn sheep. This may be due, in part, to the young age of the Witch Cave specimen, indicated by the loose sutures between the occipital, parietal, and temporal bones, and completely unworn third upper molars. Based on these comparisons, the Witch Cave bighorn is most likely assignable to *Ovis canadensis catclawensis*. It falls well within the range of this group and supports the general pattern of Pleistocene bighorn sheep being larger than modern subspecies (Harris and Mundel, 1974).

Although several records of Pleistocene bighorn sheep exist for the Great Basin region, relatively few occurrences are documented for the Southwest. The Witch Cave specimen adds to this growing data base.

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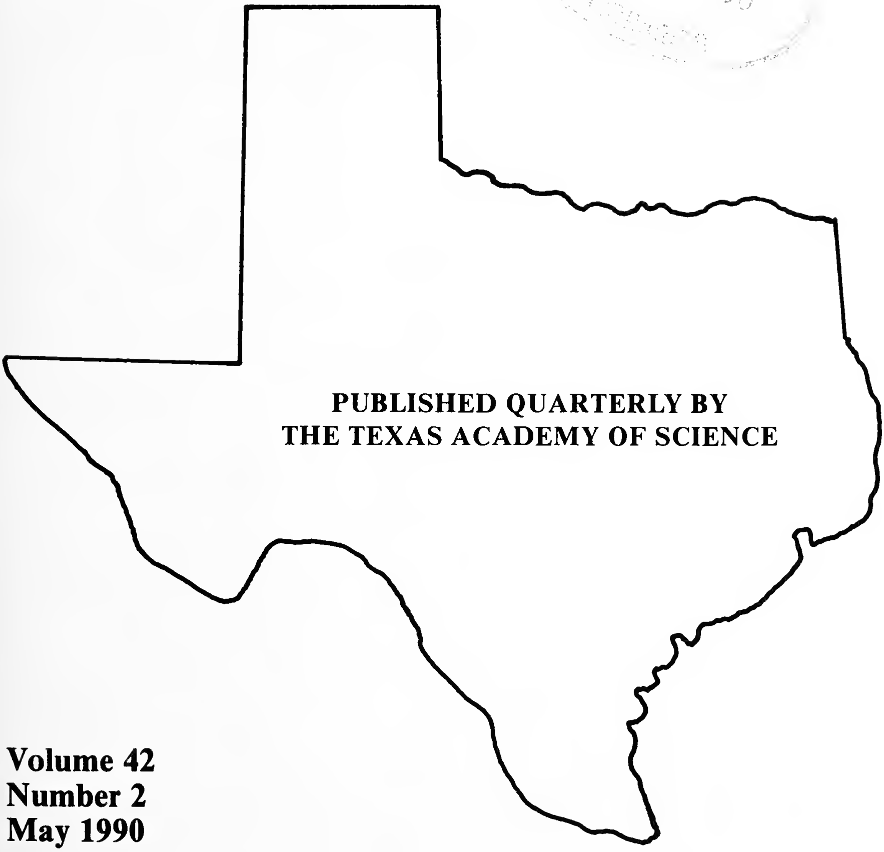

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PLANT COMMUNITIES OF THE SANTA ANA NATIONAL WILDLIFE REFUGE, TEXAS

Robin S. Vora
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Abstract.—A total of 137 plant species, including 61 woody species, was identified on 31 0.10-hectare plots. The woody species with greatest frequency (24 of 29 plots) across all vegetation types were granjeno (*Celtis palida*) and snailseed (*Cocculus diversifolius*). Plant communities follow former river channels and flooding patterns. Nine potential plant communities (and characteristic species) were identified: 1) Rio Grande riparian (*Salix* sp./ *Baccharis* sp.); 2) river bank (*Salix nigra*/*Clematis drummondii*); 3) recent accretions (*Celtis laevigata*/*Clematis drummondii*); 4) aquatic (*Scirpus californicus*/*Potamogeton* sp.); 5) seasonally flooded (*Parkinsonia aculeata*/*Mimosa pigra*); 6) former resaca bottom (*Fraxinus berlandieriana-Sapindus drummondii*/*Rivina humilis*); 7) floodplain-bottomland (*Ulmus crassifolia-Sapindus drummondii*/*Rivina humilis*); 8) floodplain-chaparral (*Pithecellobium flexicaule*/*Celtis pallida*); and 9) upland brush (*Acacia rigidula*/*Leucophyllum frutescens*).

Key words: flooding patterns; permanent plots; Rio Grande Valley, Texas; species frequency.

Ecological data are lacking for thorn woodlands in general. The U. S. Fish and Wildlife Service and Texas Parks and Wildlife administer more than 16,500 hectare of Tamaulipan thorn woodland in southern Texas, including the 801-hectare Santa Ana National Wildlife Refuge (NWR) in Hidalgo County. Tamaulipan thorn woodland is a general term for the vegetation in the lower Rio Grande Valley.

The plant communities of the lower Rio Grande Valley of southern Texas follow old flooding patterns and change with climate from the coast inland. The soils of the resaca bottoms are heavy clays, whereas the upland soils are silty clay loams or silt loams (Jacobs, 1981).

The native plant communities have not been described other than by brief summary description (Clover, 1937; Blair, 1950; Fleetwood, 1973; U. S. Fish and Wildlife Service, 1983). Clover (1937) classified much of the area into a climax association she called "mesquital," with "mesquital-chapparal the most important phase." Blair (1950) termed this area the Matamoran district of the Tamaulipan province. The native Tamaulipan thorn woodland is now relegated to islands surrounded by farm and pasture land and urban development.

The Santa Ana NWR is the largest remaining tract of native thorn woodland in the lower Rio Grande Valley. The vegetation has remained undisturbed since acquisition of the refuge in 1940, except for accretions of land along the river that occurred primarily before 1968 and the Bravo Woods addition in 1978. Fleetwood (1973) assembled a floristic list for the refuge and described 11 "ecological units": managed impoundments, dry lake beds, river, resacas, floodplain, borrow pits, mesquite groves, shrub garden, ebony woods, chaparral, and lawn areas.

Refuge managers initiated a woody plant inventory program with permanent plots in 1984 to describe the native plant communities, study succession, obtain baseline biological data, and otherwise gather information needed for management. Thirty-one plots were installed and censused. My primary objective in this paper is to present a preliminary description of the native plant communities of the Santa Ana NWR based on data from these plots. I also examined how increasing the number of sample plots affected the cumulative number of species sampled.

METHODS

Twelve points, located across the range of woody plant communities found in the lower Rio Grande Valley, were selected to test the adequacy of the 0.10 hectare plot size. From these 12 points, distances to all woody species at least five centimeters diameter at breast height (dbh) were measured to the nearest decimeter. Locations of other plants were plotted on a circular graph, represented as within two meters plus or minus of their actual location. The distances to the nearest individual of the smaller woody and herbaceous plants were estimated from the graphs. Cumulative number of species were plotted in relation to area sampled. Minimal area was defined as "the sample area at which the initially steeply increasing curve becomes almost horizontal" (Mueller-Dombois and Ellenberg, 1974).

Minimal areas varied from eight to 250 square meters for the individual plots. Minimal areas were 50 to 250 square meters for five plots with relatively high species richness (15 to 39 species) that were located across a variety of plant communities (Fig. 1). A plot size of as little as 250 square meters seems to be adequate for recording composition of plant comununities in the lower Rio Grande Valley, unless one is interested in sampling rare species.

Eight plots were located randomly within selected stands at Santa Ana NWR beginning in January 1984. An infra-red color photograph, taken from an altitude of 18,287 meters, was available later in 1984, and stands were delineated on it. These stands were grouped into 20 potential cover types based on color signatures on the aerial photographs and cursory ground reconnaisance. Five of the types had been sampled previously. Plots were located randomly within the remaining 15 types. Field study revealed additional potential cover or plant community types, and eight more plots were located randomly within selected stands to sample these areas. The centers of three of these plots had to be in the center of their respective stands because of the small size or narrow width of the stands. One plot was in a transitional riparian zone adjacent to a lake. Floristic lists were made for each 0.10-hectare plot.

The plot centers were marked permanently with steel center posts. All woody species with one stem at least five centimeters in diameter at a height of 1.4 meters (dbh) were marked with numbered stainless steel tags fastened with aluminum nails. The species and number of each tagged tree or shrub were recorded on a data sheet along with the azimuth and distance from the center of the plot. Also recorded were the dbh of the largest stem (dbh hereafter), tree height, and number of stems more than five centimeters dbh. Woody vegetation less than five centimeters dbh was not tagged, but along with dominant herbaceous species was plotted on circular graphs. These graphs were prepared in a way to approximate canopy cover for shrub, small trees, and herbaceous plants at the time data were collected. Photographs of a 2.0 × 0.5 meters density board were taken from the center of plots in the four cardinal directions. Photographs were taken with the board 17.8 meters from the plot center. A brief site description was made and any relief features noted. Additional data were collected on tree vigor, litter depth, and canopy cover on the last 11

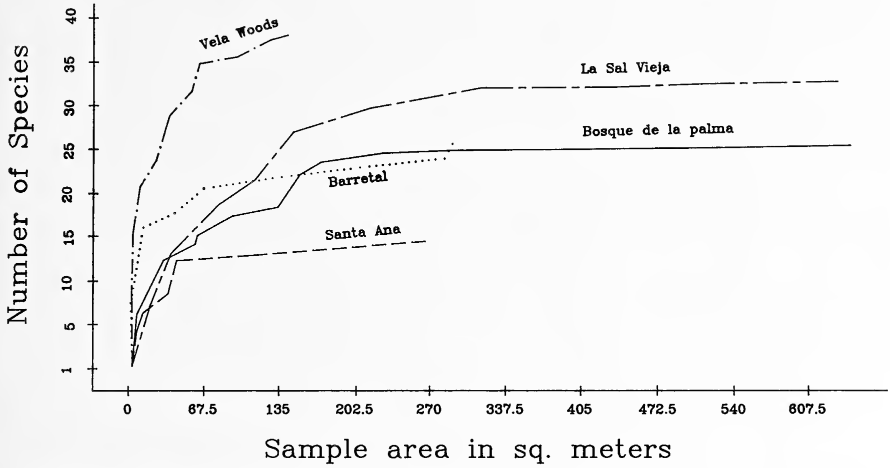

FIGURE 1. Minimal areas for five plant communities in the lower Rio Grande Valley, Texas.

plots sampled (plots 13, 14, 16, 21, 24, 27, and 29-33). Soil classification maps (Jacobs, 1981) were field-checked on 14 plots (plots 2, 5, 6, 9, 12, 14, 15, 16, 18, 21, 25, 27, 29, and 31).

Plots were grouped by tabular comparison (Mueller-Dombois and Ellenberg, 1974) of presence of woody species. These were more easily identified at any time of the year than herbaceous plants, hence data analyses focused on them. A woody species was defined as one included in Lonard et al. (1990). The constancy of each woody species across all plots was calculated. Plots were ordinated manually along a soil moisture gradient with species characteristic of wet and dry areas. Plots were grouped based on similarities and dissimilarities of their floristic lists, soil types, field observations, and, to a lesser extent, on tree cover and densities. Small sample size (n = 29), including only one or two plots in some potential community types, precluded use of more sophisticated ordination and classification techniques (Gauch, 1982). Two plots in early successional stands (plots 11 and 22) in the Bravo Woods area were excluded from this analysis because they were dominated by ubiquitous pioneer herbaceous species.

RESULTS AND DISCUSSION

Species-Plot Relations

One hundred and thirty-seven plant species were found on the 31 0.10-hectare plots (Fig. 2). This is only 33 percent of the 455 species and varieties listed by Fleetwood (1973) for Santa Ana NWR. Most plots were visited only once, and additional visits at other seasons undoubtedly would have resulted in larger floristic lists for each plot. Repeated visits to one plot produced a list of 17 herbaceous species, and this was the reason for the rise in the cumulative species curve in Figure 2 at plot 21.

Sixty-one of the 92 woody species that Fleetwood (1973) listed were found on the 31 0.10-hectare plots. Fifty (54 percent) of the woody species were found on the first 10 plots located by stratified random sampling (Fig. 2, the first 15 plots on the horizontal axis of the figure

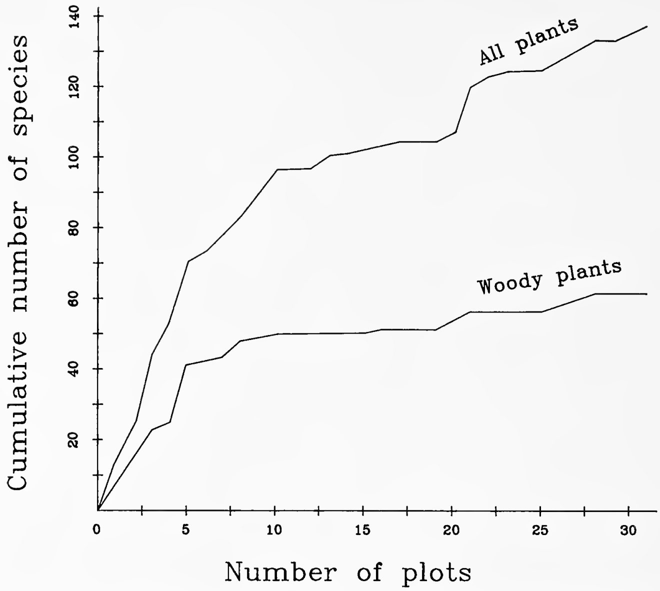

FIGURE 2. Relation of cumulative plant species to number of 0.1-hectare plots sampled on the Santa Ana NWR.

were those located randomly within cover types delineated on an aerial photograph).

The woody species found with greatest frequency (24 of 29 plots) across all vegetation types were granjeno (*Celtis pallida*) and snailseed (*Cocculus diversifolius*). Constancy was 10 percent greater (three or more of 29 plots) for 42 woody species (Table 1). The number of woody species on a 0.10-hectare plot varied from nine to 28, with a mean of 18.

Plant Communities of the Santa Ana NWR

A preliminary map of plant communities of Santa Ana NWR (Fig. 3) shows that they are intertwined and follow former river channels and flooding patterns. Discrete boundaries are found between resaca bottoms (old river channels) and more upland surroundings. Their shape creates a large amount of edge habitat between plant communities and is perhaps a reason for the large diversity of plant and animal life found in this 800-hectare thorn woodland.

Plant communities were highly varied in species composition, vegetation structure, and apparent successional stage, thereby making community classification difficult and tentative. The climax or disclimax make-up of these plant associations are unknown as it is probable that every hectare on the refuge (except recent accretions from the river) has been affected by grazing or farming before the creation of the refuge in 1940. The lower Rio Grande Valley has been settled since the 1700s, but

TABLE 1. Constancy (number of plots out of 29 in which at least one individual of the species was found) of major woody species on Santa Ana National Wildlife Refuge across all vegetation types.

Species	Constancy	Species	Constancy
Celtis pallida	24	*Tillandsia usneoides*	11
Cocculus diversifolius	24	*Leucaena pulverulenta*	10
Diospyros texana	22	*Phaulothamnus spinescens*	10
Celtis laevigata	21	*Guaiacum angustifolium*	9
Zanthoxylum fagara	21	*Ziziphus obtusifolia*	9
Amyris texana	20	*Acacia wrightii*	8
Condalia hookeri	20	*Fraxinus berlandieriana*	8
Ehretia anacua	20	*Heimia salicifolia*	8
Bumelia celastrina	19	*Malphighia glabra*	8
Rivina humilis	19	*Sapindus drummondii*	8
Ulmus crassifolia	18	*Opuntia lindheimeri*	7
Cissus incisa	17	*Sida* sp.	7
Parkinsonia aculenta	16	*Solanum triquetrum*	7
Forestiera angustifolia	15	*Amyris madrensis*	6
Serjania sp.	15	*Karwinskia humboldtiana*	6
Acacia smallii	14	*Petiveria alliacea*	6
Clematis drummondii	14	*Smilax bonanox*	6
Capsicum annuum	12	*Lantana horrida*	5
Pithecellobium flexicaule	12	*Opuntia leptocaulis*	4
Prosopis glandulosa	12	*Acacia rigidula*	3
Tillandsia recurvata	12	*Lippia alba*	3

local site histories are unknown. Flooding has been eliminated as a natural force since the 1950s, except during an occasional hurricane.

Rio Grande riparian.—Riverbanks are typically steep and five to eight meters high, except in accretion areas where they are wider with a more gentle slope. The vegetation is dense and composed of dry-land willow (*Baccharis neglecta*), seepwillow (*B. salicifolia*), black willow (*Salix nigra*), and sandbar willow (*S. exigua*). The soil type is Zalla loamy fine sand.

River bank.—On top of the bank in accretion areas, one finds black willow, dry-land willow, seepwillow, and also sugarberry (*Celtis laevigata*), cedar elm (*Ulmus crassifolia*), and Mexican ash (*Fraxinus berlandieriana*) as represented by plot 10 (Tables 2 and 3). The soil type is Zalla loamy fine sand. The overstory has a canopy cover of about 50 percent and is primarily sugarberry and black willow trees that are five to 16 meters tall, with trunks five to 55 centimeters dbh, and a density of about 270 trees per hectare. *Baccharis* sp. dominates the understory with about 50 percent canopy cover. Texas virgin's bower (*Clematis drummondii*) often forms a dense ground cover.

Recent accretions.—The river continues to make small accretions to the southern boundary of the Santa Ana NWR, although none of

TABLE 2. Relationships among woody plant species and plant communities on the Santa Ana National Wildlife Refuge.

	Plant community/plot																												
	A	B			C						D							E		F						G			
Species	10	30	19	20	31	29	1	28	9	18	21	14	23	15	16	5	12	13	24	3	25	2	27	17	6	33	7	8	32
	Differential Species																												
Salix nigra	x				x																								
Salix exigua					x																								
Buddleja sessiliflora	x																												
Baccharis salicifolia	x				x																								
Mimosa pigra		x								x																			
Lycium carolinianum		x																											
Fraxinus berlandieriana	x			x	x	x	x	x			x		x																
Sapindus drummondii			x		x	x	x		x		x	x	x																
Smilax bonanox					x	x		x	x			x	x																
Leucaena pulverulenta					x	x		x	x	x	x	x	x	x							x								
Lippia alba									x	x							x												
Ulmus crassifolia	x		x	x	x	x	x	x	x		x	x	x	x		x	x			x	x		x	x					
Celtis laevigata	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x						
Ehretia anacua	x		x	x	x	x	x	x	x		x	x	x	x	x	x			x	x	x	x	x		x				
Parkinsonia aculeata	x	x	x	x	x	x		x	x	x			x	x		x	x	x	x					x					
Acacia smallii		x	x	x	x			x	x	x	x	x		x			x	x	x				x						
Clematis drummondii	x		x	x		x		x	x	x			x	x		x	x	x	x		x								
Capsicum annuum			x	x		x	x					x	x	x	x				x				x	x	x				
Tillandsia usneoides					x	x	x	x	x		x	x			x	x					x				x				
Ziziphus obtusifolia			x				x			x		x	x					x		x	x	x							
Petiveria alliacea					x	x	x					x								x		x							
Croton sp.																										x			x
Mimosa malacophylla																										x		x	
Castela texana																										x			
Acacia rigidula																											x	x	x
Adelia vaseyi																											x		x
Bernardia myricifolia																													x
Croton humilis																												x	
Leucophyllum frutescens																													x
Lycium berlandieri																													x
Schaefferia cuneifolia																													x

TABLE 2. Continued.

	Ubiquitous Species																												
Celtis pallida			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x		x	x	
Cocculus diversifolius	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x			x
Diospyros texana					x	x	x		x	x	x	x	x	x	x	x			x	x	x	x	x	x	x	x	x	x	x
Zanthoxylum fagara			x	x	x	x		x	x	x	x	x	x	x	x				x	x	x	x	x		x	x	x	x	
Amyris texana					x	x			x	x	x	x		x	x	x		x	x	x	x	x	x	x	x	x	x	x	
Condalia hookeri			x		x	x	x	x	x	x		x	x	x	x		x			x	x	x	x		x		x	x	x
Bumelia celastrina		x	x		x	x	x	x			x	x	x	x	x					x	x	x		x		x	x	x	x
Rivina humilis			x		x	x	x		x	x	x	x		x	x	x	x	x	x		x		x		x	x		x	
Cissus incisa					x	x			x		x	x	x		x	x		x	x	x	x	x	x		x	x		x	
Forestiera angustifolia					x	x	x			x	x	x		x	x	x			x				x		x	x	x	x	
Serjania sp.		x	x		x	x	x		x		x	x		x	x				x				x		x	x			x
Pithecellobium flexicaule						x	x	x	x		x	x	x							x		x		x		x		x	
Prosopis glandulosa		x									x			x	x		x				x		x	x	x	x	x		x
Tillandsia recurvata					x		x		x		x	x			x	x					x		x		x	x	x		
Phaulothamnus spinescens			x	x				x					x				x			x		x		x	x	x		x	
Guaiacum angustifolium			x		x															x		x		x		x	x	x	x
Acacia wrightii												x			x	x									x	x	x	x	x
Heimia salicifolia						x			x						x				x		x				x	x		x	
Malphighia glabra									x	x		x								x					x	x		x	x
Opuntia lindheimeri		x								x				x	x		x	x							x				
Sida sp.						x			x	x							x		x		x							x	
Solanum triquetrum						x			x	x						x	x	x										x	
Amyris madrensis								x			x											x		x				x	x
Karwinskia humboldtiana																				x				x		x	x	x	x
Lantana horrida		x			x											x			x									x	
Opuntia leptocaulis														x							x				x	x			
Baccharis neglecta	x																	x											
Phoradendron tomentosum																							x	x					

A—*S. nigra*/*C. drummondii* (river bank)
B—*P. aculeata*/*M. pigra* (seasonally flooded)
C—*F. berlandieriana*-*U. crassifolia*/*R. humilis* (former resaca bottom)
D—*U. crassifolia*-*S. drummondii*/*R. humilis* (bottomland)
E—*C. laevigata*/*C. drummondii* (recent accretions)
F—*P. flexicaule*/*C. pallida* (chaparral)
G—*A. rigidula*/*L. frutescens* (upland brush)

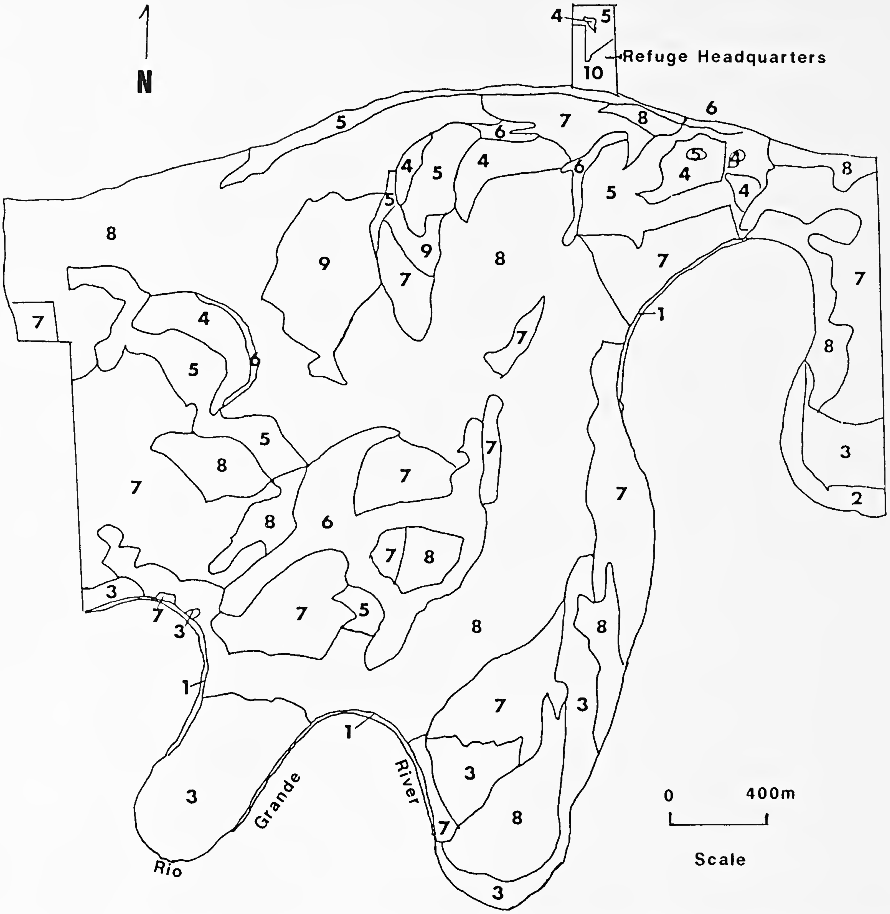

FIGURE 3. Plant communities of the Santa Ana NWR (1, Rio Grande riparian; 2, river bank; 3, recent accretions; 4, aquatic; 5, seasonally flooded; 6, former resaca bottom; 7, floodplain-bottomland; 8, floodplain-chaparral; 9, upland brush; 10, office compound and parking lot).

significance since Hurricane Beulah in 1967. Overstory cover is 50 percent in thin bands of sugarberry, huisache, and retama and less than 10 percent in open areas between the bands. Trees are up to 11 meters tall and have a dbh up to 36 centimeters (Table 3). Tree density is about 300 per hectare in the sugarberry bands and 100 per hectare in open areas. Herbaceous and vine cover is 90 to 95 percent. *Eupatorium* sp. is common. Pigeonberry is frequent in the sugarberry area, whereas the open areas are covered by a dense mat of Texas virgin's bower. These stands have remained undisturbed since the accretions occurred and are in primary succession. The sugarberry bands follow previous river courses, and with soil development and time probably will resemble mesic bottomland forests. With succession, the presently open areas more likely will resemble the chaparral community.

Aquatic.—The three pools at Santa Ana are shallow and the level is maintained by pumping from two wells. Aquatic plants include pondweeds (*Potamogeton* sp. and *Zannichellia palustris*), southern naiad (*Najas guadalupensis*), California bulrush (*Scirpus californicus*), spikesesdge (*Eleocharis* sp.), and smartweed (*Polygonum densiflorum*—Fleetwood, 1973).

Seasonally flooded.—Adjacent to resacas of oxbow lakes are seasonally flooded stands of huisache (*Acacia smallii*), sugarberry, and retama (*Parkinsonia aculeata*) (Tables 2 and 3). These trees are four to 12 meters tall, with a dbh of five to 32 centimeters, and have a density of 380 to 1060 trees per hectare. California bulrush, rattlebox (*Sesbania drummondii*), smartweed, black mimosa (*Mimosa pigra*), Carolina wolfberry (*Lycium carolinianum* var. *quadrifidum*), *Salix* sp., *Baccharis* sp., granjeno, and colima (*Zanthoxylum fagara*) comprise the understory. Herbaceous vegetation and Texas virgin's bower cover 90 to 95 percent of the ground. The soil type is Grulla clay. These communities may be an early seral stage of the community described next.

Former resaca bottoms.—Former resacas wind through the area and are typically 0.3 to 2.0 meters deep and 10 to 50 meters wide. They are characterized by Mexican ash, sugarberry, cedar elm, huisache, and retama (Table 2). The soil type is typically Grulla clay. Overstory tree cover is usually dense (more than 70 percent), and trees often form a parklike setting with a sparse understory and dense cover of litter. Dominant trees are five to 17 meters tall, with a dbh of five to 35 centimeters, and a density of 500 to 700 trees per ha (Table 3). Spanish moss (*Tillandsia usneoides*) and small ball moss (*T. recurvata*) are common in overstory trees, especially in cedar elm. Common understory brush species include those found in the overstory trees, especially in cedar elm. Common understory brush species include those found in the overstory, and retama, chapotillo (*Amyris texana*), and elbow bush (*Forestiera angustifolia*). Pigeonberry is common in the ground layer and Texas virgin's bower is found in openings. Retama and black mimosa are found in disturbed areas.

Floodplain.—On higher ground out of resaca bottoms, one finds a wide variety of plant communities that form a continuum toward a dry, upland type. Exceptions were found to every attempt made to ordinate the stands according to floristic lists or soil types. The presence of various overlapping successional stages (Huschle and Hironaka, 1980) and lack of knowledge of stand history hindered our attempts.

TABLE 3. Plant community descriptions based on inventory plots at Santa Ana National Wildlife Refuge.

Plot	Layer 1—Trees						Layer 2—Shrubs					Layer 3—Ground Cover			
and		Major Species						Major Species					Major Species		
soil type^a	Total cover^b	Code^c	Cover (%)	Height (m)	Trees/ha^d	Dbh^e	Total cover^b	Code^c	Cover (%)	Height (m)	Dbh^e	Total cover^b	Code^c	Cover (%)	Litter cover
Salix nigra/Clematis drummondii community (river bank)															
10	50	CELA	n.m.^{f}	5.15	180	5-34	50	BANE	n.m.	<5	<6	40	CLDR	n.m.	n.m.
Zalla lfs		SANI	n.m.	5-16	90	12-55		BASA	n.m.	<3	<5				
Parkinsonia aculeata/Mimosa pigra community (seasonally flooded)															
30,19,20	40-75	PAAC	20-40	3-8	240-400	5-18	20-40	PAAC	1-10	<6	<6	50-95	CLDR	0-30	
Grulla		CELA	5-30	3-8	20-940	5-16		CELA	1-10	<6	<6		ERPU	0-30	
clay		ACSM	5-30	4-8	80-120	6-32		ASCM	1-10	<6	<6				
								LYCA	1-3	<2					
Fraxinus berlandieriana-Sapindus drummondii/Rivina humilis community (former resaca bottom)															
31,29,1,	30-85	CELA	20-40	6-17	80-490	6-30	2-40	ULCR	0-10	<8	<17	1-80	RIHU	0-40	8-95
28,9,18		ULCR	10-55	10-13	10-260	5-34		CELA	0-10	<8	<17				
Grulla		FRBE	<20	9-12	0-60	11-30		CELA	0-5	<8	<17				
clay		ACSM	<10	8-10	0-30	24-34		TIUS		<8					
		PAAC	<10	5-8	0-20	6-20									
Ulmus crassifolia-Sapindus drummondii/Rivina humilis community (bottomland)															
21,14	60-90	ULCR	25-85	5-13	50-1320	20-55	30-50	CEPA	<10	<7	<6	6-10	RIHU	<5	90-98
Matamoros		LEPU	<5	7-13	10-40	20-55		CELA	<15	<9	<22				
sic		CELA	<5	5-12	50-60	6-19		DITE	<15	<7	<6				
		SADR	<6	5-11	<10	20-30		ULCR	<80	<5	<7				
		PRGL	<4	5-10	<10	30-60									
Celtis laevigata/Clematis drummondii community (recent accretions)															
13,24	8-50	ACSM	4-13	5-8	40-60	5-36	10-30	CELA	<10	<5	<5	90-95	EUS	12-30	5
Zalla		CELA	1-33	5-11	10-190	5-31		BANE	<5	<2	<5		RIHU	<50	
lfs		PAAC	<3	4-9	<50	5-20		EHAN	<5	<2	<5		CLDR	<80	
								ZAFA	<6	<2	<3				

TABLE 3. Continued.

Pithecellobium flexicaule/*Celtis pallida* community (chaparral)															
3,25,2	30-55	PRGL	<40	6-10	60-160	5-36	40-85	CEPA	<15	<7	<9	10-40	EUS	<5	<90
27,17,6		PIFL	<30	6-13	220-380	7-53		CELA	<10	<7	<10		RIHU	<10	
Rio Grande								EHAN	<5	<5	<6				
sicl								BUCE	<5	<5	<6				
sil								COHO	<5	<5	<6				
Acacia rigidula/*Leucophyllum frutescens* community (upland brush)															
33,7	1-30	PRGL	<1	4-9	10-20	8-46	80-90	AMTE	20-30	<5		<5			20-60
8,32								BUCE	5-20	<5	<21				
Reynosa								CEPA	<20	<6	<6				
sicl								ACRI	<5	<3	<5				
								LEFR	<5	<2	<5				

[a] lfs = loamy fine sand, sic = silty clay, sicl = silty clay loam.

[b] Percent canopy cover.

[c] ACRI-*Acacia rigidula*, ACSM-*Acacia smallii*, AMTE-*Amyris texana*, BASA-*Baccharis salicina*, BANE-*Baccharis neglecta*, BUCE-*Bumelia celastrina*, COHO-*Condalia hookeri*, CELA-*Celtis laevigata*, CEPA-*Celtis pallida*, CLDR-*Clematis drummondii*, DITE-*Diospyros texana*, EHAN-*Ehretia anacua*, EUS-*Eupatorium* sp., FRBE-*Fraxinus berlandieriana*, LEFR-*Leucophyllum frutescens*, LEPU-*Leucaena pulverulenta*, LYCA-*Lycium caroliinianum*, PAAC-*Parkinsonia aculeata*, PIFL-*Pithecellobium flexicaule*, PRGL-*Prosopis glandulosa*, RIHU-*Rivina humilis*, SADR-*Sapindus drummondii*, SANI-*Salix nigra*, TIUS-*Tillandsia usneoides*, ULCR-*Ulmus crassifolia*, ZAFA-*Zanthoxylum fagara*.

[d] Number of trees per hectare with one stem at least five centimeters diameter at height of 1.4 meters.

[e] Diameter (centimeters) of largest stem at height of 1.4 meters of trees with one stem at least five centimeters dbh.

[f] n.m. = not measured.

Floodplain-bottomland.—The wetter, more developed portions of floodplain soils support trees up to 14 meters tall and a diversity of species. The characteristic soil type is Matamoros silty clay. In what appear to be later successional stands, canopy cover of the overstory tree layer is 60 to 90 percent with cedar elm, tepeguaje (*Leucaena pulverulenta*), western soapberry (*Sapindus drummondii*), sugarberry, honey mesquite (*Prosopis glandulosa*), anacua (*Ehretia anacua*) the dominant species (Tables 2 and 3). Tree densities are 180 to 1500 per hectare, with a dbh range of five to 55 centimeters, and heights of five to 13 meters. Spanish moss is common in the trees. Understory shrub cover is 30 to 50 percent and includes overstory species as well as Texas persimmon (*Diospyros texana*), granjeno, chapotillo, and colima. Ground cover is less than 10 percent and consists primarily of pigeonberry (*Rivina humilis*) and tree seedlings. Litter cover is 90 percent.

In earlier successional stages of this type of community, dominant trees are retama, sugarberry, and cedar elm. Overstory tree cover is 10 to 75 percent with heights up to 14 meters, dbh up to 39 centimeters, and densities of 200 to 690 per hectare (Table 3). Common understory brush species include Texas persimmon, granjeno, anacua, retama, and Wright's acacia (*Acacia wrightii*). Pigeonberry and Texas virgin's bower are frequent in the understory. The earliest successional stands are characterized by huisache, dry-land willow, retama, and Texas prickly pear (*Opuntia lindheimeri*).

Floodplain-chaparral.—The community found in the somewhat drier portion of the floodplain is characterized by the absence of species found in more mesic or xeric regions (Table 2). The characteristic soil types are Rio Grande silt loam and Rio Grande silty clay loam. Soils on three plots (3, 22 and 27) are mapped as Reynosa silty clay loam, a soil type more characteristic of 'ancient stream terraces' found immediately north of the levee along the northern refuge boundary (Jacobs, 1981). Overstory cover varies from 30 to 100 percent, with Texas ebony (*Pithecellobium flexicaule*), cedar elm, and honey mesquite the dominant species. Tree heights in the overstory are five to 13 meters, with dbh up to 53 centimeters, and densities of 160 to 380 per hectare. Understory shrub canopy cover is much denser (40 to 85 percent) than in the previously described communities, and typical species are granjeno, Texas ebony, coma (*Bumelia celastrina*), guayacan (*Guaiacum angustifolium*), anacua, brasil (*Condalia hookeri*), colima, Wright's acacia, cedar elm, and lotebush (*Ziziphus obtusifolia*). Species of *Eupatorium* sp. are common in the herbaceous layer. A field that was cultivated eight years previously now has an 80 percent cover of Texas virgin's bower and common sunflower (*Helianthus annuus*).

Open honey mesquite groves were found in these upland areas. Fleetwood (1973) noted that the ground cover is buffalograss (*Buchloe dactyloides*), with scattered clumps of lotebush and Texas prickly pear. These are also the only areas in which hair-covered cactus (*Mammillaria multiceps*) is found. I do not know if these groves represent another type of plant community, or if honey mesquite eventually will die out, making room for other invader species. Archer et al. (1988) suggested that honey mesquite trees serve as foci for clusters of woody plants.

Upland brush.—The dry, open shrub community found along the northern portion of Jaguarundi trail is more characteristic of vegetation found to the north of the floodplain. Fleetwood (1973) called this area "shrub garden." The overstory consists of scattered honey mesquite trees (10 to 20 per hectare) that are four to seven meters in height, up to 46 centimeters dbh, and form a cover of less than 30 percent. The characteristic shrub layer includes *Croton* sp. vine mimosa (*Mimosa malacophylla*), blackbrush (*Acacia rigidula*), allthorn (*Castela texana*), vasey adelia *(Adelia vaseyi*), oreja de raton (*Bernardia myricifolia*), cenizo (*Leucophyllum frutescens*), and desert yaupon (*Schaefferia cuneifolia*—Table 2). This shrub layer is up to five meters tall and the canopy cover is 80 to 90 percent. Dominant species are chapotillo, coma, granjeno, guayacan, stem-leaf goldeneye (*Viguiera stenoloba*), and oreja de raton. Herbaceous cover is less than five percent.

The reason for the occurrence of this community in the floodplain is unclear; perhaps it is due to the manner in which soils were laid down by flooding of the river. The soil is mapped as Reynosa silty clay loam as are other areas on the Santa Ana NWR that support more treelike vegetation. During further investigation of the soils with J. Jacobs, of the Soil Conservation Service, we discovered that the B horizon of the soil was a silt loam instead of silty clay loam found in Reynosa soils elsewhere in the Santa Ana NWR (about 10 percent less clay), and it is also more calcareous. The latter accounts for the presence of cenizo and blackbrush, which are more common in calcareous soils in the eastern part of the lower Rio Grande Valley. We also observed an abundance of shells associated with calcareous soils and this community type.

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ADDITIONS TO THE DISTRIBUTIONAL ECOLOGY OF TWO PARTHENOGENETIC CLONAL COMPLEXES IN THE *CNEMIDOPHORUS LAREDOENSIS* SUBGROUP (SAURIA: TEIIDAE) IN TEXAS AND MEXICO

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Abstract.—An investigation of the parthenogenetic *Cnemidophorus laredoensis* subgroup in the upper, middle, and lower Rio Grande Valley of Texas and México between Ciudad Acuña-Del Rio and the Gulf of Mexico has resulted in four significant new distributional records for clonal complex LAR-B and five for clonal complex LAR-A. The new data support the view that LAR-B is limited to habitats situated within 10 kilometers of the Rio Grande in the upper and lower parts of the valley and that the clonal complex is absent in all except the southern part of the middle valley. Newly collected specimens in northern Webb County establish the presence of LAR-A in the upper valley and significantly change our previous zoogeographic conception of this clonal complex. LAR-A also is reported for the first time in areas well removed from the river in parts of the the middle and lower valley. The loss of habitat at four sites indicates that previous statements pertaining to the survival of the LAR clones outside areas under state or federal protection may have been overly optimistic. *Key words*: distribution; habitats; parthenogenetic *Cnemidophorus*.

The two parthenogenetic clonal complexes of whiptail lizards in the *Cnemidophorus laredoensis* subgroup (Walker, 1986) are among the most unusual vertebrates in the fauna of Texas and México with reference to their evolution, ecology, and distribution. Both clonal complexes evolved through independent hybridizations of the gonochoristic species *C. sexlineatus* and *C. gularis* (McKinney et al., 1973; Wright et al., 1983; Parker et al., 1989). To date, morphotype (that is, clonal complex) LAR-A (= *C. laredoensis sensu* McKinney et al., 1973) has been reported from 36 sites in Texas and México (Walker, 1987*a*) and morphotype LAR-B from 26 sites in Texas and México (Walker, 1987*b*). The geographic ranges for the clonal complexes as mapped by Walker (1987*a*, 1987*b*) are so unusual geographically and so restricted ecologically, especially in comparison to other southwestern *Cnemidophorus*, that we conducted additional field work to determine whether these ranges are real or artifactual as previously represented. The purpose of this report is to further clarify the distributional ecology of the *C. laredoensis* subgroup, including documentation of recent losses of habitat through catastrophic destruction.

Methods

This report is based upon eight periods of study between August 1987 and May 1989. The following geographic designations are used: (URGV) upper Rio Grande Valley (within

10 kilometers of the Rio Grande in Val Verde, Kinney, Maverick, and northern Webb counties, Texas, and from Lake Amistad, Coahuila, to the Nuevo León border); (MRGV) middle Rio Grande Valley (near the Rio Grande in Webb, Zapata, and Starr counties, Tamaulipas from about 50 kilometers north of Laredo-Nuevo Laredo to the vicinity of Rio Grande City, and away from the Rio Grande in Dimmit, LaSalle, and Starr counties); and (LRGV) lower Rio Grande Valley (within 25 kilometers of the Rio Grande in Starr, Hidalgo, and Cameron counties, and Tamaulipas from the vicinity of Rio Grande City to near the Gulf of Mexico).

Specimens utilized in this study are deposited in the University of Arkansas Department of Zoology (UADZ) and University of Kansas Museum of Natural History (KU). The coded localities and specimens of *Cnemidophorus* from each are listed below.

Results and Discussion

Nine new records for the LAR clones, from among more than 40 additional sites searched, are presented in geographical sequence from north-northwest to south-southeast by county in Texas and state in México. The locality codes and the whiptail association codes are consistent with those introduced by Walker (1987*a*, 1987*b*). Habitat characteristics of newly discovered sites are summarized in Table 1.

Texas (URGV). Val Verde Co.: (V-13^{++}) Del Rio, 13.1 km. NW jct. Spur 239 and U. S. Hwy. 90-277 (♀♀ LAR-B, UADZ 3140; ♀♂ *C. gularis*, UADZ 3138; ♀♂ *C. marmoratus*, UADZ 3139). Webb Co.: (W-15^{*+}) 96 km. N Laredo (or 79 km. S Eagle Pass) along FM 1472-1054 (= "Mines Road") (♀♀ LAR-A, UADZ 3483; ♀♀ LAR-B, UADZ 2209-2212, 2217-2222, 3027, 3032, 3033, 3039, 3041-3044, 3046, 3048; ♀♂ *C. gularis*, UADZ 2213, 2223-2231, 3031, 3034-3036, 3038, 3040, 3045, 3047, 3049).

Texas (MRGV). Zapata Co.: (Z-3*) Falcon Lake, end of FM 496 *ca.* 4.8 km. SW U. S. Hwy. 83 in Zapata (♀♀ LAR-A, UADZ 2460-2461; ♀♂ *C. gularis*, UADZ 2462-2463). Starr Co.: (S-12*) 13.6 km. N Rio Grande City on unsurfaced road off FM 755 (♀♀ LAR-A, UADZ 2527-2528; ♀♂ *C. gularis*, many observed).

Texas (LRGV). Hidalgo Co.: (H-1^{++}) Los Ebanos, at ferry landing (♀♀LAR-B, UADZ 2954; ♀♂ *C. gularis*, KU 199960-199964, 200038-200040); (H-5^{++}) Hidalgo, few km. upriver from international bridge (♀♀ LAR-B, UADZ 2531-2533; ♀♂ *C. gularis*, UADZ 2537); (H-7*) 10 km. N U. S. Hwy 83 at La Joya, then 200 meters W of first intersection on FM 2221 (♀♀ LAR-A, UADZ 2924-2931, 2933-2940, 2946-2948, 3514-3517, 3538; ♀♂ *C. gularis* UADZ 2941-2945, 3518).

Mexico (LRGV). Tamaulipas: (T-6^{+}) ferry landing across from Los Ebanos, road leading to Ciudad Diaz Ordaz (♀♀ LAR-A, UADZ 3536; ♀♀ LAR--B UADZ 3513); (T-13^{++}) Ejido Guadalupe, *ca.* 5.0 km. W Matamoros (♀♀ LAR-B, UADZ 2534-2536; ♀♂ *C. gularis*, UADZ 2538).

Additions to the Distributional Ecology in the Upper Rio Grande Valley

We found only LAR-B and *C. gularis* on our first five visits to W-15^{*+} in northern Webb County in 1987, 1988, and 1989 (Walker, 1987*b*). Thus, we were astonished when the only two specimens collected on a short visit to W-15^{*+} on 10 May 1989 included an adult LAR-A and a triploid hybrid LAR-A x *C. gularis*. This record, which extends the range of LAR-A 100 kilometers upriver from W-3 (Walker, 1987*a*—Laredo, Webb County) and 48 kilometers southward from D-3* (Walker, 1987*a*—Catarina, Dimmit County), significantly changes our zoogeographic

TABLE 1. Habitat characteristics of new sites where LAR-A and LAR-B have been collected; records are presented on the basis of geographical relationships from northwest to southeast in Texas and Tamaulipas. Abbreviations and symbols: letter = county or Mexican state code, number = locality code, $^{+}$ = LAR-A (♀♀) and LAR-B (♀♀), $^{++}$ = LAR-B and *C. gularis* (♀♂), * = LAR-A and *C. gularis*, $^{*+}$ = LAR-A, LAR-B, and *C. gularis*, BG = bunchgrass(es), CA = cactus, WE = weeds, ME = mesquite, TS = thorn shrub, MF = mixed forest, SS = sandy soil, LS = loamy soil, GS = gravelly soil, $^{+}$ = yes, — = no.

Site-sample code, date		Habitat characteristics	Catastrophic alteration	Steady degradation	Proximity to thorn shrub	Vegetatively comples	Topographically complex	Soil type
V-13^{++}	1988	BG-WE-TS	+	+	+	+	+	SS, LS, GS
W-15^{*+}	1989	BG-WE-ME	—	—	—	+ to —	—	SS, LS, GS
Z-3*	1987-89	WE-TS	—	—	+	+	—	SS, GS
S-12*	1987	BG-WE-ME	—	+ to —	+ to —	—	—	SS
H-1^{++}	1988	WE-ME-MF	—	+ to —	+ to —	+	+ to —	LS, GS
H-7*	1988-89	BG-WE-ME	+ to —	+ to —	+ to —	—	—	SS
H-5^{++}	1987-88	BG-WE, BG-WE-ME	+ to —	+ to —	—	+ to —	—	SS, LS
T-6^{+}	1989	BG-WE-MF	—	+	—	+	+ to —	SS, LS
T-13^{++}	1987	BG-WE-ME	—	+ to —	—	+	—	SS, LS, GS

conception of this clonal complex. Site W-15*+ is located about 6.4 kilometers from the Rio Grande along notorious "Mines Road," a remote unsurfaced stretch of highway (1472-1054) between Laredo and Eagle Pass. The part of W-15*+ that has been found to support parthenogens involves a narrow corridor of about 200 meters in length comprising remnants of sandy grass-weed-mesquite habitat extending about 10 meters from each side of the sandy roadbed to fenced pastureland. Attempts to find other sites for LAR-B and LAR-A between Laredo and Eagle Pass along 1472-1054 only have produced specimens of the ubiquitous *C. gularis*.

A specimen collected at site V-13++ (located about four kilometers upriver from the previous record for LAR-B at V-10++—Walker, 1987*b*) marks only the second record for LAR-B in Val Verde County as well as the second example of sympatry between LAR-B, *C. gularis*, and *C. marmoratus* (the other being CO-4++ directly across the Rio Grande in the suburbs of Ciudad Acuña—Walker, 1987*b*). LAR-B is far more numerous and widely distributed in urban and suburban Ciudad Acuña, Coahuila (five visits to three sites have produced 36 LAR-B), than across the Rio Grande in urban and suburban Del Rio where gonochoristic *C. gularis* dominates nondesert habitats (15 visits to nine sites have produced only three LAR-B because of the haphazard approach to urban and suburban development in México, which generates numerous patches and enclaves of disturbed habitat that are favored by parthenogens (Walker, 1987*c*).

Additions to the Distributional Ecology in the Middle Rio Grande Valley

Site Z-3* near Zapata is only the third record for LAR-A in Zapata County known to us. Here, LAR-A was found in a narrow band of habitat dominated by grasses and weeds along the shoreline of Falcon Lake, whereas *C. gularis* was present in a bordering tract of thorn shrub. In August and October 1987, we attempted to determine the distribution of LAR-A away from the Rio Grande along FM 755 between Rio Grande City and La Gloria, Starr County. A new record for LAR-A and *C. gularis* located 13.6 kilometers north of Rio Grande City at S-12* (comprising the weedy margin of a sandy roadbed) marks the most distant point from the Rio Grande established for LAR-A in this area. A number of sandy roadsides bordered by habitat that appeared to be suitable for LAR-A north of S-12* were found to support only *C. gularis*. The ecological basis, as no geographic barriers are apparent, for abrupt absence of LAR-A at sites north of S-12* along FM 755 is unclear.

Additions to the Distributional Ecology in the Lower Rio Grande Valley

Numerous visits to H-1++ (Los Ebanos, thorn shrub habitat near ferry landing—Walker, 1987*b*) have resulted only in the collection of *C.*

gularis. Thus a single specimen of LAR-B collected within 30 meters of the Rio Grande where thorn shrub merges with a narrow zone of riparian forest remnants represents the first record for this parthenogen at the site. Our first opportunity to thoroughly investigate site T-6+ in Tamaulipas (directly across the Rio Grande from H-1++) revealed the presence of a different whiptail community; sandy riparian habitat with numerous trails and small open spaces in the remnant forest vegetation supports large numbers of both LAR-A and LAR-B there, but apparently no *C. gularis*. Site T-6+ is presently the only site known in México where both LAR-A and LAR-B parthenogens occur together in large numbers.

Site H-7* located 10 kilometers north of La Joya, or 13 kilometers northeast of H-2*+, is the first site away from the immediate vicinity of the Rio Grande in the LRGV where LAR-A has been discovered. Here, large numbers of LAR-A and a few *C. gularis* occur within remnants of grass-weed-mesquite between an unsurfaced road and fenced pastureland not unlike site W-15*+ in the URGV.

Walker (1987*a*, 1987*b*) reported that sites T-7*+, T-8, T-9*, and T-10+ in Tamaulipas (consisting of xeric degraded thorn shrub habitats in the suburbs of Reynosa) are inhabited by large numbers of LAR-A and only a few LAR-B or *C. gularis*, or both. Several visits to new site H-5+ near Hidalgo (directly across the Rio Grande from the suburbs of Reynosa) revealed that numerous *C. gularis*, a few LAR-B, and no LAR-A are present in mesic patchy remnants of ecotonal thorn shrub-mixed forest habitat near cultivated land.

In August 1987, we entered México at Nuevo Progresso, where both LAR-A and LAR-B were reported at T-11+ by Walker (1987*a*, 1987*b*), in an attempt to locate additional sites for parthenogens along Mexico Hwy. 2 between T-11+ and the Gulf of Mexico. Virtually no suitable habitat for parthenogens was located before reaching the vicinity of Matamoros. We located one additional site for LAR-B and *C. gularis* at T-13++ at Ejido Guadalupe; the habitat there consisted of narrow trails through thick growths of bunchgrasses and weeds, and roadsides.

Recent Habitat Losses

The geographic ranges of LAR-A and LAR-B involve areas that are intensively used by man. Thus it is not surprising that several significant losses of habitat have occurred since the publications Walker (1987*a*, 1987*b*, 1987*c*), Walker et al. (1989), and Walker and Cordes (1990). Despite repeated visits to the Texas side of the URGV since 1984, parthenogens have actually been collected at only one site in Webb County (W-15*+), two in Maverick County (M-2 and M-3++—Walker, 1987*b*), and two in Val Verde County (V-10++ and V-13++). Unfortunately, the habitat known to support LAR-B at M-2 was bulldozed in 1988 and the habitat at M-3++ bulldozed and burned in

1988. A search of M-3++ by three collectors in May 1988 resulted in no sightings of *Cnemidophorus*. Site W-3 in the MRGV in the southern suburbs of Laredo was one of only two sites known for *C. laredoensis* (= LAR-A) when described by McKinney et al. (1973); this site was also the focus of a study by Walker (1987*c*). As of the summer of 1989, a photograph from the vantage point used for the habitat photographs published by Walker (1987*c*) would show a cul-de-sac with modern homes in a new subdivision of Laredo. Finally, site W-7* in Laredo, the focus of Walker and Cordes (1990), was bulldozed in 1988, completely eliminating LAR-A and *C. gularis*.

CONCLUSIONS

The conclusions supported by this study may be summarized as follows. LAR-B is restricted to habitats located within 10 kilometers of the Rio Grande in the URGV and LRGV. Additional field work in the MRGV supports Walker's (1987*a*, 1987*b*, 1987*c*) contention that LAR-B is absent from the area between Laredo-Nuevo Laredo and Rio Grande City, Starr County—adjacent Tamaulipas (the distribution of parthenogens between Laredo-Nuevo Laredo and site W-15*+ has not been determined owing to the lack of access to habitats near the Rio Grande). The range map provided by Walker (1987*b*) for LAR-B requires only minor alteration as a result of newly acquired data. The discovery of LAR-A at W-15*+, the first record for the URGV, greatly increases the known range of this clonal complex. Although we would be less surprised to see additional local range extensions for LAR-A than for LAR-B, we doubt that subsequent field work will significantly change the newly defined geographic range for LAR-A. Finally, it appears that Walker's (1987*a*, 1987*b*, 1987*c*) statements about the future survival of the LAR clones outside of areas under state or federal protection were overly optimistic given the instances of habitat losses observed since May 1987.

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PLANT PHENOLOGY IN THE LOWER RIO GRANDE VALLEY, TEXAS

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Abstract.—Native plant growth and reproduction in the lower Rio Grande Valley of Texas were keyed to rainfall and soil moisture for most species during 1985 and 1986. The three most active growth and reproductive periods were February, late May to June, and late September through November; there were significant differences between years. The majority species dropped ripened seeds in mid- to late summer, although several species produced flowers and fruit throughout the year. *Key words*: plant phenology; lower Rio Grande Valley, Texas.

Plant phenology in the subtropical lower Rio Grande Valley of south Texas is more complex than that in temperate regions. Multiple periods of growth and reproduction have been observed in many species but little has been documented. Knowledge of plant phenology aids studies in botany, entomology, and wildlife and is valuable in landscaping and plant comununity restoration. General flowering and fruiting periods are listed in plant texts such as Correll and Johnston (1970), Vines (1960), and Lonard et al. (1990), but multiple cycles during the year are not listed.

The objective of this study was to record plant phenology for several native species over a two-year period. Woody species that are commonly planted as ornamentals or in plant community restoration efforts by the U. S. Fish and Wildlife Service (USFWS) and the Texas Parks and Wildlife Department were emphasized.

Methods

Forty-four plants of 19 species were observed for flowering, fruiting, and leaf growth and drop weekly from May 1985 to January 1987 at the Santa Ana National Wildlife Refuge (NWR) (C Trail) (Table 1). In addition, notes on plant phenology were made by several employees of the USFWS and by visitors on these 19 and other plant species. Observations were limited to tracts of native brush throughout the lower Rio Grande Valley and the Santa Ana NWR parking lot. Ideker (1985, 1987) recorded observations made in October 1985, November and December 1986, and January 1987 in the newsletter of the Native Plant Project of the Lower Rio Grande Valley. Nomenclature for woody plants and vines follows Lonard et al. (1990) and is from Correll and Johnston (1970) for other species. Rainfall was recorded at the Santa Ana NWR headquarters site (Fig. 1).

Results

Winter

Mexican ash (*Fraxinus berlandieriana*), honey mesquite (*Prosopis glandulosa*), Texas sugarberry (*Celtis laevigata*), lotebush (*Ziziphus obtusifolia*), and cedar elm (*Ulmus crassifolia*) were among the few woody species that lost most or all of their leaves in mid-December.

Several plants such as tepeguaje (*Leucaena pulverulenta*), tropical sage (*Salvia coccinea*), anacahuita (*Cordia boisseri*), pigeonberry (*Rivina humilis*), mist-flower (*Eupatorium* sp.), Turk's cap (*Malaviscus drummondii*), Indian mallow (*Abutilon incanum*), elbow-bush (*Forestiera angustifolia*), and chilipiquin (*Capsicum annuum*) continued to flower during this coldest part of the year so long as soil moisture was adequate. Tropical sage and pigeon-berry also produced new fruit in winter.

Spring

The most dramatic announcement of warmer weather in late January was the yellow-orange flower clusters of Texas huisache (*Acacia smallii*). Growth was evident by early February for many species. Texas huisache, tepeguage, lotebush, anacahuita, brasil (*Condalia hookeri*), retama (*Parkinsonia aculeata*), and coyotillo (*Karwinskia humboldtiana*) were among the first to produce new leaves. Mexican ash flowered.

By March, many more species flowered including Texas lantana (*Lantana horrida*), guayacan (*Guaiacum angustifolium*), sunflower (*Helianthus annuus*), Texas paloverde (*Parkinsonia texana*), honey mesquite, allthorn (*Koberlinia spinosa*), manzanita (*Malpighia glabra*), Texas persimmon (*Diospyros texana*), white-brush (*Aloysia gratissima*), Spanish dagger (*Yucca treculeana*), blackbrush (*Acacia rigidula*), anacua (*Ehretia anacua*), Texas baby-bonnets (*Coursetia axillaris*), leatherstem (*Jatropha dioica*), retama, and Texas prickly pear (*Opuntia lindheimeri*). During the wet spring of 1985, the species noted previously as flowering in the winter continued to flower.

By early April, Wright's acacia (*Acacia wriqhtii*), false ragweed (*Parthenium hysterophorus*), coral bean (*Erythrina herbacea*), black mimosa (*Mimosa pigra*), and Mexican hat (*Ratibida columnaris*) also bloomed along with the species mentioned in the last paragraph. Green fruits were observed on guayacan, Texas huisache, and Texas paloverde. April in 1986 was a windy, warm, and droughty month and many annuals such as tropical sage and catchweed bedstraw (*Galium aparine*) disappeared, and perennials such as pigeon-berry and mist-flower wilted. Cedar elm, Texas sugarberry and Mexican ash maintained a sparse canopy of leaves.

Cenizo (*Leucophyllum frutescens*), chapotillo (*Amyris texana*), anacua, la coma (*Bumelia celastrina*), tree tobacco (*Nicotiana glauca*), catchweed bedstraw, Texas ebony (*Pithecellobium flexicaule*), and snailseed (*Cocculus diversifolius*) bloomed in May. The development of fruits had become more visible with anacua, Mexican ash, retama, honey mesquite, brasil, Texas huisache, tepeguaje, Texas sugarberry, lotebush, granjeno (*Celtis pallida*), Texas persimmon, and colima (*Zanthoxylum fagara*) having fruit by this time. Far less fruit was produced in 1986 because of a five-month drought (January to May). Another sequence of flowering

TABLE 1. Phenological observations of 19 species at the Santa Ana NWR from May 1985 to February 1987: f—flower; F—fruit; R—ripened fruit; D—deciduous; d—partially deciduous; N—first new growth; w—wilted.

	1985								1986												1987
Species	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan
Anacahuita	FfFf	FfFf	FfFf	FfFf	FFFF	FF	fFf	FfFf	FfFN	fFfF	ffff	fFfF	fFfF	fFfF	fFfF	fFfF	fFfF	fFfF	fFfF	fFfF	fFfF
Brasil	FF	FFRR	RRR				FR			NNN			FF	FFRR	RRR				FR		
C. bedstraw	ffff	f	w	wwww	N	NN					Nwww	wwwN	ffw	Nff	w	wwww	N	ww	wwN		
C. elm					RRR		dd	dddd	dddd	d NN	N					dddd	dddd	dddd	dddd	dddd	dddd
Coyotillo	ffF	RR						FR		NNN		F	FFFR	R					F	FR	
Granjeno	FF	FFFR	RRRR										f	FFFR	RRRR	RRR					
H. mesquite	FfFf	FfRf	RfRf	RRR				ddd	dddd	dddd	NNff	ffff	FFFf	FfFf	FfFf	RRRR	RR			ddd	dddd
Lotebush	fFfR	RR					dddd	dddd	dddd	NNNN		ff	fFFR	RR					dd	dddd	dddd
M. ash	FRR							DD	DDDD	DNfN	NN		FRR							DD	DDDD
Mist-flower	ff	f					ffff	fff		Nf	f		ff	f		w w		fff	ffff	ffff	ffff
Pigeon-berry	fFf	RfRR	ffRw	wwww	ww	fRf	RfRf	RfRf	R f	fR		ww	fRfR	fRfR	R w	ww f	fwwf	ffww	ffRf	Rfff	ffff
Retama	ffFf	FfFf	RfRR	RRRf	RfRf	RfRf	RfRd	dddd	dddN	N	ffff	ffff	ffFf	RfRf	RfRf	RfRf	RRRR	few pods			
Tepeguaje	ffFf	FfFF	FRRR	RRRR	RR	ff	ffff	ffff	ffff	NfNf	ffff	ffff	ffFf	FFFF	FRRR	RRRR	RR	f	ffff	ffff	fff
T. ebony	ffF	fFfF	RRRR	RRfR	fRRR	RRRR	RRRR	RRRR					ff	FfFf	FFRR	RRRf	RRRR	RRRR	RRRR	RRRR	
T. huisache	FFFF	FFRR	RRRR	R						NfNf	ffff	FFFF	FFFF	FFRR	RRRR	RRRR	few pods				
T. persimmon	FF	FFFF	RRR				FR			N											
T. p. pear	FFFF	FRRR	RRRR			ff	FR			NN	ffff	ffff	FfFF	fRRR	RRRR			ff	FR		
T. sage	fR F	fFRw	wffF	RRww	ww	fffR	fRfR	ffRw	wwww	wwww	www		Nf	ffRf	RfRw	ww	www	wffF	wwff	RfRf	ffRR
T. sugarberry	FFF	FFFR	RRRR	RRR	few fruit			DD	DDDD	DDNN	N		FF	FFFR	RRRR	RRRR	few fruit			D	DDDD

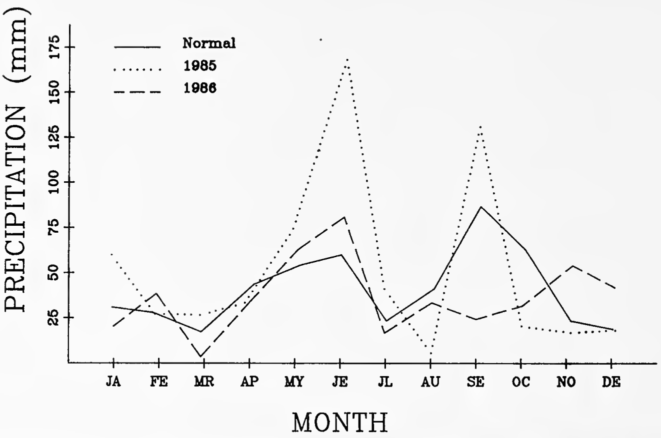

FIGURE 1. Precipitation in 1985 and 1986 at the Santa Ana National Wildlife Refuge, Texas.

among annuals and low perennials was triggered by rains in late May and early June.

Summer

Texas sabal palms (*Sabal texana*) bloomed and began producing fruit in June. Retama, Texas ebony, tepeguaje, anacahuita, catchweed bedstraw, tropical sage, mist-flower, and pigeon-berry continued flowering. By late June the fruit of Texas huisache, retama, Texas prickly pear, anacua, brasil, coyotillo, lotebush, and coral bean were mature. Snailseed also produced fruit.

Fruits of spring flowers ripened for many species in July and August. These included Texas sugarberry, guayacan, granjeno, chilipiquin, tepeguaje, Texas ebony, Wright's acacia, colima, blackbrush, cenizo, honey mesquite, Texas persimmon, elbow bush, brasil, black mimosa, Texas paloverde, snake-eyes (*Phaulothamnus spinescens*), and desert yaupon (*Schaefferia cuneifolia*). These months were relatively dry except for occasional afternoon thundershowers, and many plants wilted or dropped leaves under the intense heat (high temperatures usually more than 35°C). Plants such as retama, Texas ebony, tropical sage, pigeon-berry, and honey mesquite continued to flower with sufficient soil moisture. Tenaza (*Pithecellobium pallens*) was one of the few plants with peak flowering in August.

Autumn

The autumn rains arrived in mid-September in 1985 and initiated vigorous plant growth and flowering in the latter part of that month and in October. Retama, manzanita, white bush, chilipiquin, chapotillo, Berlandier wolfberry (*Lycium berlandieri*), Texas ebony, tropical sage, pigeon-berry, cenizo, black mimosa, Texas lantana, Texas kidneywood (*Eysenhardtia texana*), Texas paloverde, tenaza, la coma, tepeguaje, mist-flower, and anacahuita flowered. This flowering period continued into November. Cedar elm fruits dropped in late September and early October.

In November of 1985, species such as Texas persimmon, western soapberry (*Sapindus drummondii*). retama, brasil, Texas prickly pear, tasajillo (*Opuntia leptocaulis*), and urvillea-vine (*Urvillea ulmaceae*) developed fruits. Some legumes, such as Texas ebony and huisachillo, continued to hold pods with mature seeds through the autumn and early winter.

Rains did not arrive until late November in 1986 (Fig. 1). Some flowering and growth occurred at that time, but not of the intensity observed in 1985. August through mid-November was a period of inactive growth for most species in 1986.

Discussion

Plant growth and reproduction were keyed to rainfall and soil moisture for most species; these were, however, reduced by cool weather between late November and the first of February. The three most active growth and reproductive periods were February, late May-June, and late September through November. Cycles varied considerably with species. Warm weather plants had two or more growing seasons. Some species were partly or completely deciduous in hot, dry period in response to moisture stress. Species such as tropical sage and pigeon-berry went through a complete reproduction cycle each time there was sufficient soil moisture, except during cold periods (perhaps less than 7°C, but actual temperatures were not recorded). Other species, such as Texas huisache, bloomed once in spring (late January to March) and seeds ripened by June.

Rainfall was highly variable from year to year and between areas, resulting in yearly and spatial differences in plant growth and reproduction. Growth was minimal during the five-month spring and autumn droughts of 1986. Many species, especially those producing fleshy fruits such as Texas persimmon, brasil, and Texas sugarberry, had little fruit that year. The cedar elm seed crop was also much reduced from that of the previous year. Plants in the eastern part of the lower Rio Grande Valley grew vigorously and produced abundant fruit after heavy fall rains. Rainfall in the western part of the valley, however, was 75 to 200 mm less than in the eastern areas during that period, resulting in the same species showing little activity. Anacahuita produced flowers and fruits year-round when it received sufficient water (as when used as an ornamental), but reproduction was limited to spring, early summer, and autumn in its native dry upland sites.

Winter severity also varies from year to year. The two winters in the study period were relatively mild with temperatures staying above freezing the entire winter of 1986-87. Many plants such as tepeguaje, tropical sage, anacahuita, and pigeon-berry continued growth and reproduction through the winter. Severe winters do occur once every 10 to 20 years, as in 1983-84, and several species were damaged by that severe freeze (Lonard and Judd, 1985).

Soil moisture appears to be the key to plant growth and should be carefully monitored in revegetation efforts. Plants such as tropical sage and pigeon-berry may provide a good index to soil moisture, and planting should perhaps be avoided when those species are not flowering or producing new vegetative growth. Most species drop ripened seeds in mid- to late summer in anticipation of autumnal rains. Many species, especially legumes, have hard seed coats and require weathering action to soften the coats before water can be absorbed. This protects the seed from germinating too early as a result of short-term summer thunderstorms.

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A RECORD OF *BOOTHERIUM BOMBIFRONS* (ARTIODACTYLA: BOVIDAE) FROM HUNT COUNTY, TEXAS

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Abstract.—A third cranial record of the extinct musk ox, *Bootherium bombifrons* (=*Symbos cavifrons, Gidleya zuniensis*, and synonyms), from Texas is described and illustrated. This specimen was found in the channel of the South Sulphur River, southwest of Commerce, Hunt County, probably having eroded from sediments considered to be latest Wisconsinan in age. Remains of other extinct mammals recovered from these sediments include *Mammuthus* and *Bison*. A southward salient of the range of *Bootherium bombifrons*, which incorporates all records of this species from Texas, also is identified. *Key words*: *Bootherium bombifrons*; musk ox; Texas; paleontology; Sulphur River Formation.

The musk ox group comprises the genera *Ovibos* de Blainville, 1816, *Bootherium* (Harlan), 1825, and *Praeovibos* Staudinger, 1908. *Praeovibos* appeared near the end of the early Pleistocene. *Ovibos* and *Bootherium* appeared during the middle Pleistocene (McDonald et al., 1990). *Praeovibos* and *Ovibos* were Holarctic in distribution, whereas *Bootherium* evidently occurred only in North America. *Bootherium* was the most widely distributed genus of musk ox in North America; the southern boundary of its known range passed through Texas, and it is the only genus of musk ox known to have occurred in the state (Fig. 1). As used in this paper, *Bootherium* incorporates the nominal genera *Symbos* (Leidy, 1852) and *Gidleya* (Gidley, 1906) and their synonyms, all of which have been placed in the monotypic species *Bootherium bombifrons* by McDonald and Ray (1989).

To date, only two records of crania of *Bootherium bombifrons* from Texas have been documented in the literature (Hesse, 1942; McDonald, 1985). We describe and figure a third cranium and provide information on its geological provenience and zoogeographical significance. The specimen (ET 5301) is now in the collection of the Department of Earth Sciences at East Texas State University.

Previous Reports of Musk Oxen from Texas

Two records of *Bootherium bombifrons*, based on cranial remains, have been reported from Texas. A partial cranium of a mature female was collected from a sand bar in or along the Brazos River at Pitts Bridge, in Brazos County (Hesse, 1942). This specimen, TAMC 2553, became the holotype of *Bootherium brazosis* Hesse, 1942, since referred by Ray (1966) to *Bootherium sargenti* and McDonald and Ray (1989) to *Bootherium bombifrons*. TAMC 2553 is now in the collection of the University of Texas, Balcones Research Center, Austin.

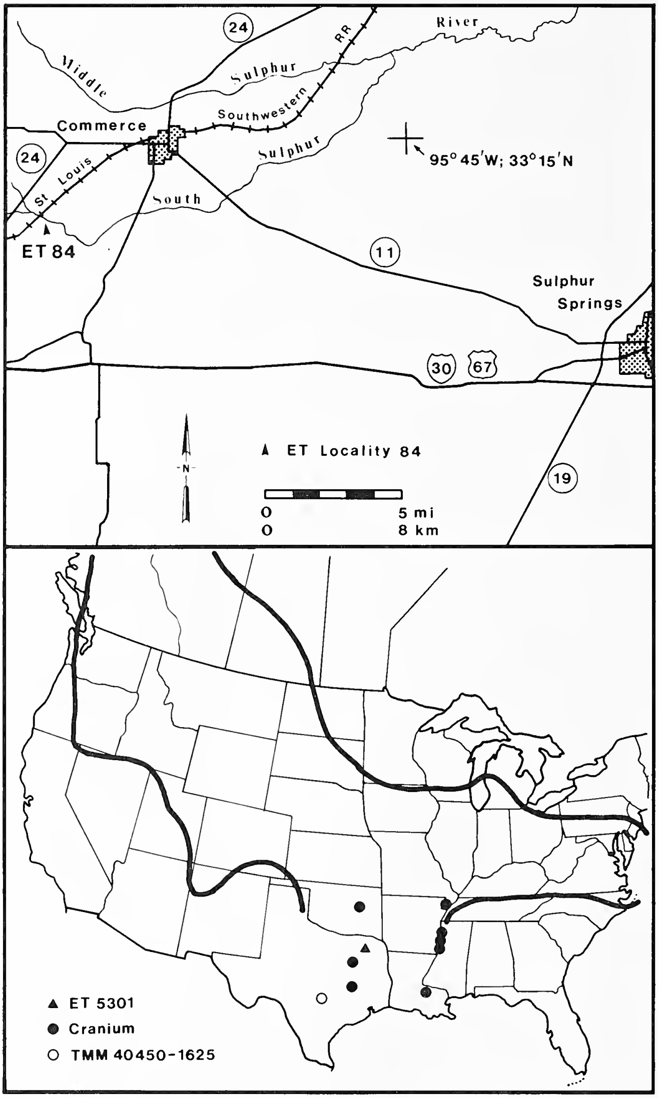

FIGURE 1. Top: the provenience of ET 5301, found about 100 yards east of ET Locality 84 in the channel of the South Sulphur River. Bottom: records of *Bootherium bombifrons* from south of latitude 35° N, along with the next-nearest northerly records, which form the conspicuous southern salient of the range of the species. Heavy lines demarcate the boundary of the range of the species as presently known.

The second cranial record is a mature male (referred to *Symbos*) found in 1969 along Lower Brushy Creek, southwest of Kaufman in Kaufman County (McDonald, 1985). This specimen, SMU-SMP 69127, is in the collection of the Shuler Museum of Paleontology, Southern Methodist University, Dallas. A third phalanx (UT 40450-1625) from Cave Without

A Name in Kendall County is in the collection of the University of Texas, Balcones Research Center, Austin (Lundelius, 1967). Our comparison of a cast of the Cave Without A Name specimen (which was referred to *Symbos* by Lundelius—personal communication, 13 April 1989) and the third phalanges of *Bootherium bombifrons, Euceratherium collinum, Ovibos moschatus, Bison bison*, and *Alces alces* indicated that UT 40450-1625 most closely conforms to the third phalanges of the pes of *Bootherium (=Symbos) bombifrons.*

Provenience of the Hunt County Specimen

ET 5301 was obtained in September 1984 by Richard L. Tarpley, a local rancher, who found the specimen in the gravel bed of the artificial channel of the South Sulphur River, southwest of Commerce, Hunt County (Fig. 1). The partial skull was discovered lying on top of alluvium, along the bank of the channel, about 100 yards downstream (east) of ET Locality 84 (approximately 0.25 mile downstream [east] of the trestle of the St. Louis Southwestern Railroad) under high tension electric wires on the Eugene Bickley ranch (*ca.* 33° 12′ 30″ N; 95° 58′ 30″ W). The area was searched subsequently in an effort to locate additional parts of the skull, but none was found.

The specimen presumably eroded from Pleistocene (probably latest Wisconsinan) gravels or sandy clays that crop out a short distance upstream from where it was found, because preservation of the bone is similar to that of bones from partial skeletons of *Mammuthus* and *Bison* collected *in situ* from gravels at Locality 84.

The gravels and sandy clays of ET Locality 84 are presumed to be an extension of, or correlative with, the Sulphur River Formation, an "extensive alluvial deposit" described from exposures in and near the Sulphur River in the vicinity of Ben Franklin, Delta County, located some 15 to 20 miles northeast of Commerce (Slaughter and Hoover, 1963). Slaughter and Hoover (1963) recognized the occurrence of this formation along some 40 miles of the Sulphur River, including the North Sulphur River as far west as western Fannin County, northwest of Commerce. The Sulphur River Formation also was observed in the channels of the lower parts of the Middle and South forks of the Sulphur River. The large-mammal faunule from the Sulphur River Formation contained several extinct taxa, including *Mammut americanum, Mammuthus* cf. *columbi, Equus* sp., *Mylohyus* sp., and *Bison* sp. Radiocarbon dates obtained on charcoal and mussel shells from the Delta County localities indicate an age of about 11,000 to 9500 years BP for the sediments (Doering, 1983; Slaughter and Hoover, 1963). If the Hunt County gravels from which ET 5301 is presumed to have eroded are westward extensions of the Sulphur River Formation, and if the radiocarbon dates on material from the Sulphur River Formation are

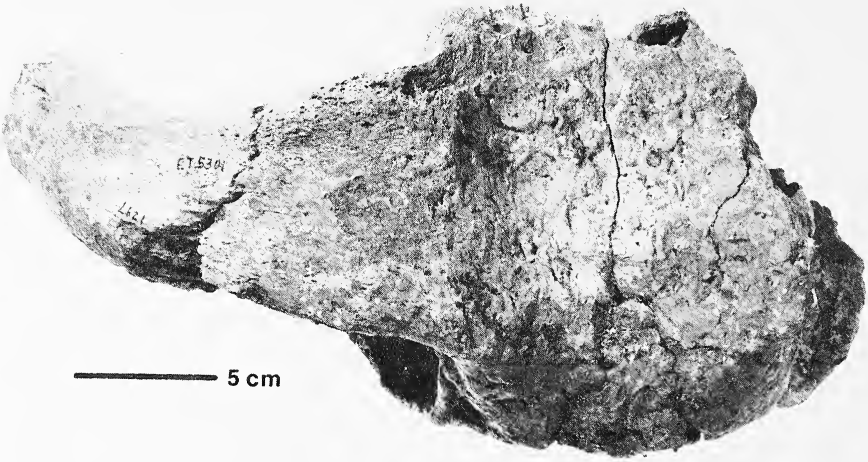

FIGURE 2. View of dorsal surface of ET 5301.

accurate, the specimen is approximately 10,000 years old. This would make it one of the geologically youngest records for the species. (A radiocarbon date of 10,900 ± 190 years B.P. was obtained from bone from the Cave Without A Name fauna—Lundelius, 1967.)

IDENTIFICATION AND DESCRIPTION OF THE SPECIMEN

ET 5301 is identified as *Bootherium bombifrons* on the basis of the placement, shape, and orientation of the horn cores, and the depth of the frontoparietal sinus region. The horn cores in *Ovibos* do not emanate laterally from the cranium, they do not curve significantly in *Ovibos*, and they curve in a different pattern in *Praeovibos*. The frontoparietal sinuses of *Ovibos* and *Praeovibos* typically are not expanded dorsoventrally. The presence of secondary bone (exostosis in this case) across the dorsal surface of the cranium and the fact that the bases of the horn cores attach to both the frontal and parietal bones identify this specimen as a male.

ET 5301 is much damaged. When recovered, the specimen was broken into four relatively large pieces and several smaller pieces. All fragments were punky and friable. Included are most of the dorsal elements, the lateral elements excluding the zygomatic processes, the occiput, and the caudal half of the basioccipital (Figs. 2-3). The pattern of bone loss in ET 5301 is consistent with that seen in skulls of male *Bootherium*

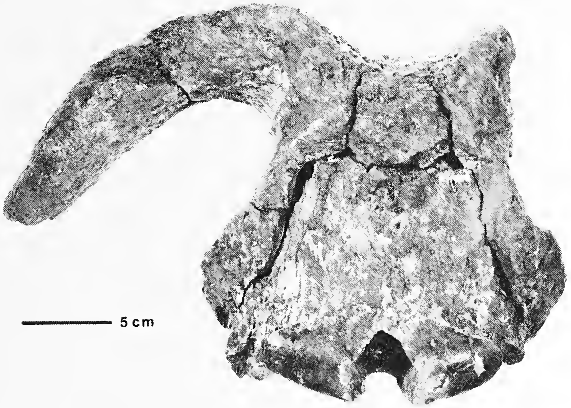

FIGURE 3. View of occipital surface of ET 5301.

bombifrons that have been found in coarse fluvial sediments. All observable features preserved in ET 5301 are typical of male specimens assigned to *Bootherium bombifrons* as described in McDonald and Ray (1989). Measurements of ET 5301 are given in Table 1.

DISCUSSION

The pattern of damage to ET 5301—the loss of the face, all or part of both horn cores, and most of the minor prominences on other parts of the cranium, in conjunction with relatively large missing chips of bone—is consistent with patterns of damage seen in male crania of *Bootherium bombifrons* that have been recovered from coarse fluvial sediments and are presumed to have been damaged by abrasion in high-energy fluvial currents. ET 5301 weathered to a punky state during diagenesis, however, and did suffer breakage during or following erosion from its former host sediments. The differences in color and texture between break surfaces that occurred before diagenesis and after exposure indicates that most of the loss of bone occurred before or during deposition, not after exposure. The available gross taphonomic evidence is consistent, therefore, with the notion that ET 5301 eroded from gravels near the point at which it was found by Mr. Tarpley.

Although records of *Bootherium bombifrons* are uncommon south of about latitude 35° N, a conspicuous concentration of records of the species in the south-central part of the United States is emerging. Prior to 1985, only one record of *Bootherium bombifrons* was known from south of 35° N (Hesse, 1942). Now, however, ET 5301 and six other crania, along with various postcranial elements, are known from south of 35° N in Mississippi, Louisiana, and Texas (Hesse, 1942; Lundelius, 1967;

TABLE 1. Measurements of characters of ET 5301 (in mm). Values in parentheses are estimates based upon nearly complete characters. Numbers in parentheses following the written descriptions of some measurements identify numbered measurements for *Bos* given by von den Driesch (1976).

Minimum breadth of cranium across dorsal surface of parietals	137.4
Length of horn core at base	Left 120.1
Depth of horn core at base	Left 66.4
Actual length of remaining segment of horn core, measured along dorsal surface	Left 242.0
Greatest breadth of basioccipital	(77.0)
Greatest breadth of occipital condyles, primary (26)	(137.1)
Greatest breadth of foramen magnum (28)	41.5
Height of foramen magnum: basion-opisthion (29)	44.5
Height of occiput, opisthion-nuchal line	113.3
Width of occiput at external acoustic meatus	(220.0)

McDonald, 1985; McDonald and Corkum, 1987; McDonald and Ray, 1989), and collectively constitute a distinct southern salient of the known range of *Bootherium bombifrons* (Fig. 1).

The reasons for, and significance of, this salient, however, are not clear. None of the seven crania has been found *in situ* in host sediments and none has been radiocarbon dated, so direct evidence of the absolute geologic ages, environments of entombment, and faunal associates of the specimens is lacking. Most of the crania are considered to be middle or late Wisconsinan in age, but such age assignments—even if probably correct—are without factual confirmation. The spatial pattern of records mapped in Figure 1 could reflect a true salient in the range of *Bootherium bombifrons* resulting from ecological opportunities that existed at some period(s) in the past. Alternatively, the pattern possibly could reflect a natural sampling bias resulting from the relatively great quantities of fluvial sediments in the region or an artificial recovery bias resulting from the intensive utilization of that region by humans during the historic period.

ACKNOWLEDGMENTS

We wish to thank Mr. Richard L. Tarpley of Commerce, Texas, for collecting and donating this specimen to East Texas State University. Ernest L. Lundelius, Jr., University of Texas, kindly loaned a cast of UT 40450-1625 for our examination. Clayton E. Ray, National Museum of Natural History, arranged for the restoration of ET 5301 and otherwise greatly facilitated our collaboration on the study of this specimen.

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CHANGES IN NATIVE VEGETATION FOLLOWING DIFFERENT DISTURBANCES IN THE LOWER RIO GRANDE VALLEY, TEXAS

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Abstract.—Permanent plots established in 1981 were censused again in 1986 at the Palmview tract of the Rio Grande Valley National Wildlife Refuge in southern Texas. Successional changes from bareground to communities dominated by dry-land willow (*Baccharis neglecta*) and huisache (*Acacia smallii*) were documented. In formerly grazed woodlands, overstory honey mesquite (*Prosopis glandulosa*) trees grew an average of 2.5 meters in height over the five-year period. Understory honey mesquite trees were dying, and cover of herbaceous vegetation declined. Cover of woody species such as coma (*Bumelia celastrina*), granjeno (*Celtis pallida)*, brasil (*Condalia hookeri*), and Texas ebony (*Pithecellobium flexicaule*) were increasing beneath honey mesquite. *Key words*: grazing; mesquite; old fields; *Prosopis;* succession; Texas.

Few ecological studies have been conducted in the plant communities of southern Texas and little is known about successional changes in this vegetation. In an area 175 kilometers to the north of the Rio Grande River near Alice, Texas, Archer et al. (1988) demonstrated that honey mesquite (*Prosopis glandulosa*) invades grasslands, and the trees serve as foci for bird-disseminated seeds of other woody species. The resulting shrub clusters represent an intermediate stage, eventually coalescing to form closed-canopy woodlands on more mesic sites. On the San Antonio River terraces (350 kilometers north of the Rio Grande River), Van Auken and Bush (1985) observed that the number of woody species, total density, and total basal area increased with stand age and that the community changes with succession from a low-nitrogen, high-light habitat dominated by huisache (*Acacia smallii*) to one of high-nitrogen, low-light characterized by Texas sugarberry (*Celtis laevigata*).

In 1981, the U. S. Fish and Wildlife Service began a woody plant inventory program by establishing nine permanent plots in the Palmview tract of the Rio Grande Valley National Wildlife Refuge (RGVNWR) to obtain data on secondary succession in thorn woodlands of the lower Rio Grande Valley. In this paper, we compare the vegetation from the time of establishing the plots in 1981 to resampling in 1986. The Palmview tract offered an opportunity to document changes following different situations such as fire, removal of cattle, seasonal flooding, abandonment of a gas well, and old field succession.

Study Site

Soils of the lower Rio Grande Valley have been formed by alluvial deposits through flooding of the Rio Grande. Palmview is five kilometers west of Mission on the second major terrace north of the floodplain. Soil textures vary from fine sandy loam to saline clay, and soils are a mixture of upland (Hidalgo and Raymondville) and terrace (Harlingen and Runn) types (Jacobs, 1981).

The site is in the Matamoros District of the Tamaulipan Biotic Province (Blair, 1950). The potential natural vegetation of the Province has been classified as *Prosopis-Acacia-Andropogon-Setaria* savanna (Küchler, 1964). This site, however, may have been a mesic floodplain with perhaps a gallery forest. At present the area has islands of subtropical thorn woodland surrounded by large agricultural fields and urban development.

A portion of the Palmview tract was cultivated until its acquisition by the U.S. Fish and Wildlife Service in 1981. The rest was grazed by cattle. The grazed portion included pasture, woodland, and a seasonal wetland. No grazing or cultivation of crops occurred after 1981. A gas well was also abandoned at that time. A man-caused fire burned a portion of the former pasture on 30 January 1982.

METHODS

The Palmview tract was typed as grazed woodland, pasture, cultivated field, or wetland in January 1981. Seven plots were located using a stratified random sampling procedure in the main vegetation types. Three plots (4, 5, and 6) were grazed woodlands. Plot 7 was located at the edge between woodland and pasture; the pasture portion was burned by the previously mentioned fire. Two plots (8 and 9) were in formerly cultivated fields, and plot 3 was located in a seasonal wetland. Two additional plots were established in disturbed sites; one (plot 2) was established on a manmade levee at the edge of a woodland and another (plot 1) was located on the abandoned gas well site.

Sampling was conducted in plots 0.1 hectare in diameter; the center of each plot was marked permanently with a steel post. Two groups of vegetation were sampled in each plot. The first group consisted of larger woody species—one stem at least five centimeters diameter at 1.4 meters height (dbh). Each individual in this group was identified to species, numbered, and marked with a stainless steel tag. Information recorded for each individual included azimuth and distance from the center of the plot, dbh of the largest stem, plant height, and the number of stems at least five centimeters dbh. The second group sampled consisted of woody vegetation less than five centimeters dbh and dominant herbaceous species. Individual locations were plotted on circular graphs. Canopy cover was estimated ocularly for each species with the aid of the graphs. Density estimates for each plot were obtained from photographs of a 2.0 × 0.5-meter density board located 17.8 meters from plot center. Photographs were taken from the center of plots in the four cardinal directions. In addition a species list was made for each plot. Plots were sampled in 1981 and again during March 1986.

RESULTS

Old fields.—Cultivated fields (bare soil) were colonized by dry-land willow (*Baccharis neglecta*), which formed an overstory with a canopy cover of 65 to 80 percent and was one to five meters tall. Exotic Washingtonia palms (*Washingtonia* sp.) invaded plot 8 (they were present nearby on the tract in 1981). Understory grass cover was 60 to 80 percent and was dominated by exotics, primarily buffelgrass (*Cenchrus ciliaris*) and bermudagrass (*Cynodon dactylon*).

Former pasture and succession after fire.—This disturbance type was represented by the southern half of plot 7. Photographs show all herbaceous vegetation and woody plant seedlings removed by the fire on 30 January 1982. Fire did not enter the woodland. By 1986, large shrub and tree canopy cover in the burned pasture was 30 to 50 percent and was dominated by dry-land willow, huisache, retama (*Parkinsonia aculeta*), and honey mesquite. Tree heights were up to six meters, and the dbh of the largest stems were 8.5 cm. Dry-land willow plants had 10 or more stems, and the total basal area of one of these plants was often 100 square centimeters at 1.4 meters height. The understory in 1986 was typically a dense mat of Texas virgin's bower (*Clematis drummondii*) and bermudagrass. The portion of the pasture that burned in 1982 had a denser cover of woody vegetation than the unburned portion.

Abandoned gas well.—This once-denuded site had 25 percent overstory canopy cover of honey mesquite and Washingtonia palms in 1986. The major understory species were dry-land willow, honey mesquite, buffelgrass, and whorled dropseed (*Sporobolus pyramidatus*), the last-listed an indicator of saline soil (Raymondville clay loam).

Man-made levee.—By 1986, overstory large shrub and tree cover was 5 percent and was primarily retama and honey mesquite. The understory was dominated by dry-land willow, retama, buffelgrass, and bermudagrass.

Seasonal wetland.—Plant cover in 1988 was 95 percent and one to four meters tall, and was dominated by dry-land willow and cat-tail (*Typha domingensis*). Abundance of these species did not change much over the five years. The northeastern portion of the plot, however, changed from cat-tail to dry-land willow and an island of dry-land willow in the western part changed to cat-tail. Photographs showed dry-land willow to be taller and denser in the southern and eastern parts of the plot in 1986 relative to 1981. The one huisache tree measured on the plot in 1981 had died and rotted. Honey mesquite seedlings found scattered near the plot center in 1981 were no longer there in 1986, perhaps killed by flooding.

Woodland.—Plot 6 and the northern half of plot 7 were similar. Cattle grazed there until 1981, and a narrow road once passed through plot 6. The overstory in 1986 was dominated by honey mesquite with a canopy cover of about 70 percent and a density of about 230 trees per hectare (Table 1). The height of the dominant tree layer varied from 5.9 to 8.8 m, and the average five-year height growth was three (1.5 to 5.0) meters. At least 20 percent of the crown of all honey mesquite trees was composed of dead material, and about half of them had at least 60 percent dead material. The dbh of the largest stem of these overstory trees varied from 5.3 to 30.9 centimeters, and average increase in dbh of this stem was three (one to six) centimeters.

The understory brush had a canopy cover of about 20 percent. Plant heights were up to six meters, and dbhs were up to 18 centimeters. The dominant understory species were honey mesquite, granjeno (*Celtis pallida*), brasil (*Condalia hookeri*), mist flower (*Eupatorium odoratum*), huisache, coma (*Bumelia celastrina*), ivy treebine (*Cissus incisa*), snake-eyes (*Phaulothamnus spinescens*), coyotillo (*Karwinskia humboldtiana*), and guayacan (*Guaiacum angustifolium*). Thirteen of 28 honey mesquite trees with crowns below the dominant overstory had died over the five-year period. A comparison of photographs between the two measurements showed an increase in shrubs obscuring the density boards.

Plots 4 and 5 were similar in appearance and appeared to be a later successional stage than plots 6 or 7. Overstory canopy cover was also about 70 percent and dominated by honey mesquite in 1986. Trees such as Texas ebony (*Pithecellobium flexicaule*), coma and huisache entered the upper canopy to a minor extent. The density of trees in the overstory was about 250 to 380 per hectare. Tree height varied from 5.3 to 9.6 meters, and average five-year growth was 2.5 (one to four) meters—Table 1. Diameter at breast height of the largest stem varied from 5.4 to 37.8 centimeters, and average five-year dbh increase was about three (zero to nine) centimeters for all overstory trees. Vigor of honey mesquite trees was similar to that on plots 6 and 7. Other species had less dead material in their upper crowns.

Understory shrub cover was 20 to 40 percent, with heights of up to 5.5 meters, and dbh of the largest stem up to 14.1 centimeters. The species in the understory shrub layer did not appear to have changed much over the five years. Photographs showed shrub biomass higher in 1986, and density boards not visible at 17.8 meters. They also showed less herbaceous vegetation in 1986 (cover less than 10 percent). Major understory species included brasil, granjeno, honey mesquite, coma, elbowbush (*Forestiera angustifolia*), Berlandier wolfberry (*Lycium berlandieri*), Texas ebony, snake-eyes, and the exotic guinea grass (*Panicum maximum*).

Discussion

The development of woody assemblages at this site seems to fit the Relay Floristic (Egler, 1954) or Facilitation (Connell and Slayter, 1977) models of plant succession, although the data from this study are not sufficient to demonstrate theories because only a few seres were present. Theory suggests that each successive type establishes itself because the preceding type modifies the site in a way favorable to its successor (Clements, 1916). Species may be killed in competition with later species, although this had not yet occurred with honey mesquite at this site. Archer et al. (1988) suggested that succession on their study site fit the Facilitation Model. Early successional communities seem to change from low-nitrogen, high-light to high-nitrogen and low-light as suggested by Tilman (1982) and supported by Van Auken and Bush (1985). Tilman, in his "resource-ratio" theory, suggested that species with a lower requirement for a limiting resource (that is, light) may displace others (that is, Texas ebony may replace honey mesquite).

Later successional species were not present initially. The environment at this site has been modified by humans and dormant seeds of later successional species may not be present. Seed dispersal from other areas

TABLE 1. Five-year changes in mean density, stem area, and heights of honey mesquite trees. Standard deviations are given in parenthesis.

	Plot and year of measurement														
	Early succession (old fields)						Later succession (formerly grazed woodlands)								
	Plot 1			Plot 7			Plot 6			Plot 4			Plot 5		
Variable	1981	1986	∆	1981	1986	∆	1981	1986	∆	1981	1986	∆	1981	1986	∆
Density[a]	40	160	+120	180	170	−10	430	400	−30	520	600	+80	430	420	−10
Stem area[b]	63	68	−5	285	311	−26	148	245	−97	192	184	−8	183	253	−71
	(44)	(84)	(78)	(82)	(369)	(290)	(22)	(206)	(241)	(31)	(212)	(132)	(27)	(207)	(283)
Height[c]	4.9	4.9	0	4.1	5.4	+1.3	3.9	6.4	+2.5	4.9	5.6	+0.7	4.7	6.8	2.1
	(1.0)	(0.6)	1.2	(0.3)	(2.8)	(2.2)	(0.2)	(1.8)	(2.2)	(0.2)	(1.4)	(1.7)	(0.2)	(1.6)	(2.3)

[a] Trees per hectare with one stem at least five centimeters in dbh.

[b] Mean cross-sectional area (cm^2) of largest stem at 1.4 meters height of trees with one stem greater than five centimeters dbh.

[c] Heights (m) of trees with one stem greater than five centimeters dbh.

by birds and mammals may be necessary. Van Auken and Bush (1985) observed that mature forest species, except Texas sugarberry, first occurred about 30 years after disturbance in their study site. Several of the understory brush species in plots 4, 5, and 6, such as brasil, coma, snake-eyes, coyotillo, guayacan, elbowbush, Berlandier wolfberry, and Texas ebony, are thought to be 'mature' woodland species because they are common on the Santa Ana National Wildlife Refuge, which has remained undisturbed for more than 40 years, but former disclimax (flooding) or climax species are unknown.

Dry-land willow, buffelgrass, and bermudagrass were dominant species after five years of old-field succession. Dry-land willow may prepare the site for colonization by pioneer tree species such as honey mesquite, huisache, and retama on more mesic sites. The tall dry-land willow plants may provide shade and retention of surface soil moisture for seedlings of other species. The exotic buffelgrass and bermudagrass probably inhibit establishment of other species by successfully competing for soil moisture, light, growing space, and the former possibly by allelopathy (Akhtar et al., 1978; Hussain et al., 1982). Van Auken and Bush (1988) observed that little bluestem (*Schizachyrium scoparium*) reduced biomass of honey mesquite in a greenhouse experiment.

Grazing and fire may reduce the vigor of grasses and provide the seed bed necessary for establishment of woody species, as long as the intensity and frequency are low enough to permit establishment of woody species (Vora, 1989). Fire may remove some of the inhibitory allelopathic effects. Woody plants were far more prevalent in the pasture (burned and unburned portions) than in the formerly cultivated fields, and the burned portion of the pasture had a denser cover of woody vegetation. Fire tends to be restricted to grassy fields in this area as live fuel moisture in woodlands is usually too high for it to burn except possibly under extreme conditions.

Texas virgin's bower probably also reduces colonization by woody species by forming a dense, smothering mat allowing little light penetration. Portions of new accretions from the Rio Grande on the nearby Santa Ana National Wildlife Refuge that have not been disturbed for 40 years remain covered with a dense mat of this species. Fire may be needed to remove it.

The seeds of the three colonizing leguminous trees, honey mesquite, huisache, and retama, probably require animal dissemination. Plants of these species proliferate in areas where cattle have grazed, especially once cattle are taken off the site (personal observation). Livestock transport seeds, scarify them, deposit them in a nutrient-rich media (dung), and reduce herbaceous competition by grazing (Archer et al., 1988).

Periodic flooding will drown seedlings and large trees of these species depending on the duration, depth, and time of year as in most bottomland hardwood stands (Wharton et al., 1982). Most of these trees cannot live under prolonged flooding during the growing season, and seasonal flooding has maintained plot 3 in a mixture of dry-land willow and cat-tail. Honey mesquite seedlings present in 1981, and established presumably during a dry period, were gone in 1986. Decomposition is rapid as evidenced by the complete disappearance of a huisache tree on plot 3 in five years. The effects on vegetation of regular flooding of the Rio Grande before dams and diversions are unknown.

The successional role of exotic Washingtonia palms is undocumented. Presumably they are an early successional species and will die out when enveloped by later successional trees.

The Palmview tract did not have the intermediary early seral stages to demonstrate if honey mesquite trees serve as foci for cluster development of woody species as suggested by Archer et al. (1988), although there was no reason to doubt it. Several woody species, such granjeno, brasil, coma, ivy treebine, snake-eyes, coyotillo, guayacan, elbowbush, Berlandler wolfberry, and Texas ebony, were growing under the honey mesquite canopy on plots 4, 5, 6, and 7.

The older woodland stands (plots 4, 5, and 6), which are known to have been in existence for at least 20 years, were still dominated by honey mesquite. The dominant honey mesquite trees had not yet realized their growth potential and were still growing an average of 0.5 to 0.6 meters per year. Dominant trees seemed to be shading out intermediate and suppressed honey mesquite trees as indicated by the loss of 13 of 28 such trees over five years on plot 6. Honey mesquite did not seem to be replacing itself, and in time will presumably be reduced by competition from tree species presently in the understory. Light intensities under adult tree canopies may be insufficient for honey mesquite seedlings, but this alone may not explain lack of seedling establishment (Bush and Van Auken, 1987).

Huisache and retama may play a role similar to honey mesquite, although Archer et al. (1988) concluded that *Acacia farnesiana* played no role in cluster development; they suggested that its canopy architecture was unattractive to perching birds. All three leguminous trees probably facilitate survival and growth of other species by enhancing soil nutrient levels (especially nitrogen and carbon), water-holding capacity and infiltratation, and mineralization potential (Van Auken and Bush, 1985; Bush and Van Auken, 1986; Archer et al., 1988) and by providing shade for tolerant species.

These data are the first repeated measurements of individual trees showing plant community change in the lower Rio Grande Valley. They begin to provide growth rates needed to determine time frames for succession.

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FISH ASSEMBLAGE STRUCTURE IN AN INTERMITTENT TEXAS STREAM

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Abstract.—A total of 34 fish taxa were collected from August 1988 to July 1989 in Sister Grove Creek, an intermittent stream in north-central Texas. *Cyprinella lutrensis, Gambusia affinis, Pimephales vigilax, Menidia beryllina,* and *Fundulus notatus* were the five most abundant taxa collected, respectively, comprising 79 percent of the total number of fish obtained. Species diversity and richness were greatest in the lower reaches of the creek, adjacent to Lake Lavon. Increased diversity and richness of lower reaches relative to headwaters appeared to be a function of greater habitat availability in the form of permanent pools as well as migration from Lake Lavon. As alteration of intermittent streams becomes more frequent, a better understanding of the ecological functioning of these ecosystems will be increasingly important and should not be neglected from land-use planning. *Key words*: fish assemblage structure; intermittent streams; spatial variability; species diversity; species richness.

Intermittent streams are unique habitats essential to the ecosystems of the southern Great Plains, a region of the United States where perennial streams are uncommon. Despite this, few studies have been conducted on the fish assemblage structure of intermittent streams, particularly in Texas (Zale et al., 1989). Differences in ecological conditions among intermittent prairie streams may be as great as those between prairie and upland streams. Accordingly, basic descriptions and comparisons of biotas are recommended as necessary for future investigations of these habitats (Matthews, 1988).

This study was conducted to examine the fish assemblage structure of Sister Grove Creek, an intermittent stream in north-central Texas. Specific objectives were: 1) to describe the fish species composition of Sister Grove Creek, and 2) to examine spatial variation in fish assemblage structure. Fish assemblages were defined as all species collected at a site.

Study Area

Sister Grove Creek has a drainage area of 215.3 square kilometers in Grayson and Collin counties, Texas. Approximately 60 kilometers long, Sister Grove Creek empties into Lake Lavon, a 9000-hectare impoundment near McKinney, Texas. The study area included the entire length of the stream from the headwaters to the mouth. Stream width at normal flow ranged from 3.5 meters in the headwaters to 7.5 meters in the middle reaches. Although the mouth of Sister Grove Creek maintained a defined channel, particularly during low flow, its extended floodplain (about 50 meters wide) graded into Lake Lavon, forming the Sister Grove Creek arm of the lake. Primary substrate was clay throughout much of the stream from the mid-reaches to the mouth. In headwaters, substrates were dominated by sand, pebbles, and limestone bedrock. Data on stream discharge were obtained from a U. S. Geological Survey gauging station (no. 08059400) located about mid-reach on Sister Grove

Creek and indicated that average annual discharge from 1975 to 1985 was 1.26 cubic meters per second.

Materials and Methods

Collections were made monthly from August 1988 to July 1989 by seining in daylight at eight locations (Fig. 1) along the stream, using a 0.5-centimeter mesh seine (4.25 meters by 1.55 meters). The 0.5-centimeter mesh allowed capture of fish as small as 15 millimeters standard length, but permitted postlarvae and small young-of-year to escape. A longitudinal reach of about 100 meters was seined at each site for approximately 45 minutes. Every effort was made to sample all possible habitats.

Spatial variation in the fish fauna of Sister Grove Creek was examined using principal components analysis. Catch data for each taxon were compiled by site. Only the 14 numerically dominant taxa were included to prevent uncommon taxa from having a disproportionate effect. Shannon-Wiener diversity (H′) was calculated at each site using the formula

$$H' = \sum_{i=1}^{s} (p_i)(\log_e p_i),$$

where s = number of different taxa and p = proportion of the total number of taxa in the ith taxon. Principal components analysis was conducted using SAS (SAS Institute Incorporated, 1985). Diversity was conducted using Ecological Analysis Software (Ekblad, 1989).

Results

A total of 34 fish taxa (including 7099 individuals) was collected from August 1988 to July 1989 (Table 1). No collections were made in May 1989 as discharges greater than 55 cubic meters per second made field work impossible. *Cyprinella lutrensis, Gambusia affinis, Pimephales vigilax, Menidia beryllina,* and *Fundulus notatus* were the five most abundant taxa collected, respectively, comprising 79 percent of all individuals obtained. Species diversity for Sister Grove Creek was 2.28.

Number of taxa ranged from 10 at site 4 to 26 at site 2 (Table 2). Diversity also was lowest at site 4 and greatest at site 2. *Fundulus notatus* was the most abundant species in the headwaters, comprising at least 41 percent of the total number of individuals collected per site at sites 6, 7, and 8. *Gambusia affinis* was the dominant taxon in the mid-reaches, representing 34 to 56 percent of the total number of fish caught per site at sites 3, 4, and 5. *Cyprinella lutrensis* and *M. beryllina* were the most abundant species collected at sites 1 and 2, respectively.

Principal component analysis of the fish fauna of Sister Grove Creek revealed differences in fish assemblage structure among sites. The first two components accounted for 61 percent of the total variation. In an ordination of these components, there was no overlap among two groups, with separation of these groups primarily along the first principal component (Fig. 2). Fish assemblage structure at sites 4, 5, 6, 7, and 8 were similar and differed from that of sites 1, 2, and 3. Correlations of the first component and abundance of each taxon indicated that

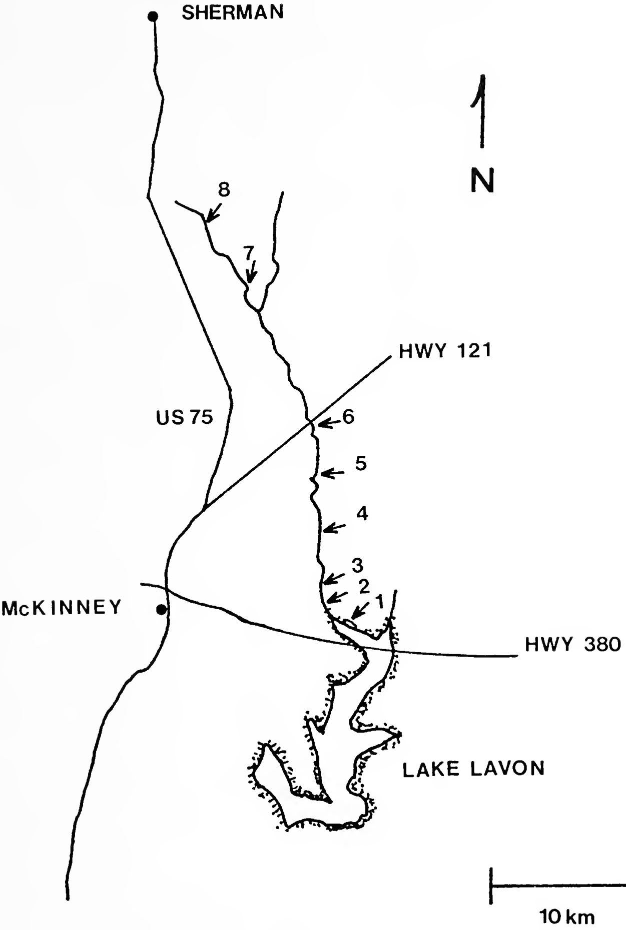

FIGURE 1. Location of eight sampling sites in Sister Grove Creek, Texas.

differences between these groups were largely the result of greater catches of *L. humilis, P. annularis,* and *L. macrochirus* at sites 1, 2, and 3 ($r > 0.60$, $P < 0.05$). Correlations of the second component and catch of *F. notatus* and hybrid sunfish (*Lepomis* sp.) indicated greater catches of these taxa at site 3 than site 1 ($r > 0.60$, $P < 0.05$). Catch of *M. beryllina* was negatively correlated with this component and corresponded to high catches of this species at site 1 ($r < -0.60$, $P < 0.05$).

DISCUSSION

The fish fauna of Sister Grove Creek was similar to fish communities in other intermittent prairie streams. Zale et al. (1989) in a review of studies of fishes in intermittent prairie streams, indicated that the most common fishes included *C. lutrensis* and *F. notatus*, with numbers of fish

Table 1. Species composition and percent abundance of 7099 fishes collected in Sister Grove Creek, Texas, from August 1988 to July 1989.

Species	N	Percent	Species	N	Percent
Cyprinella lutrensis	1583	22	*Etheostoma gracile*	11	<1
Gambusia affinis	1068	20	*Notemigonus crysoleucas*	10	<1
Pimephales vigilax	1041	15	*Cyprinus carpio*	10	<1
Menidia beryllina	934	13	*Percina caprodes*	10	<1
Fundulus notatus	595	9	*Minytrema melanops*	9	<1
Lepomis sp.	187	3	*Lepomis gulosus*	7	<1
Lepomis macrochirus	173	3	*Ictalurus natalis*	7	<1
Lepomis megalotis	169	2	*Noturus gyrinus*	6	<1
Dorosoma cepedianum	160	2	*Aplodinotus grunniens*	5	<1
Lepomis humilis	151	2	*Pimephales promelas*	5	<1
Dorosoma petenense	149	2	*Etheostoma chlorosomum*	5	<1
Pomoxis annularis	127	2	*Lepomis microlophus*	4	<1
Lepomis cyanellus	65	1	*Ictalurus melas*	3	<1
Micropterus punctulatus	59	1	*Pomoxis nigromaculatus*	2	<1
Morone chrysops	31	<1	*Pylodictus olivarus*	1	<1
Percina macrolepida	31	<1	*Etheostoma spectabile*	1	<1
Ictalurus punctatus	29	<1	*Carpiodes carpio*	1	<1

taxa for intermittent streams in Texas ranging from six to 46. Matthews et al. (1988) reported the occurrence of 30 fish taxa for Brier Creek, a prairie-margin stream in south-central Oklahoma. The fish fauna of Sister Grove Creek was dominated by high abundances of relatively few species, characteristic of intermittent streams (Zale et al., 1989). Data collected in this study suggested that Sister Grove Creek supported a viable fish fauna typical of prairie intermittent streams.

Fish species diversity and richness were greatest for lower reaches of Sister Grove Creek. Whiteside and McNatt (1972) observed low species richness in the headwaters of the Plum Creek drainage of south-central Texas relative to lower reaches. In a study of Brier Creek, it also was reported that species diversity and richness increased downstream (Smith and Powell, 1971). These authors reported that *P. vigilax, C. lutrensis, L. cyanellus, L. humilis, L. megalotis, L. macrochirus, L. microlophus,* and *F. notatus* were among abundant fishes collected in the intermittent reaches of Brier Creek. In lower perennial reaches emptying into Lake Texoma, the preceding species were collected as well as *G. affinis, M. beryllina, D. cepedianum, D. petenense, Aplodinotus grunniens, M. chrysops,* and *P. annularis*. These additional species were considered temporary inhabitants of the stream that entered it from the reservoir. Spatial patterns in fish assemblage structure reported by Smith and Powell (1971) for Brier Creek seemed to apply in general to Sister Grove Creek. *Menidia beryllina, D. cepedianum, D. petenense, M. chrysops,* and *P. annularis* were collected in the lower reaches of Sister Grove

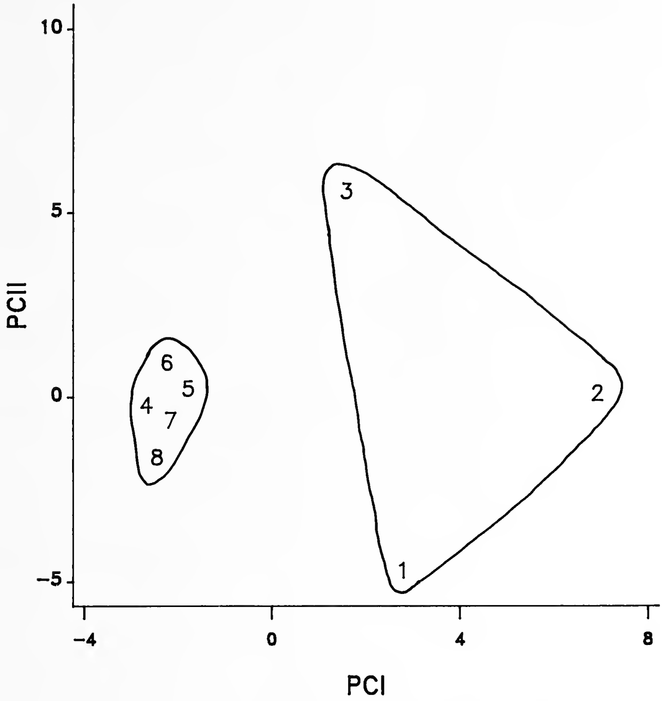

FIGURE 2. Ordination of the first (PCI) and second (PCII) components of a principal components analysis of fish assemblages at each of eight sampling locations in Sister Grove Creek.

Creek and likely were itinerant inhabitants, migrating from Lake Lavon. The influence of species from Lake Lavon on the Sister Grove Creek fish fauna appeared to be extend no further upstream than site 3, a distance of 5.6 kilometers from the reservoir. However, in Sister Grove Creek, as in Brier Creek, the presence of a man-made reservoir exerted a definite influence on the fish fauna of a tributary stream.

Spatial patterns in fish assemblage structure corresponded to the geomorphology of the stream channel. Porous gravel substrate in the headwaters of Sister Grove Creek provided little refuge for fishes during periods of summer low flows and drought. However, clay and sand substrates in the lower reaches, particularly at sites 2 and 3, held water and allowed formation of large stable pools conducive to the survival of fishes during summer drought conditions. Studies have revealed that pools in intermittent streams can be important refuges for fish and a source of potential colonists (Evans and Noble, 1979; Matthews, 1987; Schlosser, 1987). Although 22 of the 46 species collected in Big Sandy Creek were taken in the headwaters, the authors suggested that this was due to the geomorphology of the stream channel that resulted in

Table 2. Number of fish taxa collected, species diversity (H′), most abundant species, and percent abundance at each of eight sampling locations along Sister Grove Creek. Collections were made from August 1988 to July 1989.

Site	Number of taxa	Diversity (H′)	Most abundant species	Percent
1	22	1.54	*Cyprinella lutrensis*	41
2	26	2.35	*Menidia beryllina*	26
3	24	2.19	*Gambusia affinis*	34
4	10	1.17	*Gambusia affinis*	56
5	11	1.49	*Gambusia affinis*	54
6	12	1.37	*Fundulus notatus*	41
7	15	2.11	*Fundulus notatus*	41
8	16	1.79	*Fundulus notatus*	46

permanent pools upstream, rather than downstream. Geomorphology of the lower reaches of Sister Grove Creek conducive to the formation of pools during low water may have been an important factor influencing fish assemblage structure in this part of the stream.

Intermittent streams generally are regarded as poor habitat for fish owing to the instability of the flow regime and, therefore, have received little consideration in land-use planning. Unfortunately, many intermittent streams have been modified by such activities as channelization, grazing, construction of headwater impoundments, and effluents (Zale et al., 1989). Knowledge of fish species composition, spatial patterns of fish assemblage structure, and extent of available pool habitat are critical to an understanding of the ecological functioning of these important ecosystems and should not be neglected from future land-use planning efforts.

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SOIL DIFFERENCES BETWEEN NATIVE BRUSH AND CULTIVATED FIELDS IN THE LOWER RIO GRANDE VALLEY OF TEXAS

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Abstract.—Soil fertility and salinity were compared between native brush and cultivated fields of flood plain and upland areas. Organic matter and zinc were higher ($P < 0.05$) in native brush surface soils of both areas. Calcium and iron were also higher ($P < 0.05$) in native brush, but only in upland soils. No significant differences ($P > 0.05$) were observed between native brush and cultivated fields for the soil parameters of pH, nitrogen, copper, sodium, and salinity. Organic matter and potassium generally decreased with depth, whereas calcium and salinity correspondingly increased; changes with depth (to 150 centimeters) were not observed with other soil parameters. *Key words*: floodplain; old fields; organic matter; soil fertility; upland; Texas.

The U. S. Fish and Wildlife Service and Texas Parks and Wildlife Department are revegetating newly acquired cultivated fields in the lower Rio Grande Valley of southern Texas with native plants to improve habitat for wildlife. Plant growth may be reduced if cultivation has significantly lowered soil fertility. Much of the water used in irrigation is slightly saline and an accumulation of salts also might stunt growth (Everitt et al., 1977; Salisbury and Ross, 1985). Preliminary tests were conducted to identify differences in soil fertility and salinity between native plant (brush) communities and cultivated fields of floodplain and upland area.

Study Area

Floodplain soils of the study area are deep, moderately well-drained, silty to clayey soils on bottomlands (Jacobs, 1981). Upland soils are deep, gently sloping, well-drained, loamy soils on ridges of middle to high stream terraces that are modified by wind (Turner, 1982.)

The lower Rio Grande Valley has a subtropical, semiarid climate, characterized by short, mild winters (< 10°C) and long, hot summers (32 to 40°C). Annual rainfall, mostly from irregularly distributed thundershowers, varies from 450 to 700 millimeters. Occasional tropical storms in late summer (September) produce heavy rains. Another rainy period occurs in late May and early June. Relative humidity is usually between 65 and 80 percent. Surface winds are common.

Methods and Materials

Surface soil samples (top 15 centimeters) were collected at 21 sites in native brush and 27 sites in cultivated fields. Twenty-four sites were located in the Rio Grande floodplain and another 25 in an upland area about 44 kilometers north of the river. Samples were taken from Matamoros silty clay, Rio Grande silt loam, Conmargo silt loam, Rio Grande silty clay loam, and Reynosa clay loam soils in the flood plain, and from Hargill fine sandy loam, Hidalgo fine sandy loam, Willacy fine sandy loam, and Yturria fine sandy loam soils in upland areas (Table 1). The five flood plain soils supported similar native vegetation as did the four upland soils. The cultivated fields in the flood plain had been irrigated.

TABLE 1. Sampling in relation to soil type and taxonomic class (Jacobs, 1981; Turner, 1982).

No. of plots		Soil	
Native brush	Field	Soil name	Family or higher taxonomic class
			Floodplain
0	1	Conmargo	Fine-silty, mixed (calcareous), hyperthermic Typic Ustifluvents
3	0	Matamoros	Fine, mixed (calcareous), hyperthermic Vertic Ustifluvents
1	0	Reynosa	Fine-silty, mixed, hyperthermic Fluventic Ustochrepts
6	13	Rio Grande	Coarse-silty, mixed(calcareous), hyperthermic Typic Ustifluvents
			Upland
4	7	Hargill	Fine-loamy, mixed, hyperthemic Udic Paleustolls
2	0	Hidalgo	Fine-loamy, mixed, hyperthermic Typic Calciustolls
1	4	Willacy	Fine-loamy, mixed, hyperthermic Udic Argiustolls
4	2	Yturria	Coarse-loamy, mixed, hyperthermic Pachic Haplustolls

Additionally, soils were sampled to a depth of 150 centimeters at six sites in both brush and cultivated fields to examine differences associated with soil depth; samples were collected in relation to changes in soil texture, not at prior-specified depths. There was no visible water erosion at any of the sample sites (slopes less than two percent). Soils in brush were sampled where dense vegetation permitted space to take a soil core, such as under a tree or in interspaces among shrubs. Information was not available on length of cultivation or crops used. Soil analyses were done by the soil testing laboratory of Texas A & M University in College Station, Texas; Welch et al. (1980) described the analytical procedures used. Readily oxidizable organic matter was used for percent organic matter. Extraction of phosphorus, potassium, calcium, magnesium, and sodium was done with a solution of 0.025M H-EDTA in 1.4M ammonium acetate and 1.0M hydrochloric acid, pH 4.2 to 4.3. A DTPA extracting solution was used for zinc, iron, manganese, and copper (ph 7). Salinity was measured with a two to one extract of water and soil. Water-extractable nitrates were measured with a nitrate electrode (Onken and Sunderman, 1970). Ratings of high, medium, and low were also provided, and were based on comparisons with research plots at Texas Agricultural Experimental Stations. Differences between brush and cultivated fields of floodplain and upland sites were analyzed with t-tests.

RESULTS

Few differences in surface soil characteristics were observed between native brush communities and cultivated fields (Table 2). Organic matter and zinc were higher ($P < 0.05$) in native brush of floodplain and upland areas. Calcium and iron were also higher ($P < 0.05$) in native brush, but only in upland soils. Manganese was higher ($P < 0.05$) in cultivated fields of the floodplain.

Differences between native brush and cultivated fields diminished with soil depth. Organic matter decreased with soil depth (from 3.5 to 0.38 percent), except in cultivated fields in upland sites. In these sites the organic matter increased between 12 and 24 centimeters (0.7 to 1.3

TABLE 2. Summary of analyses of the top 15 centimeters of soil (mean and standard deviation in parenthesis; milligrams per liter except pH and organic matter).

	Vegetation			
	Floodplain[a]		Upland[b]	
Measured parameter	Native brush (n = 10)	Field[c] (n = 14)	Native brush (n = 11)	Field[c] (n-13)
pH	8.2(0.1)	8.2(0.2)	6.7(1.0)	7.1(0.5)
O.M.[d](%)	3.5(0.6)*[e]	1.4(0.7)	2.0(0.9)*	0.6(0.4)
Nitrogen	9.1(5.5)	9.7(5.1)	1[f]	1.3(1.1)
Phosporus	50(21)	68(33)	6(7)	3(4)
Potassium	747(101)	598(254)	377(155)	318(109)
Calcium	>3,521[g]	>3,521	923(568)*	481(213)
Magnesium	>426[g]	>426	212(116)	159(63)
Zinc	1.47(0.44)*	0.67(0.43)	0.33(0.24)*	0.13(0.09)
Iron	11.4(5.5)	8.8(3.8)	13.8(7.4)*	7.1(4.5)
Manganese	2.5(0.9)	5.1(3.3)*	5.6(3.2)	6.4(2.8)
Copper	1.03(0.40)	0.69(0.22)	0.52(0.28)	0.32(0.18)
Sodium	278(58)	254(90)	185(32)	164(111)
Salinity	408(84)	528(234)	220(163)	112(48)

[a] Soil textures: silt loam, silty clay loam, silty clay, clay, clay loam, loamy fine sand.
[b] Soil texture: fine sandy loam.
[c] Field = cultivated field.
[d] Organic matter.
[e] * = significantly higher ($P < 0.05$).
[f] One sample had 23 parts per million, the remaining nine had one.
[g] Upper limit measured in laboratory.

percent) and then decreased with depth. Potassium decreased with depth in the flood plain (747 to 346 milligrams per liter).

Calcium increased with depth in upland areas (923 to more than 3521 milligrams per liter) and was high throughout the profile in the flood plain (more than 3521 milligrams per liter). Salinity (all water-soluble salts) generally increased with depth (408 to 1202 milligrams per liter).

A comparison of soil surface characteristics between floodplain and upland sites (Table 2) showed a lower, more neutral pH in the sandier, upland soils. Nitrogen, phosphorus, magnesium, zinc, calcium, copper, sodium, and salinity were all much lower in the upland sites. Organic matter was lower in upland brush than in floodplain brush.

DISCUSSION

Higher organic matter in native brush soils would be expected given the annual leaf drop of the plants and additions of organic matter by root growth. Tilling soils may lower organic matter content by accelerating decomposition and incorporating subsoil low in organic matter. Tillage may have caused changes in physical properties of soils (that is, structure) that would return more slowly to their natural state under native conditions than would soil fertility. Higher organic matter in floodplain brush soils, compared to upland brush communities, would be the result of greater, or more lush growth of the brush in the floodplain (more water).

Lower amounts of zinc and iron (upland only) in cultivated fields may have been a result of depletion through crop harvest, reduced nutrient cycling compared to native brush, and greater leaching with irrigation. Higher calcium concentration in upland brush samples than field may have been due to calcareous soils (Hidalgo) that were present only in brush samples. We do not have an explanation for the higher amounts of manganese found in floodplain fields.

Low amounts of phosphorus, magnesium, zinc, and calcium in comparison to Texas Agricultural Experimental Station research plots were characteristic of both native brush and cultivated fields in the upland area. High levels of these elements in the floodplain were not the result of irrigation because they were also high under native brush, but instead were due to less weathering of the younger floodplain soils.

The soils of the lower Rio Grande Valley were typically low in nitrogen and organic matter, and high in phosphorus, potassium, calcium, magnesium, zinc, iron, copper, and manganese. Organic matter decomposes rapidly and does not appear to influence soil pH; it may be lost through wind or water erosion in some areas. Sodium and salinity did not appear to be a problem; all sites sampled were moderately well-drained to well-drained. Areas of salt accumulation or elevated water tables could occur if areas with poor drainage were irrigated.

Soils are naturally low in nitrogen despite the presence of a large number of leguminous species. Presumably, most of the nitrogen is in the plants and litter layer, and little in mineral soil. The native plants are probably adapted to this condition. Fertilization, nevertheless, may aid establishment but probably also will enhance growth of competing vegetation if broadcast over the entire site.

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A STONE APPROXIMATION THEOREM FOR TM-PARTITION SPACES

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ABSTRACT—By a generalized Kakutani's representation theorem, a similar result of Schaefer's Stone Approximation Theorem for the so-called TM-partition space is obtained.
Key words: M-partition space; TM-partition space; Stone Approximation Theorem; inductive topology.

For terminologies not defined explicitly in this paper, the reader is referred to Luxemburg and Zaann (1971), Schaefer (1974), and Wu (1986).

A collection of positive elements $P=\{e_i: i \in \Omega\}$ in a vector lattice is said to be saturated if for any two elements e_i, e_j in P, $e_i \vee e_j$ is also in P (Wu, 1986:4). For any collection D of positive elements in V, the collection of all finite suprema of elements in D is referred to as the saturation of D. If a vector lattice V contains a saturated collection of positive elements $P=\{e_i: i \in \Omega\}$ satisfying the conditions, then (V,P) is termed an M-partition lattice with an M-partition P: 1) if $|v| \wedge e_i = 0$ for all e_i in P, then $|v| = 0$; 2) for any e_i in P and v in V, there exist e_j in P and $r > 0$ such that $|v| \wedge ne_i \leq re_j$ for all n in $\mathbb{N}$; and 3) for any e_i in P and $\epsilon > 0$, there exists e_j in P such that for all e_k in P, $e_k \wedge ne_i \leq (1 + \epsilon)e_j$ for all n in $\mathbb{N}$. If P is finite, P is termed a finite M-partition. For each e_i in P, $p_i(v) = \inf\{r > 0$: there exists e_j in P such that $|v| \wedge ne_i \leq re_j$ for all n in $\mathbb{N}\}$ is a seminorm on V. The topology T_P inducted by $\{p_i: i \in \Omega\}$ is referred to as the M-partition topology induced by P. A topological vector lattice (V,τ) is termed an M-partition space if (V, P) is an M-partition lattice for some M-partition P such that τ is equivalent to the M-partition topology T_P induced by P. For convenience, Theorem 7 in Wu (1986:12) is copied as Theorem 1 herein.

Theorem 1.—A topological vector lattice (E,τ) is homeomorphic and lattice isomorphic to a dense subspace V of (C(Y),k) for some locally compact Hausdorff space Y such that $V \cap C_\infty(Y)$ is dense in $(C_o(Y),\|\cdot\|)$ if, and only if, (E,τ) is an M-partition space. The space Y is unique up to homeomorphism.

Schaefer (1974:169) defined an orthogonal set S of nonzero positive elements in a Banach lattice E to be a topological orthogonal system (t.o.s.) of E if the ideal generated by S is dense in E. Schaefer (1974:177) obtained the so-called Stone Approximation Theorem.

Stone Approximation Theorem.—Let E be a Banach lattice, and let H be a vector sublattice in which closure contains a t.o.s. S of E. If H separates the points of $V_S(E)$, then H is dense in E, where $V_S(E)$ is the strong representation space for E.

In this paper, by Theorem 1, a similar result of this Stone Approximation Theorem will be obtained for the so-called TM-partition spaces.

TM-PARTITION SPACES AND TM-PARITIONS

Let (V,T) be a topological vector lattice containing a saturated collection $P=\{e_i: i \in \Omega\}$ of positive elements generating a dense Archimedean ideal I_P in (V,T) and satisfying the following condition(*): for every e_i in P and every $\epsilon > 0$, there exists an e_j in P such that for all e_k in P, $e_k \wedge ne_i \leq (1 + \epsilon)e_j$ for all n in $\mathbb{N}$. Then (V,T) will be called a TM-partition space with TM-partition P. It is obvious from the first section that an Archimedean topological orthogonal system of a Banach lattice E is a TM-partition of E.

Proposition 2

The ideal I_P in V generated by a collection P of positive elements in V is an M-partition lattice with the M-partition P if, and only if, P satisfies the condition (*).

Proof.—It is enough to show that (I_P,P) satisfies conditions 1) and 2) for an M-partition lattice. Let v be an element in I_P, pick $k_1, k_2,\ldots, k_m$ in $\mathbb{N}$ and $e_1, e_2,\ldots, e_m$ in P such that $|v| \leq k_1e_1 + k_2e_2 + \ldots + k_me_m$. Let $k = \max\{mk_t: t = 1,2,\ldots, m\}$ and $e_j = e_1 \vee e_2 \vee \ldots \vee e_m$. Then for every e_i in P, $|v| \wedge ne_i \leq |v| \leq k_1e_1 + k_2e_2 + \ldots + k_me_m \leq ke_j$ for all n in $\mathbb{N}$. If u is an element in I_P such that $|u| \wedge e_i = 0$ for all e_i in P. Then for any $n_1, n_2, \ldots, n_k$ in $\mathbb{N}$, $|u| \wedge (n_1e_1 + n_2e_2 + \ldots + n_ke_k) \leq |u| \wedge n_1e_1 + \ldots + |u| \wedge n_ke_k \leq n_1 (|u| \wedge e_1) + n_2(|u| \wedge e_2) + \ldots + n_k (|u| \wedge e_k) = 0$. Inasmuch as I_P is the ideal generated by P, thus $|u| \wedge v = 0$ for all v in I_P. Let K be the Dedekind completion of I_P, by Theorem 24.2 in Luxemburg and Zaann (1971:131), $I_P^\perp \oplus (I_P^\perp)^\perp = K$ and $I_P^\perp \cap (I_P^\perp)^\perp = \{0\}$. Because $I_P \subset (I_P^\perp)^\perp$ and $|u| \in I_P^\perp$, thus $|u| = 0$. For the converse, it is obvious from the definition for an M-partition lattice.

Proposition 3

An M-partition space (V,T_P) with the M-partition P is a TM-partition space with the TM-partition P.

Proof.—This is clear from Proposition 3 in Wu (1986:5) that the ideal I_P in an M-partition lattice (V,P) generated by P is dense in (V,T_P).

Corollary 4

Let V be a vector lattice having an order unit u. Then V with the order unit topology is a TM-partition space with TM-partition {u}.

Proof.—This is obvious from Proposition 5 in Wu (1986:5) that an order unit space is an M-partition space with a finite M-partition.

TM-Representation Spaces

Let (V,T) be a TM-partition space with a TM-partition P and let I_P be the ideal in V generated by P. Proposition 2 implies that (I_P,P) is an M-partition lattice with the M-partition P. Let T_P be the M-partition topology induced by P, then (I_P,T_P) is an M-partition space. By Theorem 1, there is a homeomorphism and lattice isomorphism H from (I_P,T_P) onto a dense subspace of (C(Y),k) for some locally compact Hausdorff space Y. Y is unique up to homeomorphism. This Y will be called a TM-representation space of (V,T,P).

By Proposition 8 in Wu (1986:7), for each i in Ω, the closure cl(E_i) of $E_i=\{y \in Y: H(e_i)\,(y) > 0\}$ is compact. Let I_i be the ideal in V generated by e_i. Then H(I_i) is contained in the set $C_*(cl(E_i))=\{f \in C(Y): |f|^{-1}((0,\infty)) \subset E_i\}$. For convenience, let $H_i = H_{|I_i}$, the restriction of H on I_i, $T_i = T_{|I_i}$, the relative topology on I_i, and $||\cdot||$ denote the supremum norm.

Lemma 5

The mapping H_i^{-1}: $(H(I_i), ||\cdot||) \rightarrow (I_i,T_i)$ is continuous.

Proof.—It is enough to show that H_i^{-1} is continuous at zero. Let O_i be a balanced, absorbing, solid open neighborhood of zero in (I_i,T_i). Then there is a balanced, absorbing, solid open neighborhood O of zero in (I_P,$T_{|I_P}$) such that $O \cap I_i = O_i$. By the Corollary of Proposition 8 in Wu (1986:7), there exists e_j in P such that $H(e_j)\,(x) > 1/2$ for all x in cl(E_i). Because O is absorbing, there exists $r_j > 0$ such that r_je_j is in O. Inasmuch as $r_je_j \,\Lambda\, me_i \leq r_je_j$ for all m in ℕ and O is solid, $r_je_j \,\Lambda\, me_i$ is in O for all m in ℕ. This implies that $r_je_j \,\Lambda\, me_i$ is in $O \cap I_i = O_i$ for all m in ℕ. It is claimed that $\{v \in H(I_i): ||v|| < r_j/2\}$ is contained in $H_i(O_i)$. Let u be an element in H(I_i) such that $||u|| < r_j/2$. Then $|u|\,(x) < r_j/2$ for all x in E_i and u(x) = 0 for all x in Y - E_i. Because $H(e_j)\,(x) > 1/2$ for all x in cl(E_i), $|u|\,(x) < r_j/2 < r_jHe_j)\,(x)$ for all x in Y. Hence $|u| \leq r_jH(e_j)$. Because u is in H(I_i), there exists k in ℕ such that $|u| \leq kH(e_i)$. Therefore, $|u| \leq r_jH(e_j) \,\Lambda\, kH(e_i) = H(r_je_j \,\Lambda\, ke_i)$. Inasmuch as $r_je_j \,\Lambda\, ke_i$ is in O_i and O_i is solid, this implies that |u| is in $H_i(O_i)$. Thus, H_i^{-1} ($\{v \in H(I_i): ||v|| < r_j/2\}) \subset O_i$. Therefore, H_i^{-1} is continuous.

A Stone Approximation Theorem for TM-Partition Spaces

Let H be the homeomorphism and lattice isomorphism from (I_P,T_P) onto the dense subspace of (C(Y),k) defined in the previous section. For each i in Ω, let g_i: $H(I_i) \rightarrow H(I_P)$ be the inclusion mapping and $||\cdot||$ the supremum norm on H(I_i). Let T* be the finest locally convex topology such that g_i: $(H(I_i), ||\cdot||) \rightarrow (H(I_P), T^*)$ is continuous for all i in Ω; that is, T* is the inductive topology on H(I_p) with respect to the family $\{(H(I_i), ||\cdot||, g_i): i \in \Omega\}$ (Schaefer, 1971:5). A zero-neighborhood base for T* is given by the family {U} of all radical, convex, circled subsets of H(I_P) such that for each in in Ω, g_i^{-1} (U) is a zero-neighborhood in $(H(I_i),||\cdot||)$.

Lemma 6

Let W be a vector sublattice of $H(I_P)$. If $W \cap H(I_i)$ is dense in $(H(I_i), \|\cdot\|)$ for each i in Ω, then W is dense in $(H(I_P),T^*)$.

Proof.—Let O be an open subset of $H(I_P)$ in $(H(I_P),T^*)$. Then for each i in Ω, g_i^{-1} (O) is an open set in $(H(I_i),\|\cdot\|)$. Because $W \cap H(I_i)$ is dense in $(H(I_i),\|\cdot\|)$, it follows that $(W \cap H(I_i)) \cap g_i^{-1}(O) \neq \phi$. This implies that $W \cap g_i^{-1}(O) \neq \phi$; i.e., $W \cap O \neq \phi$. Thus W is dense in $(H(I_P),T^*)$.

Lemma 7

T^* is finer than $H(T_{|I_P})$.

Proof.—By Lemma 5, for each i in Ω, H_i^{-1}: $(H(I_i),\|\cdot\|) \rightarrow (I_i,T_i)$ is a continuous function. Because H is a lattice isomorphism from I_P onto $H(I_P)$, this implies that the inclusion mapping g_i: $(H(I_i),\|\cdot\|) \rightarrow (H(I_P),H(T_{|I_P}))$ is continuous for all i in Ω. Inasmuch as T^* is the finest topology such that g_i is continuous for each i in Ω, hence T^* is finer than $H(T_{|I_P})$.

Theorem 8

Let W be a vector sublattice of a TM-partition space (V,T). Then W is dense in (V,T) if, and only if, 1) the closure cl(W) of W in (V,T) contains a TM-partition P, and 2) $cl(W) \cap I_P$ separates points of TM-representation space Y of (V,T,P).

Proof.—If W is dense in (V,T), then cl(W)= V. It is obvious that cl(W) contains a TM-partition P and $cl(W) \cap I_P = I_P$. From Wu (1986:6), it is clear that each x in the TM-representation space Y of (V,T,P) is a real continuous lattice homomorphism on I_P. If x and y are two different points in Y, then (x - y) is a nonzero real continuous lattice homomorphism on the M-partition space (I_P,T_P), by the Corollary of Proposition 3 in Wu (1986:5), there is an e_i in P such that $(x - y)(e_i) > 0$. Because $(x - y)(e_i) = x(e_i) - y(e_i) = e_i(x) - e_i(y)$. This implies that $e_i(x) \neq e_i(y)$; that is, $cl(W) \cap I_P$ separates points of Y. For the converse, it will first be shown that $H(Cl(W) \cap I_i)$ is dense in $(H(I_i),\|\cdot\|)$. Because $H(I_i)$ is contained in $C_*(cl(E_i))$, it is sufficient to show that $H(cl(W) \cap I_i)$ is dense in $(C_*(cl(E_i),\|\cdot\|)$. For all x in E_i, because $\sup\{H(e_j)(x): j \in \Omega\}= 1$, for every $\epsilon > 0$, there exists an e_x in P such that $1 \geq 1\ H(e_x)(x) \geq 1 - \epsilon$. Pick $r > 0$ such that $rH(e_i)(x) > H(e_x)(x)$. Then $H(e_x) \Lambda rH(e_i)$ is in $H(cl(W) \cap I_i)$ with $1 - \epsilon < H(e_x)(x) = H(e_x) \Lambda rH(e_i)(x) \leq 1$ and $0 \leq H(e_x)(y) \Lambda rH(e_i)(y) \leq 1$ for all y in E_i; i.e., $1 - \epsilon < \|H(e_x) \Lambda rH(e_i)\| \leq 1$. Thus, $1 - (H(e_x)(x) \Lambda rH(e_i)(x)) / \|H(e_x) \Lambda rH(e_i)\| < 1 - (1 - \epsilon) = \epsilon$. Next, it will be shown that $H(cl(W) \cap I_i)$ separates points of E_i. Because $cl(W) \cap I_P$ separates points of Y (that is, $H(cl(W) \cap I_P)$ separates points of Y), for every x, y in E_i, there exists a v in $cl(W) \cap I_P$ such that $H(v)(x) \neq H(v)(y)$. This implies that either $H(v)^+(x) \neq H(v)^+(y)$ or $H(v)^-(x) \neq H(v)^-(y)$. Without loss of generality, assume that $H(v)^+(x) \neq H(v)^+(y)$. Let $r > 0$ such that $rH(v)^+(x) < H(e_i)(x)$ and $rH(v)^+(y) < H(e_i)(y)$.

Then $rH(v)^+ \wedge H(e_i)$ is in $H(cl(W) \cap I_i)$ and $rH(v)^+(x) \wedge H(e_i)(x) = rH(v)^+(x) \neq rH(v)^+(y) = rH(v)^+(y) \wedge H(e_i)(y)$. Thus, $H(cl(W) \cap I_i)$ separates points of E_i. By the Corollary of Theorem 2 in Wu (1986:3), $H(cl(W) \cap I_i)$ is dense in $(C_*(cl(E_i)),\|\cdot\|)$, this implies that $H(cl(W) \cap I_i)$ is dense in $(H(I_i),\|\cdot\|)$. Therefore, for each i in Ω, $H(cl(W)) \cap H(I_i) = H(cl(W) \cap I_i)$ is dense in $(H(I_i),\|\cdot\|)$. Lemma 6 implies that $H(cl(W) \cap I_P)$ is dense in $(H(I_P),T^*)$. Because T^* is finer than $H(T_{|I_P})$, thus $cl(W) \cap I_P$ is dense in $(I_P,T_{|I_P})$. By the denseness of I_P in (V,T), this implies that $cl(W)$ is dense in (V,T) and, therefore, W is dense in (V,T).

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THE EASTWARD RECESSION OF THE PINEY WOODS OF NORTHEASTERN TEXAS, 1815 TO 1989

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Abstract.—Previous studies by the author indicated that publications containing descriptions and maps of the pine-oak forests and other vegetational areas of northeastern Texas were not accurate. An on-site field survey was conducted, and the current western margin of the piney woods of northeastern Texas was located and mapped. It was determined that the forest margin had been receding to the east since the region was settled in the early 1800s. Evidence is presented showing that the number of settlers was larger than usually reported; that American settlement began earlier than reported by many Texas historians; and that major human impact on the pine-oak forests in the area began about 1815 and has continued to the present. Early and current destruction of the forest, particularly along the margin, by lumbering and agricultural use is described. *Key words*: piney woods; Texas forests; Texas history; Landsat mapping; ecology.

During ecological investigations of two *Pinus echinata* Mill.-*Quercus alba* L. communities in northeastern Texas (Wilson and Hacker, 1986; Wilson, 1989), it was determined that existing maps of the distribution of the vegetation of Texas generally did not include one or both of these communities within the pine-oak forest region of northeastern Texas. A survey of the available literature revealed that the vegetational areas in the northeastern corner of the state have not been correctly reported, and existing maps do not accurately present the distribution of the vegetation of this region (Roberts, 1881; Bray, 1904, 1906; Bailey, 1905; Tharp, 1926, 1939; Gould et al., 1960; Farb, 1963; Gould, 1969; Correll and Johnston, 1970; Arbingast et al., 1973; and McMahan et al., 1984). The map provided by McMahan et al. (1984), which was based on Landsat satellite photographs, most accurately portrayed the distribution of the vegetation in northeastern Texas, but on-site observations during this and earlier studies by the author revealed numerous discrepancies between the distribution shown on the map and the actual locations of pine forest, hardwood forest, and grassland. Some areas that were shown to be pine-hardwood forest were devoid of pines, and other areas shown as hardwood forest or prairie actually supported a mature pine-oak forest.

Other observations indicated that the current margins of the Sanders Cove pine-oak forest in Lamar County, Texas, were not entirely natural, and that the separation of this relict community from the main area of pine-hardwood forest to the east had been influenced by clearing. There seemed to have been a general eastward recession of the pine-oak forests since the northeastern portion of the state was first settled. American settlement in this area began earlier, and there were more settlers, than generally has been recognized. Previous investigators have not discussed the importance of the large numbers of early settlers in this area and their effect on the distribution of the piney woods in northeastern Texas.

It also was observed that the vegetation located west of the piney woods in northeastern Texas was not described accurately or identified. The vegetation in this region does not fit the descriptions of the westerly belts of prairie and post oak savanna shown on most maps.

METHODS

A field survey was begun in 1987 to locate and record the current limits of the piney woods in northeastern Texas and to determine the extent of changes in the forested region since the area was settled. The limits of the pine-oak forest were mapped, starting at a point on Interstate Highway 30 near Mt. Vernon (Franklin County) where native pines were known to occur. The margin north of Interstate 30 was located by crossing and recrossing the edge of the piney woods on all roads that entered or exited the pine-oak forest. Observations were recorded on county highway maps published by the Texas Department of Highways. Near the end of the project, Mueller-Wille's atlas (1988), *The Roads of Texas*, was used rather than the large, cumbersome, and no more accurate county maps. After the area north of Interstate 30 had been surveyed, the area to the south of the starting point was mapped. The southern limit of the survey was set at Texas Highway 31. Approximately 3000 kilometers (1900 miles) of roadways were traveled between the autumn of 1987 and the spring of 1989. This yielded 183 mapped points marking the intersection of the pine-oak forest margin with every paved or graveled road (and some unimproved roads) that crossed the margin. From hilltops and in locations where the pine-oak forest joined prairies, the margin was sometimes visible from roadways for as much as eight to 10 kilometers, which allowed accurate mapping between margin-road intersections.

The criterion employed to identify the pine-hardwood forest was the presence of pines of any species as a significant component of the landscape. Sample counts in the forest indicated that pines represented a minimum of five to 10 percent of the standing timber in the areas that were recorded as within the piney woods. The margin of the forest was located on the basis of naturally occurring pines only. Plantations and other planted pines lying west of the eastern limit of naturally occurring pine forests were not considered to be part of the piney woods.

Pre-statehood (1846) historic sites, such as communities, cemeteries, and river crossings were recorded on county maps as they were encountered. Communities, cemeteries, and other geographic features with the word "pine" in their names also were recorded. Additional information on early settlement and place names was obtained by examining historical and geographical literature.

RESULTS

The margin of the piney woods in northeastern Texas in 1989 is shown in Figure 1. From Texarkana (Bowie County), the margin roughly parallels the Red River westward to western Red River County, then turns to the southeast and extends to a point near the confluence of the Sulphur River and White Oak Creek at the intersection of Bowie, Morris, and Cass counties. From there, the margin makes an irregular arc to the southwest, crossing Texas Highway 31, the southern limit of this study, at the western city limits of Brownsboro, in Henderson County.

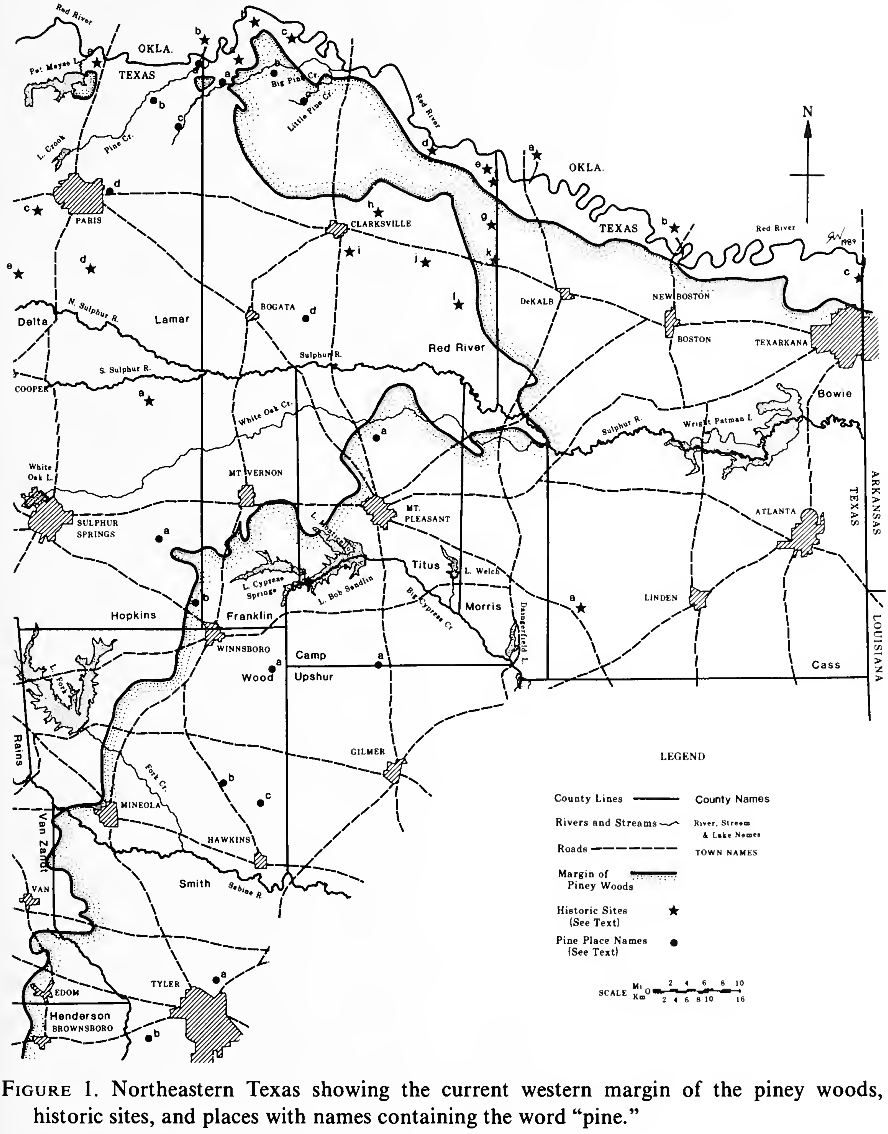

FIGURE 1. Northeastern Texas showing the current western margin of the piney woods, historic sites, and places with names containing the word "pine."

Pre-statehood historic sites and places with the word "pine" in the name are also shown in Figure 1. Historic sites are identified by a star and a county reference letter. The nature of these historic sites and their approximate ages are given in Table 1. Place names containing the word "pine" are identified on the map by a shaded circle and a county reference letter and are listed in Table 2.

TABLE 1. Pre-statehood historic sites in northeastern Texas. The symbol "b" preceding a year indicates a founding date sometime earlier than that indicated. See Figure 1.

County	Map reference	Name	Nature of site	Year founded
Bowie	a	Lewis's Ferry	Ferry	1823
	b	Trammel's Trace	River Crossing and Roadway	1813
Cass	a	Trammel's Trace	River Crossing and Roadway	1813
Hopkins	a	Sulphur Bluff	Cemetery	1837
Lamar	a	Fulton's Crossing	Community	b,1833
	b	Pine Bluff	Community and River Crossing	b,1833
	c	Central National Road, Rep. of Texas	Roadway	1844
	d	Antioch Church of Christ	Church and Cemetery	1845
	e	Shelton's Fort	Pioneer Fort	1837
Red River	a	Rock Ferry	Ferry	1840
	b	Kiomishi (spelling varies)	River Crossing and Roadway	b,1840
	c	Jonesboro (spelling varies)	Community and River Crossing	1815
	d	Pecan Point	Community and River Crossing	1815
	e	Old Rowland (Mound City)	Community and River Crossing	1839
	f	Ward's Lake	Community	1824
	g	Burkham	Community	1814
	h	Shiloh Presby. Church	Church and Cemetery	1833
	i	Clarksville	Community	b,1835
	j	Avery	Community	b,1839
	k	Annona	Community	b,1839
	l	Boxelder	Community	b,1839
Titus	a	Fort Sherman	Pioneer Fort	1834

DISCUSSION

Current Western Margin of the Piney Woods

Along the Red River, the margin of the piney woods generally followed the edge of the bluff above the river bottom. North of Texarkana, the pines closely followed this terrain feature, but in other areas (for example, western Red River County) there were bands of pasture or cultivated land as much as three to five kilometers in width between the edge of the river bottom and the edge of the forest. Except along the Red River, the margin of the pine-oak forest did not follow

TABLE 2. Geographic place names in northeastern Texas that contain the word "Pine." See Figure 1.

County	Map reference	Name	Nature of site	Direction from margin
Bowie	a	Pine Springs	Community	Within
Camp	a	Pine Tree (now simply "Pine")	Community	Within
Hopkins	a	Pine Forest	Community	Without
	b	Pine Hill	Cemetery	Within
Lamar	a	Pine Bluff	Community and Ferry	Without
	b	Pine Creek	Stream	Without
	c	Big Pine Creek	Stream	Within
	d	Pine Mill Road	Roadway	Without
Red River	a	Pine Hill	Cemetery	Within
	b	Big Pine Creek	Stream	Within
	c	Little Pine Creek	Stream	Within
	d	Pine Branch	Community	Without
Smith	a	Pine Springs	Community	Within
	b	Lost Pine Lake	Lake	Within
Titus	a	Piney	Community	Within
Wood	a	Pineview	Community	Within
	b	Pine Mills	Community	Within
	c	Pine Mills Field	Oil Field	Within

any observed natural features. Although pines have been planted in areas of blackland and red clay soils, the natural pine-oak forest was found only on sandy soils. The western margin of the piney woods, however, did not coincide with the boundary between the western clay soils and the sands to the east. This forest margin always was located on the sands east of this soil-type boundary.

Pine-hardwood forest areas containing only short-leaf pine (*Pinus echinata*) were found in parts of Franklin and Lamar counties and in other areas in the northern and western regions in the piney woods. In the eastern and southern areas, either mixtures of short-leaf and loblolly pine (*Pinus taeda* L.) and hardwoods or only loblolly pine and hardwoods were present. Loblolly and short-leaf pines have been planted throughout northeastern Texas in previously lumbered areas, in plantations outside the piney woods, and as ornamental trees in most communities as far west as Paris (Lamar County), Sulphur Springs (Hopkins County), and Athens (Henderson County). No longleaf pines (*Pinus palustris* Mill.) were observed. In the hardwood forests near the western margin of the piney woods, it was not uncommon to see pines at the tops of ridges or in otherwise nearly inaccessible locations. This suggested previous lumbering of pine timber on the lower slopes, which were relatively easy to harvest.

At the western edge of the piney woods, the mixed pine-oak forest gave way to either a hardwood forest similar in composition to the deciduous component of the mixed forest, or was abruptly replaced by grassland or cultivated fields. The margin between piney woods and prairie was usually clearly defined by a fence line, a creek bank, or a roadway. Both short-leaf and loblolly pine seedlings were sometimes found along the edges of fallow prairies, along with seedlings of various deciduous species. In some locations there was no evidence of pine reproduction, even within the forests (Wilson, 1989). Outside the piney woods, it was common to see pastures in which occasional old mature pines were scattered, providing some shade for livestock.

Athough most authorities (Gould et al., 1960; Farb, 1963; Gould, 1969; Arbingast et al., 1973) reported that the pine-hardwood forest gave way on the west to post oak (*Quercus stellata* Wang.) savanna and then to blackland prairie, this did not appear to be the case. Post oak was observed, however, in the western portions of the forest. Along the margin, the pines disappeared from the forest, leaving a mixed hardwood forest, or the forest was abruptly replaced by prairies or cultivated fields. The prairies west of the piney woods were usually pasturelands.

No attempt was made to record the locations of the numerous areas of grassland within the piney woods. These prairies, however, were not as extensive as shown by McMahan et al. (1984), nor were they static in size or location. During the course of the study, some forested areas in Franklin County were cleared for grazing, and scattered solitary pines were left standing. Fields that have not been grazed or mowed for several years are rapidly overgrown by mixed hardwood forest communities (Phelan, 1976). The natural size or occurrence of these prairies could not be determined. Native Americans are known to have cleared bottomlands for cultivation and to have enlarged prairies by burning (Phelan, 1976; Jordan et al., 1984). Northeastern Texas at one time supported a large population of Caddoans. Village sites were common along the Sulphur and Sabine rivers and on the south side of the Red River for a distance of 120 to 150 kilometers upstream from Texarkana (Clark, 1937; Swanton, 1946). Most of the small prairies recorded in Hunt, Hopkins, Delta, and Lamar counties in 1850 (Jordan et al., 1984) were not identifiable at the time of this survey; some have been overgrown with scrub woodland, and pastures and cultivated fields have replaced formerly forested areas.

Settlement of Northeastern Texas

The early and extensive influences of American settlers in Texas have not been mentioned in the literature as factors affecting the vegetation of northeastern Texas. Traditionally, American settlement of Texas has been dated 1821, beginning in the Austin Colony on the Brazos River (Fehrenbach, 1983). According to Webb (1952), however, one of the earliest communities was Jonesboro (Jonesborough, Jones Boro, or Jones Borough). A small fenced enclosure known as Houston Park, situated on a wide prairie between the piney woods and the Red River in northeastern Red River County, contained a grave stone and two Texas Historical Commission Markers. The stone marked the interment of Jane Chandler Gill, who died in Jonesboro on 20 September 1816. One historical marker commemorated the founding of Jonesboro and the Jonesboro ferry by Henry Jones in 1815. The second marker stated that Sam Houston and David Crockett both entered what was to become the Republic of Texas by way of the Jonesboro ferry. Stephen F. Austin crossed the Red River there on his second trip to Texas in late 1820. Three Jonesboro families joined him and became part of the "Old Three Hundred" settlers in Austin's colony on the Brazos River (Fehrenbach, 1983). The texts of these and other historical markers may be found in Dooley and Dooley (1985).

Jonesboro was to become the head of steamship navigation on the Red River. By the mid-1830s, the Jonesboro area supported a population of 2350 persons and was shipping more than 1000 bales of cotton each year. By 1840, Jonesboro had begun to decline, and no trace of the community remains today (Crow, 1972).

The earliest American residents of Texas were "a dozen or so fugitives from the law who spent the summer of 1811 on Pecan Point" in Red River County, 30 miles east of Jonesboro (Webb, 1952). A trading post was established at the Pecan Point crossing of the Red River in 1815 by George and Alex Wetmore. Pecan Point was the location of a large Caddoan village on the south side of the Red River which was inhabited in 1815. The community became a focal point of early settlement, with at least 50 American families in residence at Pecan Point by the winter of 1817. The nearby community of Burkham, which was established in 1814, probably was the oldest American community in Texas (Crow, 1972). These and other early settlements are shown in Table 1. By about 1825, there were at least 20,000 American settlers, plus their slaves, in communities to the south of the Red River between the current site of Texarkana and the Pine Bluff ferry, northeast of Paris, in Lamar County (Crow, 1972; Fehrenbach, 1983).

The Impact of Settlement on the Piney Woods

Although the traditional view of early Texas settlers holds that prairies and plains were to be avoided (Jordan, 1973; Phelan, 1976), actual records indicate that settlers selected sites on or at the edges of prairies (Jordan, 1973; Conrad, 1988*a*). Water and grazing for livestock were of primary consideration. Adequate grazing could not be obtained in forested areas. Additionally, timber was needed for construction of fences, houses, and barns. The ideal homesite thus would have been situated at the edge of a prairie. Later, forested areas would be cleared for increased grazing, for planting kitchen gardens, and eventually for growing cotton throughout most of northeastern Texas (Conrad, 1988*b*). The effect of American settlement in the region on the northeastern Texas piney woods was initially a gradual erosion of the western margin of the forest, followed by clearing of large areas within the forest.

Evidence indicates that pine was harvested preferentially over hardwood timber for construction purposes in areas where pine timber was available. Pine logs were easier to harvest, trim, and haul and were more suitable for log building construction than were hardwood logs. Fort Sherman, a one room log building, was constructed in 1834 on Cypress Creek in Franklin County (Jurney, 1961; Russell, 1965). At about the time that construction began in 1976 on the Lake Bob Sandlin site, the building was moved to a location near the Blodgett community (eight kilometers north of Cypress Creek) and partially restored. The walls of this small structure required from 25 to 30 trees with diameters of 30 centimeters or more at a height of six or seven meters above the ground. No estimates can be made of the requirement for the roof, as the original has not survived.

Additional evidence of the preferential use of pine timber is from Smithwick (1900), who stated that the "gubernatorial mansion" in Austin in about 1860 had been constructed of pine logs with a pine plank roof. Evidently, pine logs and boards were hauled from the Bastrop area.

After settlement, the early Texans needed a cash crop, and additional pines were harvested. The Spanish had operated sawmills in San Augustine and Nacogdoches as early as 1819 (Phelan, 1976), and other mills were built later in most northeastern Texas counties. In the Avery, Annona, and Boxelder area of eastern Red River County, pine timber is known to have been used as a cash crop as early as 1839 (Russell, 1965). According to an 1880 estimate, a half billion board feet of short-leaf pine timber remained to be harvested in southeastern Hopkins County (White and Richardson, 1940). At a reasonable estimate of 4000 board feet per hectare, this amounted to about 20,000 hectares (personal communication, Dr. David Hacker, Department of Forestry, Stephen F. Austin State University, Nacogdoches, Texas). Today, the total area of pine-oak forest in Hopkins County has decreased to about 1300 hectares. The existing town of Pine Forest is located approximately three kilometers west of the pine forest-prairie margin in southeastern Hopkins County. No lumbering is currently evident in Hopkins County, but timber harvesting is a current industry in northern Red River and Bowie counties.

Five additional sites in Lamar and Red River counties (Table 2) also bear the word "pine" in their names, but are located west of the edge of the piney woods (Tarpley, 1969). These place names probably indicate that when settlement began in northeastern Texas the pine-oak forests extended from three or four to as many as 25 kilometers further west than the location of the present western margin.

Eastward recession of the margin of the northeastern Texas piney woods has been brought about by human activities including clearing and burning by Caddoans, timber use for immigrant construction purposes, agricultural clearing by early and current residents, and early and current timber harvest. Some additional areas have been cleared within what had originally been pine-oak forest. In some places, the pine-oak forest has been replaced by prairie, whereas in other areas, the pines have been selectively removed, leaving a hardwood forest.

CONCLUSIONS

The results of this study support the following conclusions:

1. Existing maps and descriptions of the distribution of the vegetation of northeastern Texas do not accurately represent the current vegetational patterns of the region. Neither the extent of the northeastern Texas piney woods nor the descriptions and locations of the post oak belt, the prairies, or the transitions from pine-oak forest to other kinds of communities in this area were accurately reported.
2. The vegetation to the west of the piney woods was not accurately described or located in earlier literature.
3. The margin of the piney woods from the Red River to Henderson County has been receding in an eastwardly direction, making earlier maps even less accurate. This loss of pine-oak forest has been greatly influenced by human activities, such as lumbering and clearing for agricultural usage. This recession has been occurring for the last 175 years or more.
4. Human impact in northeastern Texas has been more important than has been generally recognized. The settlement of this region began earlier than many historians have reported. The number of pre-Republic and pre-Statehood American settlers in this region was much greater than has been recognized.
5. The extent and rate of vegetational changes throughout the state, and the influence of early settlement on the vegetation of the state should be investigated.
6. Human influence, both past and present has had, and continues to have, more effect on the distribution of major vegetational areas in northeastern Texas than has been reported in the scientific literature.
7. The general inaccuracy of the older literature, insofar as northeastern Texas is concerned, leads one to question the overall accuracy of the existing maps and descriptions of the vegetation of Texas.

8. The need for a general re-examination of the vegetation of Texas, with due consideration given to historical information and extensive on-site surveying is evident. Aerial surveying and satellite imaging methods may be appropriate, if more extensive and more accurate "ground-truthing" is conducted than has been done in the past.

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CROCODILIAN SLAUGHTER METHODS, WITH SPECIAL REFERENCE TO SPINAL CORD SEVERANCE

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Abstract.—American alligators (*Alligator mississippiensis*) were examined during their capture, handling, restraint, and slaughter at a crocodilian farm. Procedures were monitored with special reference to assessing the method of slaughter—spinal cord severance at the atlanto-occipital area (nape-stab) and induced hypotension—and its effectiveness from practical and humanitarian viewpoints. Although practical, the method of slaughter, refined by the studied establishment, did not produce rapid loss of consciousness. Following slaughter procedures, voluntary activities and responses to stimuli indicated that central nervous system functions, consciousness, and awareness to physical insult and trauma, anterior to the severance site, probably ranged from one hour 41 minutes to one hour 53 minutes. Recommendations are made for replacement of the current widely used nape-stab with methods involving free-projectile firearms and captive-bolt systems, which potentially provide a more humane and acceptable approach. *Key words*: *Alligator mississippiensis*; crocodilian; hypotension; hypoxia; slaughter; spinal cord severance.

Crocodilian slaughter occurs regularly in commercial operations where animals are reared for the skin, culinary, and other industries. In recent years, there has been a substantial rise in the number and production of crocodilian farms and in marketing crocodilian products (Luxmoore et al., 1985). The industry is extensive in Florida and Louisiana, and also is represented in Texas. Recommendations for slaughter-euthanasia of wild crocodilians rarely are documented and no guidelines have been issued by United States authorities that cover killing of crocodilians for commercial purposes (A. Woodward, personal communication). Perhaps largely as a consequence, there is an apparent neglect in the crocodilian farming-ranching industry to adopt humane procedures of handling and slaughter. Because the Gatorland Zoo, Kissimmee, Florida, was reported to be the most advanced and well organized crocodilian farm in the United States (B. Cook, personal communication), it seemed reasonable to examine their current slaughter method. In addition, this slaughter procedure had been refined by a biologist working with Gatorland and allegedly took into account both practical and humane considerations (F. Godwins, personal communication).

Current methods of slaughter used by the industry in general are: insertion of blade to sever the spinal cord and blood vessels at the atlanto-occipital area (sometimes termed "nape-stab"); clubbing with hammers; bludgeoning with axes; shooting through cranium from a superior aspect with free-projectile firearms; shooting into atlanto-occipital area from a posterior-diagonal aspect with free-projectile firearms.

MATERIALS AND METHODS

General

Because the study mostly involved observations, only a few materials were required. These were: small battery-operated light with focusing beam; modified screwdriver with rounded tip; 35-mm camera and flash unit; mercury thermometer; tape measure; digital watch; and cassette tape recorder. Materials used in farm slaughter practices were operated by the staff and were, therefore, separate from my materials. These were: chisel; blade; heavy-duty hammer (approximately 1.35 kilograms); and adhesive insulating tape. The camera was used to photograph the operations; verbal descriptions and observations were recorded on tape. Air and water temperatures of the outdoor environment and the alligator pond were monitored. Indoor temperature (slaughterhouse) was recorded at varying heights. Approximate temperature of each alligator was assessed by placing the thermometer both on the animal (primarily to establish the immediate environmental temperature) and inside the cloaca. Although alligators are ectothermic, it was necessary to check their temperature, particularly early in the studies, to note the variance that could occur due to reptiles only recently having been removed from the water in an outdoor enclosure and placed in the warmer slaughterhouse.

Description of Specimens

Four American alligators (*Alligator mississippiensis*) were involved in the study. These were coded 1 to 4 in accordance with the order in which they were processed. All were in good physical condition. Measurements (in meters) of alligators 1 to 4, total length (tip of snout to tip of tail) and tip of snout to vent length, respectively, were: 1.24, 0.73; 1.45, 0.80; 1.78; 0.80; 1.60, 0.79. Weights (kilograms), estimated by Gatorland Zoo personnel, in the same sequence were: 18-20; 22-25; 30; 22-25. Ages were estimated by the staff to be between four and five years for all four specimens. No attempt was made to assess the sex of the alligators.

Monitoring Activities and Responses of Alligators During and After Slaughter Procedures

Voluntary and involuntary activities of the alligators (whether stimulated by the central nervous system or the peripheral nervous system) were recorded over a period of approximately two hours. In addition, certain benign stimuli were applied to assess pupillary, corneal (blink and nictitating membrane), defense (reacting to approach with attempts to withdraw or bite), skin sensitivity, pedal, tail, and audio responses. Activities of the jaw muscles, tongue movement, and general muscular activity in the neck anterior to the spinal cord severance also were monitored. Posterior to the spinal cord severance, general somatic activity was observed and recorded. Applied stimulation included pinching between finger and thumb the webbing of the feet as well as the digits and the skin of the limbs to monitor pedal reflexes, gently running the blunt screwdriver along the ventral side of both abdomen and tail, touching by hand the closed vent, and pinching the tail progressively towards the posterior end. Potential activity within the body cavity was assessed by listening directly against the ventral surface.

Alligators were, for the most part, positioned on their backs. Stimulation, as above, except of the ventral midline areas, also was applied when animals were turned to an upright position, and reactions were monitored; thus, dorsal surface sensitivity was examined. Observations were made of activities not resulting from stimulation. On most occasions, each feature of the examination was monitored in all animals before commencing to the next. Usually no more than one minute separated completion of one examination sequence and beginning of the next.

Slaughter Procedures

Alligators for slaughter were carried singly into the slaughterhouse and placed on the floor. One person holds the tail off the ground while placing a foot on the hindquarters of the animal to reduce movement. A second person places one foot directly across the anterior part of the upper jaw and presses downward to restrain the head. Using one hand, the second person positions the 46-centimeter-long chisel midway in the atlanto-occipital region, so as to be in line with the cervical vertebrae and thus the spinal cord. The free hand is used to hold a heavy steel hammer, which is used to strike the chisel. Around five to eight strikes are made in order to reach the desired depth of incision (5.0 to 6.5 centimeters). The chisel then is used rather like a crowbar to pry the head forward from the spinal column. This is to completely sever the spinal cord and the internal jugular sinus, but the head is not severed from the body. A blade approximately 7.5 centimeters in length then is inserted into the center of the cavity, and with vertical slicing motions driven out toward the sides of the neck. This ensures a more comprehensive severance of the spinal cord and blood vessels. Depth of the incision is similar to that caused by the chisel. The total incision width is approximately seven centimeters. The insertion of the chisel causes immediate exudation of a small amount of blood. The additional severance caused by the blade results in greater, but still not profuse, blood loss.

Alligators then are dragged to a drainage channel and turned onto their backs so that they "bridge" the channel, with the snout resting on one edge and the thorax resting on the opposite edge, thus allowing more convenient drainage of blood. One animal is slaughtered at a time.

On close inspection, the incisions in alligators 1, 2, and 3 revealed the following features. 1) Fractures across the first cervical vertebra, effectively splitting it into two sections; the anterior portion remained attached to the foramen magnum, whereas the posterior part was attached to the rest of the spinal column. 2) Complete severance of the spinal cord at the site of fracture of cervical vertebrae. 3) Severance of internal jugular and vertebral blood vessels. 4) Total incision area formed approximately 30 square centimeters. Alligator 4 showed the same damage as described for above except the severance of the spinal cord was incomplete.

The general procedure is that three or four alligators of the size examined are slaughtered on each desired day. Preparation of the carcasses takes place several hours after the slaughter process. Staff at the slaughterhouse stated that movements of the body still may be present during the dressing of the animals. Additionally, individuals even may flip themselves back onto their feet. It was also reported to me that activities in the alligators, before and after the slaughter procedures, are more energetic during warmer temperatures than during cooler times.

Results of Monitoring Activities and Responses in the Alligators During and After Slaughter Process

In the slaughter process, upon first strike of the chisel the alligators responded by closing tightly the nictitating membranes and eyelids, tensing of the muscles of the jaws, tensing of the muscles of the neck, and rapid withdrawal of forelimbs; a brief general struggle (although not violent) occurred over a period of approximately two to three seconds. When the second blade was inserted, although the eyes usually remained closed, there was a general tensing of the muscles of the head in particular, followed by slight reduction in tension, then an increase, decrease, and so on, while the blade was being used to sever tissue. Somatic responses also occurred in relation to the movement of the blade while the spinal cord, blood vessels, and tissues were severed. Once turned and placed over the drainage channel, heads would strike the angular corners. When this occurred, the alligators repeated the head reactions as detailed above. Somatic responses also occurred in reaction to handling associated with the procedure of turning the alligators over and then placing them in the drainage channel.

Activities and responses in the four alligators after "slaughter" were evident, both anterior and posterior to the severance. Interest is obvioiusly mainly drawn to the activities and responses of their heads. Alligators 1, 2 and 3 generally lay with the eyes closed. However, alligator 4 usually lay with the eyes partially or fully open. Approximately 20 minutes after commencement of slaughter procedures, a member of staff turned all the alligators onto their normal upright position and cleansed the cavity of the severance site using a moderately pressured spray-type water hose. All alligators responded with sudden activities both in the heads (involving tensing of the eyelids and muscles of the jaws and tongue) and with somatic responses (writhing and sporadic movement of the forelimbs).

Although erratic, after-slaughter defense activities were present, but they diminished and failed (hour and minutes) as follows: 1, 1.31; 2, 1.41; 3, 1.40; 4, 1.39. After slaughter, pupillary reactions were apparent initially but weakened and become progressively less responsive (hour and minutes): 1, 0.59; 2, 1.02; 3, 1.04; 4, 1.06. They failed as follows: 1, 1.35; 2, 1.41; 3, 1.39; 4, 1.37. Blink and nictitating membrane reflexes frequently corresponded in their responses to stimuli. However, whereas blink reflexes were strong and readily reacted to stimulation, nictitating membrane reflexes were less obvious, just detectable beneath the eyelids. After slaughter blink and nictitating membrane reflexes weakened and became progressively less responsive upon (hour and minutes): 1, 1.09; 2, 1.19; 3, 1.23; 4, 1.23. They ceased at: 1, 1.41; 2, 1.51; 3, 1.49; 4, 1.53. General activity in the heads of the alligators in the form of tensing of the muscles of the jaws, neck, and tongue, both voluntary and in response to stimuli, were present (although not strong or wholly reliable) until (hour and minutes): 1, 1.26; 2, 1.34; 3, 1.29; 4, 1.31. Posterior to the severance, general somatic, pedal, and tail activity occurred from commencement of the slaughter process and were still strongly evident on my departure from the establishment two hours later. Activities not resulting from deliberate stimulation were as follows: lateral undulating movement of the body and tail; pedal movements usually in either a regular horizontal plane or paddling movements, with occasional corresponding digital activity; urination (up to three times by one individual); expression of the cloaca.

Gentle deliberate stimulation of the skin on the ventral surface resulted in waves of muscular activities corresponding to the movement of the stimulating object. Pinching of the webbing between the digits in order to provoke pedal reflexes proved unreliable throughout the examination. Pinching the feet, however, was a reliable method of gaining pedal responses. Pinching the skin of the limbs also proved to be reliable stimulation. Pinching from the base of the tail progressively towards the end was a reliable method of producing responses in the form of tail movements. Touching the external surface of the vent produced rapid expression of the cloaca. In the process of stimulating a particular response, another activity would commonly coincide. For example, during stimulation of skin on the ventral surface, posterior to the severance, expression of the cloaca often occurred. Upon returning alligators to upright positions, their responses posterior to the severance, both stimulated and voluntary, became far more obvious. In addition, attempted stimulation of a single aspect, for example, pedal reflexes, frequently resulted in greater stimulation of more secondary activities (lateral undulating movements of the body and tail, limb movement, and so on), than when the animals were on their backs.

An hour and a half after slaughter procedure, examinations were made to detect any breathing activity. There was some evidence of slight breathing in all four alligators. Intestinal movement of all four also was noted. Heart rates (beats per minute) were detected in all animals as follows: 1, 24; 2, 21; 3, 20: 4, 22. No responses to audio stimulation occurred in any specimen either prior to, or following, the slaughter process. Cloacal temperatures were taken approximately 15 minutes after the slaughter process and were 12.7°C, rising to 13.8°C within approximately 20 minutes.

Discussion

Head activities of the four alligators were good indicators of consciousness and awareness to physical stimuli. Coordinated defense activities indicate a largely intact set of sensory systems and consciousness. Normally, a lack of pupillary-blink-nictitating membrane responses imply a lack of consciousness. Tolerance of reptilian nerve tissue to hypoxia has been reported in Belkin (1963), W.S.P.A. (1985), and U.F.A.W./W.S.P.A. (1989). There is good evidence, mostly summarized in the latter two references, that the considerable resilience of reptilian nerve tissue to hypoxia and hypotension results in animals remaining conscious for long periods. Neurogenic shock reported to affect, for example, mammals and birds, is considered insufficient (if at all significant) in the case of reptiles (U.F.A.W./W.S.P.A., 1989). Therefore, awareness to painful stimuli and traumatic occurrences remains. Consequently, practices during the slaughter process—for example, insertion of the chisel, follow-up massive severance of tissues using the short blade, and the prizing forward of the head—probably result in short duration severe general pain and distress, followed by longer duration trauma anterior to the severance site in "slaughtered" alligators.

It is reasonable that some blood would continue to reach the central nervous system inasmuch as several major vessels remain intact. Because the phrenic and vagus nerves were not severed, there is potential for central nervous system influence over some major organ functions. However, there was no evidence to suggest the extent to which central nervous system control might affect major organ functions because, although organ activity was present, it did not noticeably change either prior to death or afterwards. Organ activities are known to occur in situations where the central nervous system has no influence (for example, following decapitation).

Because the four animals probably were conscious for periods up to one hour and 53 minutes at temperatures of 20 to 22.2°C, attempts at moving alligators following spinal cord severance before the end of this period may cause additional trauma.

A marked difference in tolerance to hypoxic and hypotensive conditions was noted in alligators 1 and 3. This probably relates to difference in size between individuals. Alligator 1 was the smallest specimen, with the highest metabolic rate, and was the least resilient individual, whereas 3 was the largest individual, with the lowest metabolic rate, and was the most resilient individual. While alligators were overturned and in the drainage channel there was a decrease in general activities. Activity increased when the alligators were temporarily returned to their upright position. These responses concur with behavior in "normal," undamaged individuals. Therefore, this suggests that reduction in activity has its origins in the spinal cord and not the central nervous system (although the latter may have some influence in this area when intact with the spinal cord). The practice of turning unharmed crocodilians onto their backs in order to calm them down is not uncommon. However, while facilitating handling of the animals, it is unlikely that this procedure would cause reduction in awareness to painful stimuli.

Prolonged somatic activity probably was attributable to tolerance of nerve and muscle tissue to hypoxic and hypotensive conditions and a far higher degree of integration of somatic responses at the spinal cord than the brain (Stewart in U.F.A.W./W.S.P.A., 1989). Although specimen 4 showed incomplete severance of the spinal cord, this specimen did not indicate conclusive evidence of central nervous system activity reaching areas posterior to the severance.

Conclusions

The intentions of those involved in refining the nape-stab method are sincere and commendable and relate to a desire to create a humane system of slaughtering alligators as well as one that is practical commercially. Spinal cord severance methods, although practical, do not

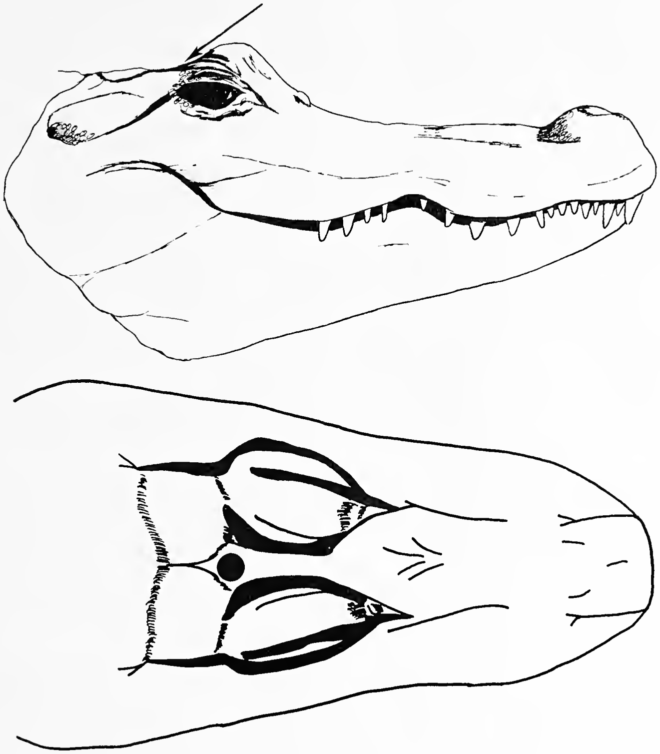

FIGURE 1. Recommended position and angle using free-projectile or captive-bolt systems in slaughter-euthanasia of crocodilians. The angle (top, arrow) offers a through-brain path for the penetrating implement, thus creating substantial and rapid brain destruction. Recommended site of entry of projectile (circle) is shown below.

constitute a humane system of slaughter or euthanasia. However, in comparison with other slaughter-euthanasia techniques (for example, the casual use of hammers), spinal cord severance is probably less traumatic, mostly due to the relative lack of general physical abuse.

First indicators of consciousness to weaken and fail are responses to pinching of the skin of the head, followed by pupillary and reflexes of the blink and nictitating membranes. Periods from commencement of the slaughter process to probable unconsciousness or death in the alligators were (hour and minutes): 1, 1.41; 2, 1.51; 3, 1.49; 4, 1.53. Cause of death of alligators probably was induced hypotension and hypoxia. Somatic activities along with pedal and tail reflexes and reactions to stimulation of the skin, both "voluntary" and stimulated, continue well after probable central nervous system functions have ceased.

RECOMMENDATIONS

A relatively humane method of slaughter should be achieved with the use of free-projectile and captive-bolt firearms (U.F.A.W./W.S.P.A., 1989). The following facilities and procedures offer guidelines for practical implementation.

1) An appropriately powered free-projectile firearm (for example, .22, .32, or .38 caliber special) or captive-bolt pistol is sufficient for killing animals of less than 2.1 meters in length. For those more than 2.1 meters in length, high powered, multi-projectile firearms are more adequate at close range and single hard-projectile guns at longer range.

2) A 30-centimeter-deep sand pit or other dense substrate, or some another absorbent surface, could provide an important base for absorption of potential excess energy from exiting projectiles.

3) The crocodilian should be placed on the soft base and shot in such a manner as to aim to cause as complete and rapid destruction of the central nervous system as possible (see Fig. 1).

Concerns for operator safety occasionally are expressed when firearms are used under circumstances such as those described above. However, free-projectile devices regularly are used in both domestic and wild animal slaughter-euthanasia situations with good safety records. Where reluctance is experienced, a captive-bolt system could be utilized for maximum safety. Silencers can be fitted easily to firearms so that noise, and thus potential distress for both people and alligators, would be greatly reduced.

Acknowledgments

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GENERAL NOTES

RANGE EXTENSION AND COUNTY RECORDS FOR TWO SPECIES OF RODENTS IN TEXAS

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Field studies during the past five years in central and north-central Texas have yielded specimens of *Oryzomys palustris* and *Thomomys bottae* that represent a range extension and county records, respectively. Voucher specimens, presently uncatalogued, will be deposited in the Texas Cooperative Wildlife Collection, Texas A&M University.

Oryzomys palustris.—Seven specimens of the northern rice rat were obtained in extreme western Hunt County (6 mi. WSW Celeste) from Countyline Prairie, a blackland-prairie preserve owned by the Texas Nature Conservancy. The nearest published records for *O. palustris* are in Lamar, Delta, and Wood counties, at least 50 kilometers to the east (Schmidly, 1983).

An intermittent stream, a tributary of Arnold Creek, is impounded by an earthen dam at the western edge of the preserve. In April, September, and November, 1989, *O. palustris* was caught in Sherman live traps baited with rolled oats in a moist, disturbed, grassy area adjacent to the intersection of the stream and dam. The predominant herbaceous vegetation in the area where rice rats were caught was Johnsongrass (*Sorghum halepense*), bermudagrass (*Cynodon dactylon*), Virginia wild rye (*Elymus virginicus*), and dallisgrass (*Paspalum dilatatum*), achieving heights of one and a half to two meters during summer. Woody vegetation was present only along the streambanks, primarily willows (*Salix*) and ash (*Fraxinus*), and along dry draws and fencelines, primarily Texas sugarberry (*Celtis laevigata*), bois d'arc (*Maclura pomifera*), and cedar elm (*Ulmus crassifolia*).

In 146 trap nights, cotton rats (*Sigmodon hispidus*, N = 3), deer mice (*Peromyscus maniculatus*, N = 2), white-footed mice (*P. leucopus*, N = 9), and one fulvous harvest mouse (*Reithrodontomys fulvescens*), were caught in the same traplines as the more abundant rice rats (N = 7). *O. palustris* was not trapped in wooded draws, along wooded fencelines, or in upland grassy (predominantly little bluestem, *Schizachyrium scoparium*; indiangrass, *Sorghastrum nutans*; big bluestem, *Andropogon gerardii*; switchgrass, *Panicum virgatum*; eastern gammagrass, *Tripsacum dactyloides*) areas. Small mammals trapped in parts of the preserve away from where *O. palustris* was found included *S. hispidus* (N = 14 in 440 trap nights), *P. maniculatus* (N = 3), *P. leucopus* (N = 36), *Neotoma floridana* (eastern woodrat, N = 3), and one *Cryptotis parva* (least shrew).

Thomomys bottae.—In October of 1986 and 1988, six adult Botta's pocket gophers were trapped by use of Victor traps in Schleicher County, 5 mi. W (on Highway 190) intersection of Highway 190 and FM 2084, in west-central Texas. The rolling terrain of this region includes elevated areas with exposed limestone and little or no soil, and gently sloping to flat areas with relatively deep soils. Gophers occur in the latter, specifically in soils of the undulating Tarrant and the nearly level Kavett-Tarrant associations along the dry drainages of Live Oak Hollow and Lake Hollow. These soils are dark grayish brown, are generally 35 centimeters or less deep, and are underlain by fractured limestone or caliche; limestone cobbles comprise up to 50 percent of the soil volume (Wiedenfeld, 1980). The minimum depth of soils in which evidence of gopher digging was found was about 7.5 centimeters.

Woody vegetation in areas occupied by *Thomomys* included predominantly plateau live oak (*Q. fusiformis*) and junipers (*Juniperus*) associated in mottes. Threeawn (*Aristida*) and buffalograss (*Buchloe dactyloides*) carpeted the low-lying areas of deeper soil. Clumps of

Yucca and prickly pear (*Opuntia*) occurred on these broad open flats as well as on rockier slopes; mounds of soil produced by gophers frequently were concentrated near yucca plants. Distribution of gophers was not continuous, but in isolated pockets of suitable substrate.

Central Texas constitutes the easternmost occurrence of *T. bottae* in North America (Hall, 1981). Hollander et al. (1987) reported *T. bottae* from surrounding counties, but did not document this species from Schleicher County. Additional reports about the distribution of this species in central Texas are needed if the taxonomic status and biogeographic history of Botta's pocket gopher are to be learned.

Thanks are due the many students in my Mammalogy and Natural History of the Vertebrates classes for their untiring efforts in the field; graduate students who contributed significantly include R. Fraze, C. Roorda, C. Swearingen, and R. Wiedenmann. I thank J. Weigel of the Texas Nature Conservancy for financial and logistic support at Countyline Prairie, and the Napier family for access to the ranch in Schleicher County.

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OCCURRENCE OF CLADOCERANS AND COPEPODS IN AN INTERMITTENT TEXAS STREAM

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Streams in general provide a less stable environment for aquatic life than lentic habitats due to variability in water level. However, prairie intermittent streams provide an extreme example of unstable water levels. Such streams generally experience seasonal fluctuations in discharge ranging from nearly dry conditions to floodwaters that exceed channel capacity (Matthews, 1988). Although lotic habitats support an abundant and diverse composition of zooplankton (Hynes, 1976), the importance of cladocerans and copepods to stream biota probably has been underestimated owing to the paucity of published studies on the occurrence of these organisms in streams (Vila, 1989). Thus, we provide information on crustacean zooplankton (Cladocera and Copepoda) collected in a Texas intermittent stream.

Sister Grove Creek is in Grayson and Collin counties in north-central Texas. The stream is about 60 kilometers long and ranges in width from about 3.5 meters in the headwaters to about 7.5 meters in the mid-reaches. Data on stream discharge were obtained from a U. S. Geological Survey gauging station located about mid-reach on Sister Grove Creek. In 1989, spring rains resulted in floods that exceeded bank capacity with discharges greater than 54 cubic meters per second. During summer and early autumn, low rainfall and runoff reduced discharge to zero, creating large pools.

Invertebrate samples were collected using stream drift nitex nets (363 μm mesh) as a part of a larger study on Sister Grove Creek. Nets were suspended from bridges at each of two sites, one located near the headwaters and one site located near the mouth. Each net was

TABLE 1. Taxa of crustacean zooplankton collected from Sister Grove Creek during December 1988 and January and April 1989. Also included is common habitat, taken from Edmondson (1959), Pennak (1966, 1978), and Hutchinson, (1967).

Species	Habitat
Copepoda	
Acanthocyclops vernalis	lentic (littoral)
Cyclops exilis	small streams
Diacyclops bicuspidatus thomasi	lentic (limnetic)
Diaptomus pallidus	lentic (limnetic)
Diaptomus siciloides	lentic (limnetic)
Eucyclops speratus	lentic (littoral)
Macrocyclops albidus	lentic (littoral, benthic)
Mesocyclops edax	lentic (limnetic
Harpacticoid species	lentic (limnetic, littoral, benthic)
Cladocera	
Bosmina longirostris	lentic (limnetic)
Ceriodaphnia lacustris	lentic (limnetic)
Chydorus sphaericus	lentic (limnetic)
Daphnia ambigua	lentic (linmetic)
Daphnia laevis	lentic (temporary ponds)
Daphnia parvula	lentic (limnetic)
Diaphanasoma leuchtenbergianum	lentic (limnetic)
Lydigia quadrangularis	lentic (littoral)
Simocephalus expinosus	lentic (littoral, benthic)

weighted such that the top was just below the water surface at mid-channel of the stream. Nets were set for two hours with samples collected four times over a 24-hour period; two during midday (generally from 1100 to 1300 and from 1300 to 1500 hours) and two during night (generally from 2300 to 0100 and from 0100 to 0300 hours). Sampling occurred on 8 and 9 December 1988, 20 and 21 January 1989, and 24 and 25 April 1989. Net contents were preserved in 10 percent formalin and stained with Phloxine B to facilitate identification (Mason and Yevich, 1967). Samples were filtered through an 841-μm mesh brass sieve to remove debris and the 210-μm fraction was saved. Identification of zooplankton was made using keys and information reported by Jones (1958), Edmondson (1959), Robertson (1970), and Pennak (1978).

Eighteen species of cladocerans and copepods (nine each) were collected in Sister Grove Creek in December 1988 and January 1989 (Table 1). Mean monthly discharges for December and January were 0.12 and 1.85 cubic meters per second, respectively. No cladocerans or copepods were taken in April 1989 when mean monthly discharge was 3.5 cubic meters per second. Of the 18 taxa collected, *Cyclops exilis* was the only one common to lotic environments (Pennak, 1978). Most of the crustacean zooplankton species collected in Sister Grove Creek have been reported as common to lentic environments (Edmondson, 1959; Pennak, 1966, 1978; Hutchinson, 1967).

Zooplankton abundance in streams previously has been demonstrated to be inversely proportional to stream discharge (Hynes, 1976; Brown et al., 1989; Vila, 1989). However, seasonally low flow in prairie intermittent streams may provide suitable conditions for the reproduction and growth of cladocerans and copepods before high discharge flushes these organisms downstream (Richardson, 1989; Vila, 1989). Whereas crustacean zooplankton taxa such as *Cyclops* sp. have been reported to be important components of temporary streams in southern Canada and the northern United States (Williams and Hynes, 1976;

Vila, 1989), the presence of cladocerans and copepods in Sister Grove Creek suggests that crustacean zooplankton may play an important role in the ecology of Texas intermittent streams.

We thank Bruce Arambula and David Partridge for assistance in the field.

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HIGH INCIDENCE OF MELANISM IN *MASTICOPHIS TAENIATUS* GIRARDI (REPTILIA:COLUBRIDAE), FROM THE CUATRO CIENEGAS BASIN OF COAHUILA, MEXICO

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The Cuatro Ciénegas Basin of central Coahuila, México, is of considerable faunisitc interest for three reasons: 1) it lies at the interface between the Chihuahuan Desert and the Tamaulipan Biotic Province (Blair, 1949); 2) it contains much permanent water, in both lentic and lotic habitats; and 3) it is surrounded by mountain ranges that have apparently acted as barriers to terrestrial animal movements (Minckley, 1969). This last factor has resulted in a high frequency of endemic and relictual animal populations. Endemic taxa of aquatic snails (Taylor, 1966), isopod crustaceans (Cole and Minckley, 1966), scorpions (Williams, 1968), fishes (Minckley, 1962, 1969; Miller and Minckley, 1963; Hubbs and

Miller, 1965; Miller, 1968), turtles (Schmidt and Owens, 1944; Legler 1960; Webb and Legler, 1960), and lizards (McCoy, 1970; Walker, 1981) are known from the Cuatro Ciénegas Basin. Relictual populations of the toad, *Bufo valliceps,* and the reptiles, *Eumeces tetragrammus, Scincella laterale, Coluber constrictor, Nerodia erythrogaster,* and *Nerodia rhombifera,* also are known to inhabit the basin (McCoy and Minckley, 1969). The zoogeography and ecology of the Cuatro Ciénegas herpetofauna were reviewed by McCoy (1984). In this note, we describe the first incidence of possible endemism of a snake inhabiting the Cuatro Ciénegas Basin.

In conducting a systematic revision of *Masticophis taeniatus*, five specimens from the Cuatro Ciénegas Basin were examined. Three of these, all females, were melanistic dorsally. An adult male (AMNH 77315), 983 mm in snout-vent length (SVL), had more dark pigment dorsally than is typical, lacking the pale nuchal collar diagnostic of the subspecies *M. t. girardi.* It was not completely melanistic, however, because five pale transverse bands diagnostic of *M. t. girardi* were present. A female (TNHC 33012), 623 mm SVL, displayed a color pattern similar to Chihuahuan Desert *M. t. girardi* but lacked the typical transverse banding. The melanistic females ranged from 823 to 885 mm SVL. These specimens were not completely melanistic ventrally. Black pigment was absent from small areas, but they had more extensive dark ventral mottling than is typical for *M. t. girardi.*

Dorsal scale formulae—15-15-11 (two specimens), 15-15-12 (two), and 15-15-13 (one)—and the head scutellation of the Cuatro Ciénegas material was typical for the subspecies. The ventrals of the females ranged from 200 to 214 (mean, 206); the mean was identical to the average for 187 female *M. t. girardi* from throughout the range of that race. The male had 193 ventrals, well within the range of 183 to 236 (mean, 205) ventrals for 257 males from throughout the range of *M. t. girardi.* Subcaudals varied from 129 to 166 (mean, 155), for the three females with complete tails. This is higher than the average of 145 subcaudals for 123 female *M. t. girardi* from throughout the range of the subspecies. The male had 155 subcaudals, which is greater than the average of 149 for 188 males of the subspecies, but within the known range of 122 to 175 subcaudals. Maxillary teeth ranged from 16 to 19, with a mean of 17.25, in the Cuatro Ciénegas females, fewer than the mean of 18.7 for all 194 female *M. t. girardi* examined. The male had 20 maxillary teeth, well within the range of 15 to 23 (mean, 19.1) from all 258 males of the subspecies examined.

The three melanistic females were collected on the floor of the basin north or east of the Sierra San Marcos, presumably in mesic habitats. The pale-colored female that lacked transverse banding was taken from the west side of the Sierra San Marcos in Chihuahuan Desert habitat. The male was obtained along the southern base of the Sierra de la Madera, in the northwestern portion of the basin, in habitat unknown to the authors. Even though some of the Cuatro Ciénegas specimens have atypical color patterns, scutellation and dentition character states fall within the known variation of *M. t. girardi.* The different color patterns of the five specimens available suggests the possibility of isolation and divergence. Because of similarity in morphology to *M. t. girardi*, the observed variation in color pattern, and the small sample size, no taxonomic conclusions are drawn at this time.

Specimens examined.—Mexico Coahuila: AMNH 77315, 3 mi. W Cuatro Ciénegas de Carranza; CM 58192, 14 km. S Cuatro Ciénegas, Tio Candido; KU 80282, 1 mi. E tip San Marcos Mtns; LACM 116256, 11 km. SW Cuatro Ciénegas de Carranza, N tip Sierra de San Marcos; TNHC 33012, 9 mi. SSW Cuatro Ciénegas, on San Pedro Rd.

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NEW RECORDS OF BATS FROM FRENCH GUIANA

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In January 1989, The Carnegie Museum of Natural History and Department of Biology, Hofstra University, conducted joint fieldwork in French Guiana to collect bats for a variety of DNA, ultrastructural, histological, and preservation studies. Bats were collected from savannah forest and secondary growth habitats in the vicinity of Sinnamary (5° 28′ N, 53° 00′ W), Remire (4° 53′ N, 52° 17′ W), and Matoury (4° 51′ N, 52° 20′ W). Among the species collected, *Pteronotus personatus, Artibeus gnomus, Vampyrops brachycephalus*, and *Lasiurus egregius* are important new records for the country, and also provide new data about the ecology and geographic distribution of these species in South America.

Measurements given below are in millimeters; those of forearms and crania were taken with Helios dial calipers, accurate to 0.1 mm. Unless otherwise indicated, specimens were preserved in 10 percent formalin after skulls and tissues were extracted. Reproductive data were acquired from gross examination of dissected specimens. All specimens reported were adults as indicated by completely fused phalangeal epiphyses. Specimens are deposited in the Recent mammal collection at The Carnegie Museum of Natural History.

Pteronotus personatus (Wagner).—This species has been reported previously from Suriname (Williams and Genoways, 1980) and farther south and east through the central interior of Brazil (Mares *et al.*, 1981). A specimen netted on 24 January from 1 km. N Remire represents the first reported from French Guiana; it also serves as a possible eastern range extension of 500 kilometers for the northern coastal region of South America. The conditions under which this specimen was taken are described in the account for *Vampyrops brachycephalus.*

The specimen, a female that evinced no reproductive activity, had the following measurements: length of forearm, 46.9; greatest length of skull, 16.1; condylobasal length, 15.0; breadth of braincase, 7.4; zygomatic breadth, 8.9; postorbital constriction, 3.6; length of maxillary toothrow, 6.5; distance across upper molars, 5.9.

Artibeus gnomus Handley.—This species recently was described by Handley (1987) and reported to occur in several areas in northern South America. A female obtained from 3 1/2 km. S and 10 km. W Sinnamary, on 21 January, is the first record from French Guiana. It was netted in a recently cleared area of primary forest. Other species of bats collected at the same location included *Saccopteryx bilineata, Carollia perspicillata, Rhinophylla pumilio*, and *Chiroderma trinitatum.*

The specimen of *A. gnomus* carried a fetus having a crown-rump length of 20. Measurements of the adult were as follows: length of forearm, 39.3; greatest length of skull, 19.1; condylobasal length, 17.0; breadth of braincase, 8.4; zygomatic breadth, 10.9; postorbital constriction, 5.0; length of maxillary toothrow, 5.6; distance across upper molars, 7.5. *Artibeus gnomus* closely resembles *A. cinereus*, but it may be differentiated by its smaller size, prominent facial markings, and presence of lower third molars. It is possible that *A. gnomus* is related to the species associated with the genus *Durmanura* by Owen (1987); however, Owen (1988) did not comment on the relationships of *gnomus.* Until further information is available, the taxonomy given in the original description (Handley, 1987) is followed.

Vampyrops brachycephalus Rouk and Carter.—The nearest geographic records for this species are in Suriname (Williams and Genoways, 1980). A male from 1 1/2 km. NE Remire (25 January) and two males and two females collected 1 km. N Remire (24 and 27 January) represent the first reports from French Guiana as well as an eastern range extension of about 350 kilometers.

At 1 1/2 km. NE Remire, nets were set over a fast-flowing stream paralleled by secondary growth, which was adjacent to a large banana garden. Other species collected at this locality included, *Phyllostomus discolor, Carollia brevicauda, C. perspicillata, Artibeus cinereus, A. jamaicensis, A. lituratus, Sturnira lilium*, and *Vampyrops helleri.* Habitat netted at 1 km. N Remire consisted of secondary growth vegetation and unmaintained gardens on a hillside. Species of bats obtained in several nets during two nights of collecting in this habitat included *Pteronotus personatus, Phyllostomus discolor, Glossophaga soricina, Carollia perspicillata, Artibeus cinereus, A. jamaicensis, Sturnira lilium*, and *V. helleri.*

Testes in each of the three males of *V. brachycephalus* measured 4 by 3; reproductive data for females included single embryos with crown-rump measurements of 15 and 35. Average measurements for the three males, followed by those of the two females, are: length of forearm, 43.3, 43.2; greatest length of skull, 23.0, 22.5; condylobasal length, 20.0, 19.9; breadth of braincase, 9.9, 9.9; zygomatic breadth, 13.6, 13.6; postorbital constriction, 5.7, 5.8; length of maxillary toothrow, 8.0, 7.9; distance across upper molars, 9.6, 9.4. This species is similar to *V. helleri*, but it can be differentiated by its slightly larger dimensions and the presence of two accessory cusps on the anterior side of the lower second premolar.

Lasiurus egregius (Peters).—This rare species is known only from three other specimens, two in the U. S. National Museum of Natural History and one in the Zoologisches Museum der Humboldt-Universitat zu Berlin. Collecting localities for these specimens are from Panamá (San Blas, Armila, USNM 11175) and Brazil (Para, Mocambo, USNM 392993, and Santa Catarina, the type locality, ZMB 3762). A female obtained 9 1/2 km. S and 11 1/2 km. W Sinnamary on 22 January, represents the first record from French Guiana and the fourth record of this rare bat. This new record, combined with those from other localities, suggests that this species may be primarily restricted to the northern and eastern coastal region of South America.

The specimen, preserved as a skin and skull, evinced no gross indications of reproductive activity. It was netted over a stream, adjacent to a bridge. The area was surrounded by grassy flats bordering the road followed by mature secondary vegetation mixed with tropical forest. Species of bats collected in the same place included *Micronycteris megalotis, Phyllostomus elongatus, P. hastatus, Carollia perspicillata, Sturnira lilium, Uroderma bilobatum*, and *Myotis nigricans.*

The female of *L. egregius* from French Guiana is somewhat smaller than the three previously known specimens. The type specimen is a male in which the forearm measures 49.3 and the greatest length of skull measures 17.3 (Carter and Dolan, 1978). The specimen from Mocambo is a fluid-preserved female with a forearm measurement of 50.3. Measurements for females from French Guiana and Panamá are as follows: length of forearm, 45.3, 49.9; greatest length of skull, 16.6, 16.7; condylobasal length, 16.0, 16.2; breadth of braincase, 8.6, 8.8; zygomatic breadth, 11.7, 12.1; postorbital constriction, 4.8, 4.6; length of maxillary toothrow, 5.8, 5.9; distance across upper molars, 7.7, 7.8.

The authors extend their appreciation to Dr. Leon Sanite for assistance in acquiring permits from French Guiana, to Drs. Alfred Gardner and Charles Handley for examining specimens and providing relevant information, to Drs. Karen Anderson and Herndon Dowling for field assistance, and to Dr. Duane Schlitter for critically reviewing the manuscript. This fieldwork and research was supported by the North American Mammal Research Institute (SLW) and NIH grants DE 07648-01A1 (CJP and B. Tandler) and GM 42563-01 (DEP and CJP), and Hofstra University HCLAS grants (DEP and CJP).

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FIRST RECORD OF THE MOLE, *SCALOPUS AQUATICUS*, ON THE LLANO ESTACADO OF WESTERN TEXAS

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The eastern mole, *Scalopus aquaticus*, has been reported as common at some locations along the Canadian River, the breaks of which form the northern boundary of the Llano Estacado, and its tributaries in the northern Texas Panhandle (Jones et al., 1988). Furthermore, Yates and Schmidly (1977) mapped localities of record for this species from east of the escarpment of the Llano in Briscoe and Dickens counties. Specimens in the collection of Recent mammals at The Museum, Texas Tech University, also include individuals from east of the escarpment in Motley County. All of these moles were collected in suitable habitats such as in sandy creek and river bottoms, on golf courses, and in other areas of generally friable soil. Presumably, the escarpment and its soils have inhibited *S. aquaticus* from colonizing the Llano Estacado.

While setting traps for rodents on 8 October 1989, J. K. Jones, Jr., and R. W. Manning noticed mole burrows atop the Llano Estacado at a site 1.5 mi. N and 4 mi. E McAdoo, Dickens Co., Texas. In an attempt to collect moles, several return visits to this location were made, and I was successful in trapping an adult female (TTU 57566) there on 23 January 1990. The local habitat in which the mole was taken was adjacent to a fenceline, and was approximately six feet wide and a quarter of a mile long. It is bordered on the east by FM 193 and situated a few hundred meters from the edge of the escarpment. Many mole runs were observed there.

The roadside is closely mowed. The slightly elevated fenceline contains rank vegetation (such as Johnsongrass, various other grasses, and carelessweed), and is bordered on the west by a cotton field. The few areas in the immediate vicinity that are not planted to row crops consist of overgrazed mesquite rangeland dominated by short grass species. The soil at the trapsite is of the Pullman series, with a high clay content (Girdner and Richardson, 1970), a substrate type normally avoided by moles (Davis, 1974).

Scalopus aquaticus has been taken just east of this location (the nearest record is nine miles away), but the substrate there is sandy, and much of the intervening terrain is inhospitable to moles. The escarpment of the Llano Estacado near the trapsite is more gentle than farther to the north or south, but soils on the scarp are both gravelly and have a high clay content. Soils may have been a greater barrier to invasion of the Llano Estacado by moles than was the escarpment itself. The subspecies of northwestern Texas is *S. a. aereus*.

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DISTRIBUTIONAL RECORD OF *LIOMYS SALVINI* FROM HONDURAS

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Salvin's spiny pocket mouse, *Liomys salvini*, typically is associated with dry tropical lowland forest along the Pacific slopes of the mountains of Central America, reaching an altitude of about 1500 meters. The only region in the Caribbean drainage in which *L. salvini* is common is in the dry habitat in Guatemala along the Río Motagua and the Río Negro and its tributaries as far as San Pedro Sula in northern Honduras (Carter and Genoways, 1978). *L. salvini* also ranges throughout central Honduras as far east as Catacamas, Department of Olancho (Genoways, 1973; Hall, 1981). Based on known records, the two northeasternmost localities for the species in Honduras are Catacamas and El Caliche Orica, Department of Francisco Morazán (Genoways, 1973).

On 27 February 1989, one of us (FJS) trapped two female *L. salvini* inside Camp Dakota, a support base for road building activities by United States Army Reserve and North Dakota National Guard soldiers. Camp Dakota is located 1.7 km. SE Sabana Larga, Department of Yoro, along the north side of the Río Aguan. Between 1 March and 23 April, a male and five additional females were captured on the base. This new locality is approximately 77 kilometers northeast and 140 kilometers northwest, respectively, of the two previous northeasternmost localities of record in Honduras (see above), and the specimens are the first captured in the Caribbean drainage of the northeastern part of that country.

External measurements (mm) of the male are: total length, 234; length of tail, 122; length of right foot, 25; length of ear from the notch, 16. External measurement for the seven females are: total length, 225, 233, 223, 221, 201, 219, 207; length of tail, 113, 118, 114, 121, 109, 109, 106; length of right foot, 27, 26, 26, 26, 27, 26, 23; length of ear from the notch, 16, 15, 15, 15, 13, 14, 15. All specimens are deposited in the Texas Cooperative Wildlife Collection, Texas A&M University.

We would like to thank Dr. J. Knox Jones, Jr., for critical review of the manuscript and for helpful suggestions, Dr. Hugh H. Genoways for confirming identification of the specimens, and Sergeant Martin and Specialists Hankle and Paul for helping collecting specimens.

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CNEMIDOPHORUS GULARIS SEPTEMVITTATUS (TEIIDAE) FROM PECOS COUNTY, TEXAS

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On 1 September 1989, a subadult male *Cnemidophorus* (University of Arkansas Department of Zoology [UADZ] 3839) was collected 21.0 km. W jct. US 90 and US 285 (102° 37′ 41″ W, 30° 08′ 54″ N) in Pecos County, Texas. The habitat, located in Sanderson Canyon at an elevation of 1013.5 meters, is comprised of widely-spaced mesquite separated by bare ground and/or patches of lechuguilla, prickly pear, crucifixion thorn, composites, mixed grasses, and forbs growing in calcareous soil, an assemblage that is typical of a 'succulent desert' (Gehlbach, 1979).

The specimen (Fig. 1A) has six dorsal stripes with colors grading from cream anteriad to tan posteriad, a partial tan vertebral (seventh) stripe extending from the occipital region to one-sixth the length of the trunk, cream-beige spots in the upper lateral and dorsolateral fields, bluish-brown dorsal surfaces of the hind limbs and tail, bluish-gray ventral surfaces of the throat, abdomen and distal one-half of the tail, 88 granules around midbody, 209 granules from occiput to rump, five granules separating the paravertebral stripes, 5.7 percent of the granules around midbody lying between the paravertebral stripes, 38 femoral pores combined, 31 subdigital lamellae of the longest toe of the left pes, nine circumorbital scales combined, 20 lateral supraocular granules on the left side, eight supraocular scales combined, 15 mesoptychial scales bordering the gular fold, and large platelike postantebrachial scales (analyses follow Duellman and Zweifel, 1962; Walker, 1981).

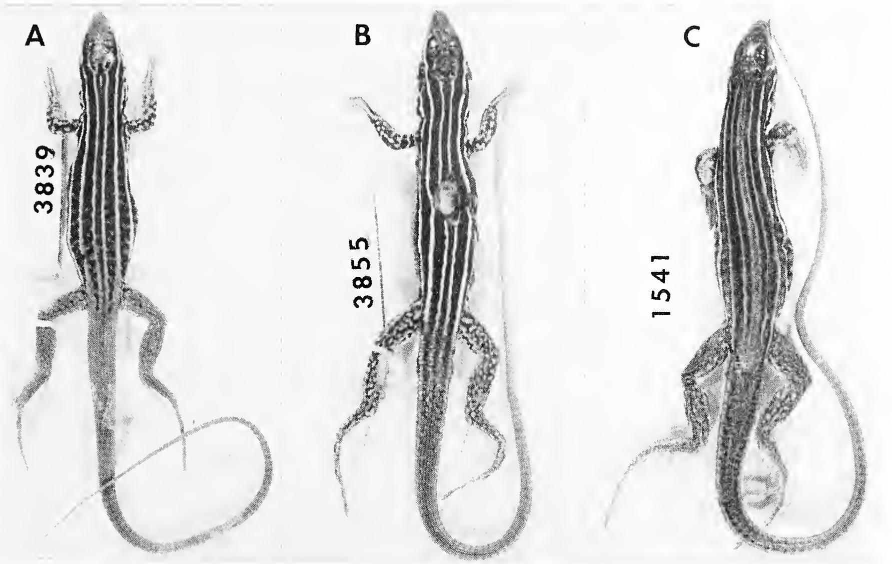

FIGURE 1. Verification of the identity of *Cnemidophorus gularis septemvittatus* (A) from 21 km. W jct. US 90 and US 285, Pecos Co., Texas (UADZ 3839, male, snout vent length 52 mm) as compared with *C: g. septemvittatus* (B) from San Antonio Canyon, Presidio Co., Texas (UADZ 3855, male, SVL 50 mm), and *C. g. gularis* (C) from Langtry, Val Verde Co., Texas (UADZ 1541, male, SVL 60 mm).

Comparison of UADZ 3839 with samples of the gonochoristic species *C. inornatus, C. marmoratus,* and *C. gularis* from geographically proximate localities indicate that it belongs to *C. g. septemvittatus* rather than to *C. g. gularis* (*sensu* Walker, 1981; Fig. 1). Based upon Dixon, 1987 (*C. septemvittatus* sp. = *C. gularis septemvittatus*), UADZ 3839 represents a new distribution record for Pecos County, filling the apparent hiatus between Brewster and Terrell counties. Although Dixon (1987) also listed records for Presidio, Jeff Davis, and Hudspeth counties, we found no evidence that *C. g. septemvittatus* has been collected in the latter two. The Texas range of *C. g. septemvittatus*, therefore, is limited to the mountain foothills and canyons in Presidio, Brewster, Pecos, and Terrell counties.

An adult male (UADZ 3838) and female (UADZ 3837) *C. g. septemvittatus* were collected on the same day at a nearby site in Sanderson Canyon, Terrell County (11.3 km. W jct. US 90 and US 285), representing only the second locality (fourth and fifth specimens) for the subspecies from that county (Morris, 1978). These specimens and those from Grapevine Hills, Brewster County (Degenhardt, 1966, in which *C. sacki* = *C. g. septemvittatus*), represent the lowest elevations (945 meters) recorded for *C. g. septemvittatus* in Texas.

Field research in Texas was conducted under authority of Texas Parks and Wildlife permit no. 61 provided through the assistance of Mr. David Riskind, Texas Parks Division, and Mr. George C. Adams, Texas Resources Protection Branch. Mr. Al Real, general manager of the Mesquite Ranch, Presidio County, provided lodging and field assistance. The Graduate Studies Committee, University of Arkansas, provided a Graduate Grant-in-Aid of Research Award in support of field work associated with this study.

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ADDITIONAL RECORDS OF BATS FROM THE BLACK MESA REGION OF OKLAHOMA

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In mid-September 1983 and in mid-October of 1985 and 1987, students in mammalogy classes at Texas Tech University, under the direction of R. J. Baker and R. K. Chesser, collected mammals near Kenton, in the Black Mesa region, Cimarron Co., Oklahoma. In a recently published book, Caire et al. (1990) summarized information on Oklahoman mammals, but inexplicably they did not include mention of specimens taken by these field parties, some of which provide interesting distributional records.

Most of the bats here reported came from Tesesquite Canyon, to the southeast of Kenton, and at an approximate elevation of 4400 feet. Mist nets were strung over pools in the drainage of Tesesquite Creek, and over a stock tank above the valley. Mature cottonwoods were the most conspicuous deciduous trees along the floor of the canyon, which cuts through rough mesa country on its way to the Cimarron River east of Kenton. Rocky slopes above the canyon support juniper, whereas the immediately adjacent terrace is dominated by semiarid vegetation such as mesquite, prickly pear, and short grasses.

In the following accounts, catalogue numbers refer to the collection of Recent mammals in The Museum at Texas Tech University. All measurements are given in millimeters.

Myotis ciliolabrum ciliolabrum (Merriam, 1886).—Four specimens of the western small-footed myotis were listed from Cimarron County by Mares (1990:423, under *M. leibii*). A male (43201), preserved in alcohol, was netted along with *M. yumanensis* and other species on 13 October 1985 at a place 3 mi. S and 1.5 mi. E Kenton. It is distinguishable from *yumanensis* by its paler, golden-colored pelage, distinct keel low on the calcar, noticeably smaller hind foot, and short forearm, which measured 30.9. Length of forearm averaged 35.1 (34.4-36.0) in 10 male *yumanensis* from the vicinity of Kenton.

Myotis yumanensis yumanensis (H. Allen, 1864).—This species is one of the common bats in the Black Mesa region, and there are numerous records from Cimarron County. Specimens in our collection, taken in all three years, are as follows: 3 mi. N, 1 mi. E Kenton, 4 (48983-86); 1.5 mi. S, 3 mi. E Kenton, 6 (43197-200, 43202-03); 3 mi. S, 2 mi. E Kenton, 6 (39724-26, 39729, 39731, 40680); 4.3-4.5 mi. S, 2.4 mi. E Kenton, 4 (39727-28, 39730, 48951); 5 mi. S, 2 mi. E Kenton, 3 (39722-23, 41951). Bats from the locality first listed were netted over the Cimarron River. All others were taken in Tesesquite Canyon.

Lasionycteris noctivagans (Le Conte, 1831).—Although the silver-haired bat is to be looked for as a migrant in spring and again in late summer and early autumn in any part of Oklahoma, previous records all are from the central or eastern parts of the state. We have examined eight specimens (both sexes) from Cimarron County, two (40677-78) netted 3 mi. S and 2 mi. E Kenton on 18 September 1983 and six (43182-87) captured 1.5 mi. S and 3 mi. E Kenton on 12 October 1985.

Lasiurus borealis (Müller, 1776).—The eastern red bat, now regarded as a monotypic species (Baker et al., 1988), is known from most Oklahoma counties, but has been recorded from the Panhandle only on the basis of a single specimen from Texas County (Mares, 1990:412). Two females (43188-89) were captured in mist nets on 12 October 1985 in Tesesquite Canyon, 1.5 mi. S and 3 mi. E Kenton. Likely these were migrants, but a few female red bats rear young in summer in the Texas Panhandle (Jones et al., 1988).

Lasiurus cinereus cinereus (Palisot de Beauvois, 1796).—The hoary bat has been recorded from all three counties of the Oklahoma Panhandle (Glass, 1990:134), but from a total of only four specimens. Probably the species does not reside in the region, but rather migrates through it seasonally. In any event, our material contains 20 specimens, 18 (including two females) taken in September and two, both males, netted in October as follows: 1.5 mi. S, 3 mi. E Kenton, 2 (43190-91); 3 mi. S, 2 mi. E Kenton, 12 (39707-12, 39714-16, 39719-20, 40679); 4 mi. S, 2 mi. E Kenton, 2 (40777-78); 4.3-4.5 mi. S, 2.4 mi. E Kenton, 4 (39713, 39717-18, 56070).

Antrozous pallidus bunkeri Hibbard, 1934.—Specimens from Cimarron County and also from Harmon County, Oklahoma, were reported previously by Manning et al. (1988). We follow them in use of the subspecific name *bunkeri* for all pallid bats from Oklahoma.

Tadarida brasiliensis mexicana (Saussure, 1860).—The Brazilian free-tailed bat has been recorded from numerous localities in southern and western Oklahoma, including several from Cimarron County. We have examined seven specimens (both sexes) all collected in September 1983, as follows: 3 mi. S, 2 mi. E Kenton, 5 (39738-42); 4.4 mi. S, 2.4 mi. E

Kenton, 1 (40788); 4.5 mi. S, 2.4 mi. E Kenton, 1 (56074). It may be noteworthy that no *T. brasiliensis* were taken in the two October visits to Cimarron County.

Nyctinomops macrotis (Gray, 1839).—Only three specimens of this large, free-tailed species have been reported previously from Oklahoma—two from Texas County and one from Oklahoma County (Glass, 1990:151). A female with incompletely fused phalangeal epiphyses and thus a young of the year (40681), likely a migrant, was netted 3 mi. S and 2 mi. E Kenton on 18 September 1983. External measurements: total length, 128; length of tail, 50; length of hind foot, 11; length of ear, 18; length of forearm, 59.5.

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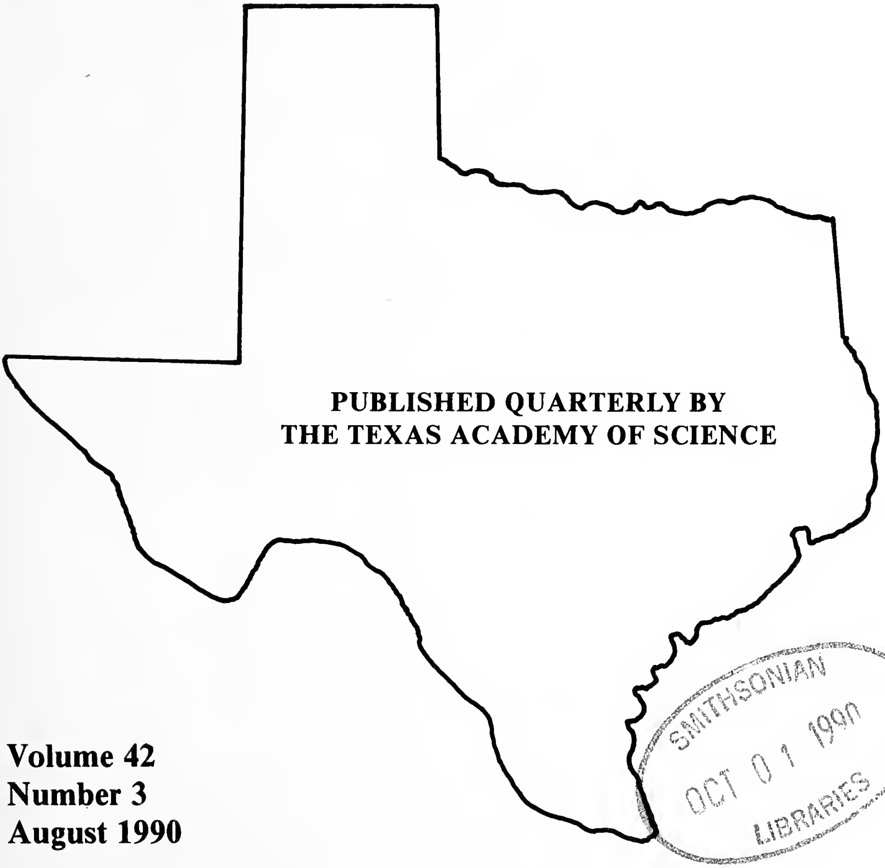

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OPTIMIZATION BY SIMULATED ANNEALING: EXPERIMENTAL APPLICATION TO QUADRATIC ASSIGNMENT PROBLEMS

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Abstract.—Recent research has revealed a useful connection between the behavior of physical systems in low energy states and the processes of combinatorial optimization in large complex systems. This analogy has been exploited with considerable success in the solution of certain optimization problems. This new perspective on traditional iterative optimization is discussed, and implementations are presented that have been applied to several quadratic assignment problems. Computational results are reported, and suggestions are given for future work on simulated annealing heuristics for quadratic programming problems. *Key words*: combinatorial optimization; simulated annealing; assignment problems; quadratic integer programming.

Within the field of combinatorial optimization, many important problems have been shown to belong to a class currently characterized as computationally intractable. Therefore, considerable research effort is being directed toward the discovery of ways to improve the speed with which suboptimal heuristic methods operate and the quality of the solutions that they produce. Conspicuously innovative progress seems to have been made recently by Kirkpatrick et al. (1983), who had the insight to perceive an analogy between the behavior of a physical substance in low energy states and the nature of the iterative improvement that can be made in a large and complex system that is in a nearly optimal configuration. States of low energy in the physical system are viewed as being analogous to the nearly optimum configuration (measured by a low objective function value) in a minimization problem.

In statistical mechanics, standard methods (Metropolis et al., 1953) are available that are used to model the evolution of a physical system through a series of slowly decreasing temperatures (an annealing process) into a state of high order and low energy. During the annealing process, temperature is reduced slowly in order to maintain system equilibrium with respect to temperature. Both positive and negative energy fluctuations are admitted, in contrast to a rapid quenching that would result in a disordered system.

The analogy in combinatorial optimization is just a variation on conventional iterative improvement methods, which begin with an initial feasible solution, repeatedly generate and consider changes in the current configuration, and accept only those that improve the objective function. Iterative improvement methods characteristically converge rapidly to a local optimum by using heuristic techniques that may fail to discover the global optimum. In anticipation of locating a more global optimum, simulated annealing methods probabilistically accept configurations that temporarily deteriorate the quality of the system. The acceptance probability exp $(-\Delta F/kT)$ is computed from ΔF (the change in the objective function) and a temperature indication (replaced by a simpler parameter Θ because physical temperature has no absolute meaning in the optimization case). As the temperature is appropriately reduced (this is referred to as the "annealing schedule"), fewer nonimproving moves are accepted; thus a coarse global search evolves into a fine local search for optimality, and the probabilistic "jumps" provide an escape from nonglobal optima. We were specifically interested in the application of simulated annealing heuristics to certain zero-one quadratic programming problems.

In the next section of this paper, the basis for simulated annealing in statistical mechanics, and the analogy to combinatorial optimization are described. Next, several quadratic assignment problems to which we have applied simulated annealing heuristics are defined, followed by a description of our heuristic methods and the results of computational experimentation. The final section summarizes our work and outlines several areas for further study.

SIMULATED ANNEALING IN STATISTICAL MECHANICS AND THE ANALOGY TO COMBINATORIAL OPTIMIZATION

The correspondence between the statistical properties of combinatorial optimization and the statistical mechanical properties of physical systems was first perceived by Kirkpatrick (1984) at IBM Thomas J. Watson Research Center. We briefly describe this analogy, and cite preliminary implementation guidelines found in the literature.

Annealing in Statistical Mechanics

All physical systems are composed of large numbers of atoms, and only the most probable behavior of the system is observed when it is in thermal equilibrium at a constant temperature. This behavior is characterized by the nature of the fluctuations of atoms or molecules about their mean positions within the system.

In order to observe different behaviors of a system, atoms are allowed to change their atomic positions by altering the temperature and letting the system attain thermal equilibrium again. The most stable state of a system is the state associated with the lowest energy level. Under the assumption that atoms with configurations close to ground states dominate the properties of the system at low temperature, it is desirable to lower the temperature of the system in search of the ground state.

The process of lowering temperature slowly so that thermal equilibrium always is maintained is termed an annealing process. A mathematical

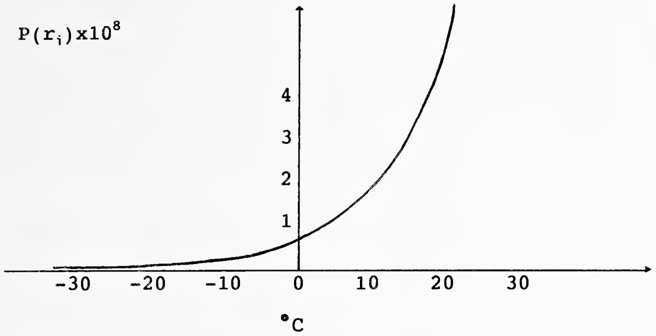


FIGURE 1. Boltzmann distribution.

model describes a system in a stable state (that is, the most probable state with respect to temperature). Each configuration of the system is defined by the Boltzmann probability factor $P(r_i)=\exp\{-E(r_i)/kT\}$, where each configuration is defined by the set of atomic positions r_i, and $P(r_i)$ is the probability of a configuration r_i, $E(r_i)$ is the energy (in joules) of the system, K_B is the Boltzmann constant (in joules/°K), and T is temperature in degrees Kelvin.

As is shown by the nature of the curve in Figure 1, as T approaches a low value, the probability of occurrence of a new configuration approaches zero because the system is already in a nearly stable state. At extremely low temperature (that is, when the system is in either liquid or solid state), the absolute value of the exponent becomes large and hence $P(r_i)$ approaches 0.

Our interest in annealing is motivated by an analogy between the annealing process and the processes of combinatorial optimization. At this point, we consider methods of studying annealing in statistical mechanics, and will subsequently show how these methods apply to combinatorial optimization.

Metropolis et al. (1953) developed an algorithm that is used to provide an efficient simulation of a collection of atoms in equilibrium at a given temperature. In each step of this algorithm, an atom is given a small displacement. Before a displacement is admitted, initial energy E_i of the system is noted, and final energy E_f of the system is measured after the displacement. The difference between these two energy states can be calculated as $\Delta E=E_f - E_i$. If E_f is less than E_i, then the system has moved from a high energy level (state) to one at low energy level, which is obviously more stable than the previous one and hence this displacement is "accepted," and the system now assumes this new configuration. In short, when $\Delta E \leq 0$ (when $E_f \leq E_i$) the displacement is accepted. But if $\Delta E > 0$, the new configuration may be rejected and the current (more stable) configuration may be maintained. (At any given temperature, the simulation must proceed long enough for the system to reach a steady state.) The acceptance criterion is based on the Boltzmann distribution. Thus the probability that the configuration will be accepted when $\Delta E > 0$ is $P(\Delta E)=\exp\{-\Delta E/K_BT\}$.

Simulated Annealing and Combinatorial Optimization

We now restate the simulated annealing procedure, using terminology that is applicable to combinatorial optimization. In general, we generate a sequence of classes of configurations (where, by "configuration," we mean some assignment of integer values to the decision variables). Within each class, a parameter Θ determines the magnitude of objective function value fluctuations. Each class is asymptotically distributed as a Boltzmann distribution, and the process of determining this distribution for any Θ is referred to as "equilibration."

Algorithm. Generate a new configuration; calculate $\Delta F=\text{obj } F_{\text{new}} - \text{obj } F_{\text{current}}$; if $\Delta F \leq 0$ then accept new configuration unconditionally; if $\Delta F > 0$ then accept new configuration only with probability $\exp(-\Delta F/\Theta)$.

It can be observed that large values of Θ imply a higher acceptance ratio (and thus a more global search), whereas small values of Θ imply a lower acceptance ratio (resulting in a more local search). A value $\Theta = 0$ reduces the simulated annealing optimization technique to the method of conventional iterative improvement.

Heat capacity (or specific heat) plays a significant role in the process of annealing. Inasmuch as specific heat is defined as the rate of change of the energy of the system with respect to temperature, it is a good measure of change in the state of order of a system. A high specific heat value can be used in the optimization context to indicate that freezing has begun and hence that successively slower cooling is required in order to avoid instability (associated with nonglobal optima in combinatorial problems).

Implementation guidelines for optimization by simulated annealing are scarce. In particular, it is generally left to the experimenter to determine the initial value of the acceptance parameter Θ, the sequence of Θ values, the number of different values of Θ, and the number of configurations to consider for each value of Θ. A probabilistic analysis (Anily and Federgruen, 1985) provides some insights into implementation. Convergence in distribution and convergence to the set of global optima with probability one is guaranteed if and only if the rate of convergence of Θ (to zero) is slower than $(K/\log K)$, where K is a problem-parameter-dependent constant.

Numerous implementation questions remain, and several of these will be discussed in the last section of this paper.

QUADRATIC ASSIGNMENT PROBLEMS

Quadratic assignment problems belong to a special class of mathematical programming problems in which the objective function contains products of boolean decision variables that measure interactions among the elements of large complex systems. Examples include problems of allocating software (tasks or files) among multiple processors in distributed systems where there is some communication between the software modules, and scheduling events over time periods wherein the interactions are manifest as conflicts between events that must not occupy the same time period. These applications are representative of the wide variety of resource-management problems (occurring in military, financial, and industrial systems), which can be solved by optimizing some quadratic function of many independent variables, subject to certain constraints.

In a distributed computing system, it is important to assign software to processors in ways that take advantage of the power and flexibility of the system. Distributed programs are characterized by the computational requirements of the software modules and the nature of the interactions among the modules. Software allocation models are aimed at matching these characteristics with the corresponding computational and communication capabilities of distributed computing networks.

In our first task allocation model, modules were assigned among nonidentical processors, but sequencing of task executions was not considered. Two kinds of costs were defined.

1. Each module has an execution cost that depends on the processor to which it is assigned. Let e_{ij} represent the cost of executing module i on processor j.

2. Any two modules that communicate during program execution incur a penalty if they are assigned to different processors. (It is assumed that the cost of such communication is zero when the reference is made between modules residing on the same processor.) Let the amount of communication between modules i and k be denoted by c_{ik}.

An optimal assignment is one that minimizes the sum of execution costs of the modules on the processors and the intermodule communication costs incurred when communicating modules are assigned to different processors. Thus the objective is to meet the conflicting goals of clustering tightly-coupled modules on the same processor while satisfying the generally diverse computational requirements of the modules that best may be served by assigning modules to different processors (Price and Krishnaprasad, 1984).

The problem can be formulated as a zero-one quadratic programming problem as follows.

Minimize

$$\sum_{i=1}^{m} \sum_{j=1}^{n} e_{ij}x_{ij} + \sum_{i=1}^{m} \sum_{k=1}^{m} \sum_{j=1}^{n} \sum_{l=1}^{n} c_{ik}d_{jl}x_{ij}x_{kl}$$

subject to the constraints

(c1) $x_{ij} = 0$ or 1 for $i=1,\ldots, m$, and $j=1,\ldots, n$,

(c2) $\sum_{i=1}^{m} s_i x_{ij} \leq p_j$ for $j=1,\ldots, n$ (limited memory at each processor),

(c3) $\sum_{j=1}^{n} x_{ij} = 1$ for all i (each module is assigned to exactly one processor),

where m is the number of software modules and n is the number of processors, and the decision variable $x_{ij} = 1$ means module i is assigned to processor j and otherwise $x_{ij} = 0$. Other problem parameters have the following interpretations: e_{ij}—cost of executing module i on processor j; c_{ik}—number of "units" of data (messages) sent from module i to module k; d_{jl}—cost of sending one "unit" of data over the data link from processor j to processor l ($=\infty$ if no link exists and $=0$ if $j=l$); s_i—size of module i (amount of code or data); p_j—buffer size at processor j.

In this set of test cases, we further assumed identical data links connecting every pair of processors, thus each nondiagonal element of the D matrix is equal to one.

In our second application, we considered a special case of the general task assignment problem in which the fully connected network is replaced by a nearest-neighbor interconnection pattern, all processors are identical, and the tasks are components of a finite element analysis (Bokhari, 1981). Thus the matrix E=0, and the matrix D displays a specialized banded structure. We further added the constraints

$$\sum_{i=1}^{m} x_{ij} \leq 1 \text{ for all } j = 1,\ldots, n$$

to specify that at most one task may be assigned to each processor (hence $m \leq n$).

Our third application, examination timetabling, can be modeled by the objective function above if the interaction matrix C is viewed as registering conflicts (Cole, 1964). Because conflicts occur when events are assigned to the same time period (whereas task communication costs were incurred when tasks were assigned to different processors), we negated the conflict measures and let $c_{ik} = -1$ denote that events i and k should not be assigned to the same time period (and $c_{ik} = 0$ otherwise). Because all conflicts carry the same weight (regardless of which time period is involved in the conflict), we allowed matrix D to be the same as for uniform, fully connected, processor networks.

Conventional methods for determining assignments of tasks to processors or events to time periods include exhaustive enumeration, implicit enumeration (branch and bound), constructive assignment (in which partial assignments are completed to yield feasible assignments) and iterative improvement (in which complete feasible assignments are repeatedly altered in ways that improve the objective function).

Exhaustive search to find an optimum is impractical for task allocation because an exponential number (n^m) of configurations must be examined. Implicit enumeration techniques may be designed to yield effective allocations, but they also may degenerate in the worst case into an exhaustive search. Constructive assignment methods (without backtracking) may be efficient but cannot in general guarantee optimal results. Iterative improvement methods operate by generating a sequence of possible changes in the allocation configuration and incorporating ("accepting") those changes that directly improve the objective function. Such methods have performed well in practice but tend to converge rapidly to a local optimum. Efficient heuristics that generate new configurations by making small changes in the present systems usually are not powerful enough to expose vastly different configurations having somewhat better quality. Such new configurations may be "inaccessible" via a given heuristic mechanism and in that case global optima never will be discovered.

Because of the various inadequacies of traditional methods, we applied simulated annealing optimization techniques to our three quadratic assignment problems. Results of computational experimentation are presented in the following section.

COMPUTATIONAL RESULTS

Implementations of the simulated annealing heuristic algorithms were developed in FORTRAN for Honeywell Level 66/DPS/B3 CP-6 system. For each application, we begin with an arbitrary initial assignment configuration. Our mechanism to generate "neighboring" configurations (to be accepted or rejected according to the Boltzmann criterion) is a variation of the well-known 2-opt heuristic (Lin and Kernighan, 1973). Given an initial feasible assignment, we looked for individual tasks (or events) that could be moved profitably. Finding none, we considered communicating (or conflicting) pairs that could be moved as a pair, or a separated pair that could be brought together.

We report on two instances of the software allocation problem to which we have applied simulated annealing. In one problem, $m = 7$ modules were assigned to $n = 5$ processors in one equilibration (with Θ

= 5) to obtain an optimal objective function value of 19. (Our traditional heuristic methods all fail to achieve this optimum.) In a second problem instance (m = 5 and n = 6), simulations were performed for Θ values 5, 3, 1, and .5. Most frequent objective function values were, for each Θ respectively, 26, 21, 18, and 18.

The distributions of objective function values in these two cases, for the various Θ values, are displayed in Figures 2A and 2B. The second case (shown in Fig. 2B) is actually more typical of the simulated annealing process.

Our second application problem represents a system for structural analysis of a ship radar tower (Bokhari, 1981). In the assignment of software for a finite element machine, we have m = 25 modules and n = 25 processors. The initial assignment objective was z = 61. Simulations were performed for Θ values 10, 5, 1, .5, .25, .125, and .0625. Results are illustrated in Figure 3 by means of a graphical display of the improvement of the objective function (with decreasing values of the acceptance parameter Θ). For each value of Θ, the curve shows the distribution of objective function values obtained. At the lowest acceptance parameter, an objective of 16 was obtained. A solution with z = 13 is known to exist; the optimal is unknown. In each class of 500 simulations, 1.2 seconds of computation time were required, for a total of 8.4 seconds.

In the time-tabling application, m = 34 examinations are to be scheduled into n = 7 time periods (Cole, 1964). In the initial assignment there are 28 conflicts (z = 28). Simulations were performed for Θ values 20, 10, 2, 1, .5, .25, .125, and .0625. The acceptance ratios and the most frequent solution for each value of the parameter Θ are shown in Figure 4. At the lowest acceptance parameter, an objective function = 1 was obtained. This is the optimal solution to this problem. Six seconds of computation time were required for each simulation of 500 configurations, for a total of 48 seconds. The implementations require $O(n^3)$ computational effort.

SUMMARY AND DIRECTIONS FOR FUTURE STUDY

We have described the analogy drawn between certain analytical techniques used in physics and optimization processes for combinatorial systems. In particular, we have applied simulated annealing techniques to quadratic programming problems in order to minimize various interaction costs among elements in a system (such as communication among software modules in multiprocessor computer systems and conflicts among events in timetabling applications.)

We have performed preliminary experimentation on several quadratic programming problems, with encouraging results. However, certain

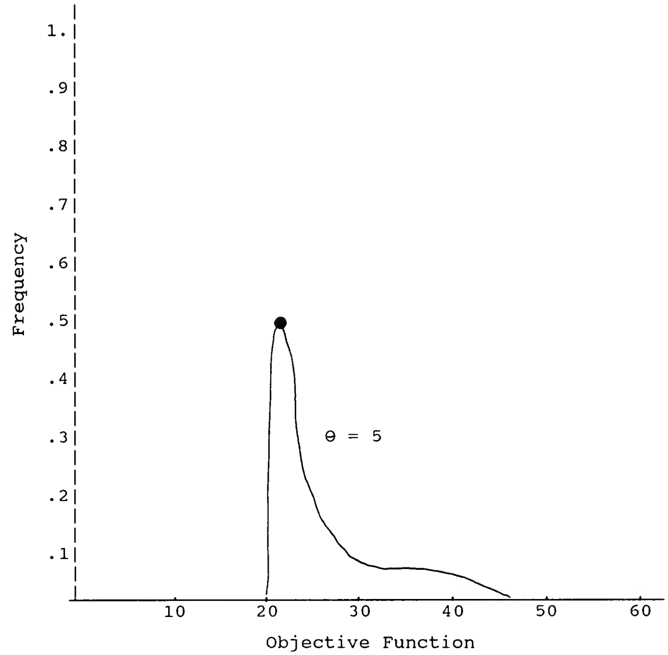


FIGURE 2A. Task allocations (m = 7 and n = 5).

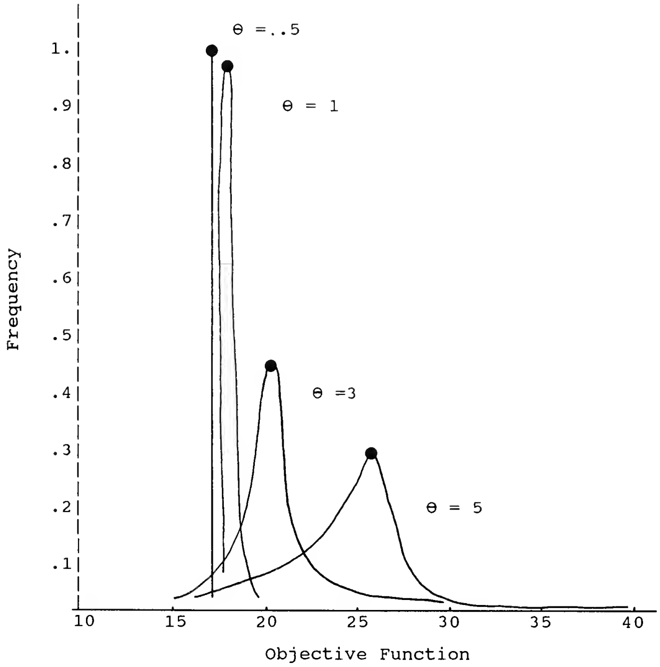
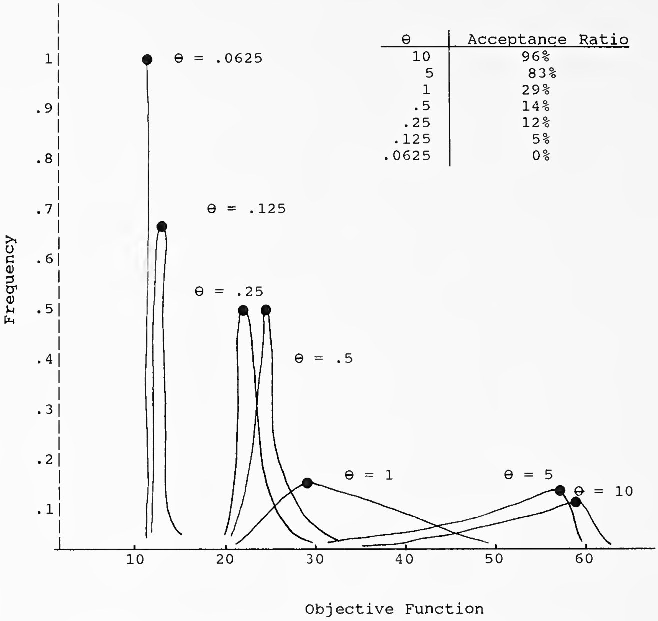


FIGURE 2B. Task allocation (m = 5 and n = 6).



θ	Acceptance Ratio
10	96%
5	83%
1	29%
.5	14%
.25	12%
.125	5%
.0625	0%

FIGURE 3. Finite element machine (m = 25 and n = 25).

aspects of the simulated annealing concept have not been mapped precisely into the domain of combinatorial optimization, thus general implementation guidelines remain ill-defined.

1. Annealing schedules are typically determined by trial and error or dynamically through real-time observations of the optimization process. It would be useful to develop either a fixed annealing schedule that is appropriate within certain classes of quadratic programming problems or a method for computing a schedule a priori from given problem parameters.

2. From each problem configuration, heuristic techniques are employed to generate new candidate configurations. Central to the simulated annealing concept is the requirement that new configurations be generated "randomly," but typical heuristic mechanisms by definition preclude the desired randomness. To give meaning to the "randomness" requirement, a statistical distribution on the set of all configurations must be defined. In support of this, it is appropriate to define two metrics—one to describe the distance between two configurations with respect to the actual number of reassignments (relocations), and another to define distance with respect to the (objective function) values of two configurations. Insights into this task were provided by Hammer and Rubin (1970), where distances were defined for purposes of establishing the quality of upper and lower bounds. With these tools, it is then

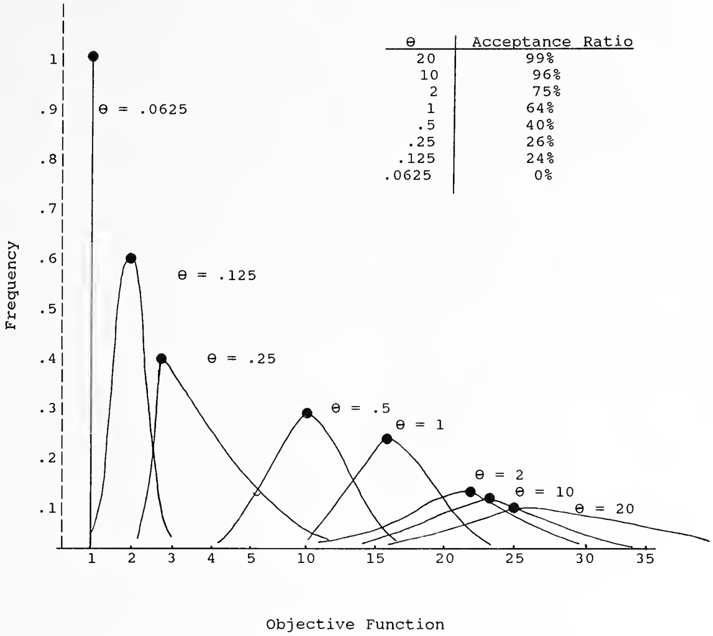


FIGURE 4. Timetabling (m = 34 and n = 7).

possible to describe to what extent new configurations ("near" the current one) are being generated randomly. If it happens that these distances actually predict the probability of a transition from one configuration to another, then the entire simulated annealing procedure can be treated as a Markov process and analyzed accordingly.

3. At each "temperature," some large number of different configurations must be generated in order to determine the most probable (most frequent) configuration for that temperature. The suggestion (Kirkpatrick, 1984) of running at each temperature until every movable object has been moved some fixed number of times is arbitrary and apparently without statistical foundation. We have outlined a straight-forward statistical analysis to determine the smallest "sample size" (number of new configurations to generate) in estimating the most representative configuration for a given temperature. The criterion for evaluating the quality of this estimate is dependent on the type of problem being solved. It would be useful to establish such a criterion for the class of quadratic programming problems and use this to determine the number of configurations to generate. (This criterion has a profound effect on the amount of computation time required for optimization by simulated annealing.)

An investigation and understanding of these questions will provide a more predictable optimization process, with a behavior that can be characterized with greater certainty.

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DESCRIPTION OF A NEW SUBSPECIES OF *BOGERTOPHIS SUBOCULARIS* (BROWN) FROM NORTHERN MEXICO (SERPENTES: COLUBRIDAE)

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Abstract.—Study of geographic variation in features of scutellation and pattern prompts recognition of a new subspecies of *Bogertophis subocularis.* Pattern features are most distinctive. The new subspecies, confined to México, occupies the southwesternmost part of the range of the species in the state of Durango. *Key words*: Reptilia; Serpentes; Colubridae; *Bogertophis subocularis*; morphological variation; subspecies.

In this report, and on the basis of precedent only, I follow Dowling and Price (1988), who proposed the new genus *Bogertophis* for inclusion of the two species *Coluber subocularis* Brown, 1901, and *C. rosaliae* Mocquard, 1899 (both formerly species of *Elaphe*). *C. subocularis* was designated as type species of *Bogertophis.*

In a previous study of variation in a large sample of *Bogertophis subocularis* from the Franklin Mountains, El Paso County, Texas (Webb and Ferguson, 1986), attention was directed to a specimen from the Mexican state of Durango, figured in that paper, that had a peculiar dorsal pattern. Study of Mexican specimens of *B. subocularis* indicates consistent geographic differences in pattern and minor differences in scutellation when compared with other specimens from throughout the range of the species. The population of *B. subocularis* in Durango is described as a new subspecies. Dowling (1957) described the species in detail, and Worthington (1980) provided a synoptic review of the species.

Methods

Scutellation data recorded for comparative purposes include counts of ventrals (Dowling method, 1951), subcaudals (including terminal scale at tip), dorsals (counted about one head length posterior to head, at approximate midbody, and just anterior to anal plate), supralabials (penultimate largest), anterior temporals, and lorilabials. Anterior temporals include all scales between supralabials and parietals that touch postoculars; the lateralmost part of parietal often has an incomplete seam suggesting an additional uppermost anterior temporal. Lorilabial scales include those subtending and entering orbit (suboculars), any anteriormost scales (not entering orbit) wedged between preocular-loreal and supralabials (may be staggered, or two scales one above the other), and occasionally a posteriormost scale (not entering orbit) that touches subocular but not the lowermost postocular and is wedged between the lowermost anterior temporal and supralabial. The size and shape of these posteriormost scales is variable with some small, roundish scales suggesting posteriormost lorilabials; if scale touches lowermost postocular (usually two postoculars), it is regarded as the lowermost anterior temporal (any other scale behind is disregarded). Posterior lorilabials are usually absent. Thus, total numbers of lorilabials are fewer than recorded by previous authors. Lorilabial counts may be expressed in text as 5(2-3-0), which indicates total (anteriormost-subocular-posteriormost) number of lorilabials.

Pattern features quantified include width of anteriormost parts of black paravertebral neck stripes (number of longitudinal scale rows), degree of constriction of body blotches on posterior fourth of body compared to length of pale interspaces (counts of scales in vertebral row), and numbers of body and tail blotches. Width of black neck stripes may be expressed in text as 1/2-1-1/2, which indicates black covering one complete longitudinal scale row and halves of each adjacent row. Counts of blotches include the anteriormost paired, slight expansions on neck, primarily laterad blotches that transcend vertebral area, and adjacent dorsal blotches that are continuous laterally.

I have not attempted an examination of all material from the United States (Texas and New Mexico), but have examined most specimens from México. Localities of specimens examined are listed in Appendix I.

Bogertophis subocularis amplinotus, new subspecies

Holotype

UIMNH 62817; from 90.5 road miles or 145.7 kilometers north (via Highway 45) of Ciudad Durango (=about 10.5 road miles or 17 kilometers south Rodeo), Durango, México; obtained by Rudolph G. Arndt and Wade Sherbrooke on 26 June 1963.

Description of holotype

Female, about 790 (body) + 140 (tail) mm, with 269 + 3 ventrals, 75 subcaudals, 33-35-25 dorsal scale rows, 12-12 supralabials, 4-4 anterior temporals, and 5(2-3-0)/5(2-3-0) lorilabials. Blotches number 23 on body, 10 on tail. Anteriormost parts of black paravertebral neck stripes are of uniform width, with each stripe occupying 1/2-2-1/2 scale rows. Vertebral parts of posterior dorsal body blotches are longer (narrowest constriction covering about eight scales) than that of pale interspaces (about four scales). Lateral extensions of body blotches may reach ventral scales; these markings and the intercalary lateral blotches are dark and enlarged. The belly has only a few dark dots posteriorly; underside of tail is pigmented with dark patches on each subcaudal, except for a midventral dark line toward tip of tail. The holotype is illustrated in Webb and Ferguson (1988:120, fig. 1).

Diagnosis

A subspecies of *Bogertophis subocularis* distinguished from *B. s. subocularis* (features in parenthesis) by the following combination of characters: 1) anteriormost parts of black paravertebral neck stripes (extending posteriorly about one and one-half head-lengths) of uniform width and occupying at least 1/2-2-1/2 scale rows (black stripes usually not of uniform width, consisting of alternating wide and narrow segments with narrowest segments not exceeding 1/2-1-1/2 scale rows); 2) primary body blotches on posterior fourth of body only slightly biconcave with length of vertebral constrictions usually longer than vertebral length of pale interspaces (vertebral parts of interspaces usually much longer than those of blotches—Table 1); 3) markings on side of body enlarged and dark (markings usually pale, indistinct), differences in pattern are

TABLE 1. Variation in number of ventrals, subcaudals, dorsal scale rows at midbody, total supralabials and lorilabials, body and tail blotches, and vertebral length (scales) of body blotches and interspaces in *Bogertophis subocularis amplinotus*, intergrades between subspecies, and two samples of *B. s. subocularis*. Data include sample size, mean plus or minus one standard error of the mean, one standard deviation of the mean, and range of variation.

		B. s. amplinotus x *B. s. subocularis*	*B. s. subocularis*	
Character	*B. s. amplinotus*		New Mexico-Texas	Chihuahua
Ventrals				
Males	1,270	10,270.2 ± 1.19, 3.77, 265-278	40,270.1 ± 0.57, 3.60, 263-277	11,263.0 ± 0.45, 1.48, 261-266
Females	7,272.3 ± 1.91, 5.06, 268-282	9,271.8 ± 1.47, 4.41, 266-279	33,269.3 ± 0.73, 4.17, 260-279	5,264.2 ± 1.16, 2.59, 261-268
Total	8,273.3 ± 1.82, 5.15, 268-282	20,271.0 ± 0.88, 3.95, 265-279	74,269.7 ± 0.45, 3.89, 260-279	16,263.4 ± 0.47, 1.89, 261-268
Subcaudals				
Males	1,75	9,78.1 ± 0.61, 1.83, 75-80	37,73.7 ± 0.38, 2.30, 69-81	9,75.0 ± 0.41, 1.22, 73-77
Females	7,75.4 ± 0.57, 1.51, 73-78	6,76.0 ± 0.73, 1.79, 73-78	26,71.5 ± 0.58, 2.94, 65-78	5,73.2 ± 1.56, 3.49, 67-75
Total	8,75.4 ± 0.50, 1.41, 73-78	15,77.3 ± 0.53, 2.05, 73-80	64,72.8 ± 0.35, 2.78, 65-81	14,74.4 ± 0.63, 2.34, 67-77
Dorsal scales	9,35.1 ± 0.31, 0.93, 33-36	20,33.8 ± 0.30, 1.33, 31-35	73,33.0 ± 0.11, 0.98, 31-35	16,33.5 ± 0.30, 1.21, 31-35
Supralabials	9,22.7 ± 0.40, 1.20, 21-24	19,21.4 ± 0.26, 1.12, 20-24	72,21.1 ± 0.12, 1.01, 20-24	16,20.3 ± 0.25, 1.01, 18-22
Lorilabials	9,9.1 ± 0.73, 2.20, 6-12	19,7.1 ± 0.35, 1.54, 4-9	71,7.3 ± 0.14, 1.19, 4-10	14,6.6 ± 0.44, 1.65, 4-9
Blotches				
Body	8,22.5 ± 0.38, 1.07, 21-24	20,23.6 ± 0.43, 1.90, 21-28	72,24.9 ± 0.18, 1.56, 22-28	16,24.5 ± 0.43, 1.71, 21-28
Tail	8,10.3 ± 0.37, 1.04, 9-12	16,9.4 ± 0.24, 0.96, 8-11	61,8.6 ± 0.10, 0.78, 7-11	15,8.6 ± 0.24, 0.91, 7-10
Length (scales)				
Body blotches	9,6.5 ± 0.44, 1.33, 5-9	19,4.6 ± 0.21, 0.90, 3-6	72,3.7 ± 0.06, 0.52, 3-5	15,3.9 ± 0.18, 0.70, 3-5
Interspaces	9,4.2 ± 0.15, 0.44, 4-5	19,6.1 ± 0.23, 0.99, 5-8	72,7.3 ± 0.10, 0.82, 6-9	15,7.1 ± 0.22, 0.83, 6-9

expressed in Figures 1-3, and in more detail in the section on comparisons; 4) more subcaudals, dorsal scale rows at midbody, supralabials, lorilabials, and tail blotches, but fewer body blotches (see comparisons and Table 1).

Description and Variation

Pattern.—Dorsally, the body and head are yellowish or buff to yellow-gray with the head patternless. The venter is usually immaculate but small dark spots may occur on posterior two-thirds of belly, more concentrated posteriorly (KU 174802); dark lateral blotches may encroach onto lateral ends of ventral scales. The underside of tail, immaculate in smallest specimens (UMML 5525, UTEP 9596), otherwise has extensive dark pigment.

The anteriormost parts of black paravertebral neck stripes, extending posteriorly for distance equal to about one and one-half head lengths, are usually of uniform width, occupying 1/2-2-1/2 scale rows; some scales of adjacent rows are almost entirely black. The anterior neck striping of AMNH 96622 is unusual in having paired, slightly widened neck segments (covering three, almost four, complete rows and half of each adjacent row) and intervening narrower segments occupying 1/2-2-1/2 scale rows; the narrowest segments are never this wide in *B. s. subocularis* (see comparisons). The width of these black neck stripes in *B. s. amplinotus* may narrow to 1/2-1-1/2 scale rows just before the first dorsal blotch (UTEP 9596). The anterior black neck striping of one Durangan specimen of *B. s. amplinotus* (UMML 5525) is not unlike that of *B. s. subocularis*.

Primary dorsal body blotches are only slightly biconcave (not prominently H-shaped); vertebral constrictions of these blotches (posterior part of the body) may be about the same length as (UMML 5525, UTA 7033), but are usually longer than, the vertebral length of the intervening pale interspaces. Variational data in number of scales occupied by vertebral length of blotches and interspaces, and in number of body and and tail blotches are in Table 1. Posterior dorsal blotches are often irregular or asymmetrical in having the lateral elongate parts of each blotch staggered. Vertebral parts of interspaces may have small dark marks (UMML 5525). Scales of vertebral parts of blotches are pale with dark edges, whereas scales of the longitudinally elongate lateral parts of blotches are usually completely dark-pigmented. Patches of scales in the center of the vertebral parts of some blotches are variably devoid of pigment (pale spots within each blotch, MCZ 146391). Posterior body (and tail) blotches have lateral extensions (often triangular-shaped) that may reach ventral scales; scales of these and intercalary lateral blotches overall are dark, enlarged (some triangular), and well defined.

Scutellation.—Variational data for numbers of ventrals, subcaudals, dorsal scale rows at midbody, supralabials, and lorilabials are in Table 1. Preoculars are usually 1-1 and postoculars 2-2. Dorsal scale row combinations varied from 31-33-23 to 35-35-25 with the most frequent counts 33 anteriorly ($\bar{x}$ 33.0, 31-35, $N = 8$), 35 at midbody (Table 1), and 23 or 25 posteriorly ($\bar{x}$ 24.0, 23-25, $N = 9$). Supralabial scale combinations varied in number from 10-11 (in two), 10-12 (in one), 11-12 (in three), and 12-12 (in three of nine). Lorilabial scale combinations (one side of head) varied from 6(3-2-1) and 6(3-3-0) to 3(1-2-0) and 3(0-3-0) with the most frequent combination of counts 5(2-3-0) in eight of 18; suboculars usually number three (78 percent) instead of two (22 percent), and if only two suboculars the scales are not separated by one supralabial entering orbit (as occurs frequently in *B. s. subocularis*). Anterior temporal combinations varied from 3-3 to 4-5 with the most frequent counts 3-4 and 4-4, respectively, in six and nine specimens; the mean number of these scales on one side of head is 3.8 (3-5, $N = 18$), or on both sides of head is 7.6 (6-9, $N = 9$).

Etymology

The subspecific name combines two Latin terms—*amplio* (enlarge, expand, widen) and *nota* (mark) in allusion to the pattern of larger body blotches than in *B. s. subocularis*.

TICKS

The host-specific tick *Aponomma elaphense* (see Keirans and Degenhardt, 1985, and references therein) occurred on five Durangan specimens of *B. s. amplinotus*: UMML 5525—male, about 513 (body) + 94 (tail) mm; ticks of varying sizes, extending from fourth and fifth dorsal scale rows to lateral ends of ventrals on middle third of body; 45 ticks on right side, 44 on left side (as many as two ticks under one scale). AMNH 96622—female, about 630 + 113 mm; only two ticks (right side) of moderate to large size attached at lateral ends of ventral scales at about midbody (ventrals 135 and 141). UTEP 9596—female, 343 + 60 mm; only one small tick (left side) attached between lateralmost ends of ventrals 81 and 82. UIMNH 62817—female, about 790 + 140 mm; four ticks (two large, two small, all right side) embedded under scales of first dorsal scale row (opposite ventrals 106 and 137) and lateral ends of ventral scales 139 and 144. MCZ 146391—female, about 1095 + 185 mm; ticks of varying sizes; right side with eight between ventrals 94 to 104 attached between lateral ends of ventrals (three), or under scales of first (four) or second (one) dorsal row, and with one tick posteriorly under lateral end of ventral 143; left side with 30 ticks between ventrals 123 to 155, all under lateral ends of ventral scales except one under scales of first dorsal scale row; as many as two ticks under one scale ($N = 8$).

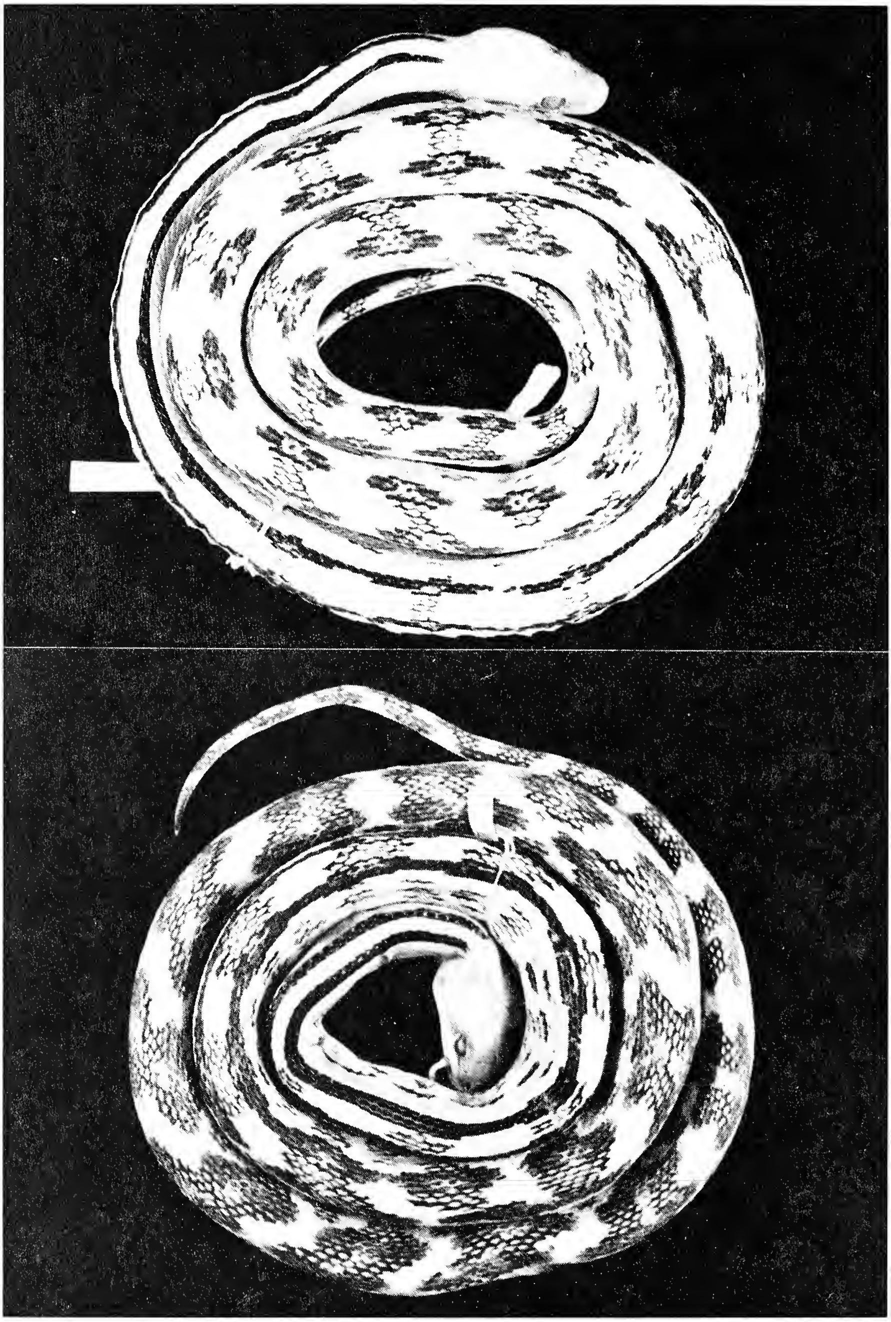

FIGURE 1. *Bogertophis subocularis subocularis* (above, TCWC 44005, Chihuahua) and *B. s. amplinotus* (below, KU 174802, Durango) showing differences in pattern.

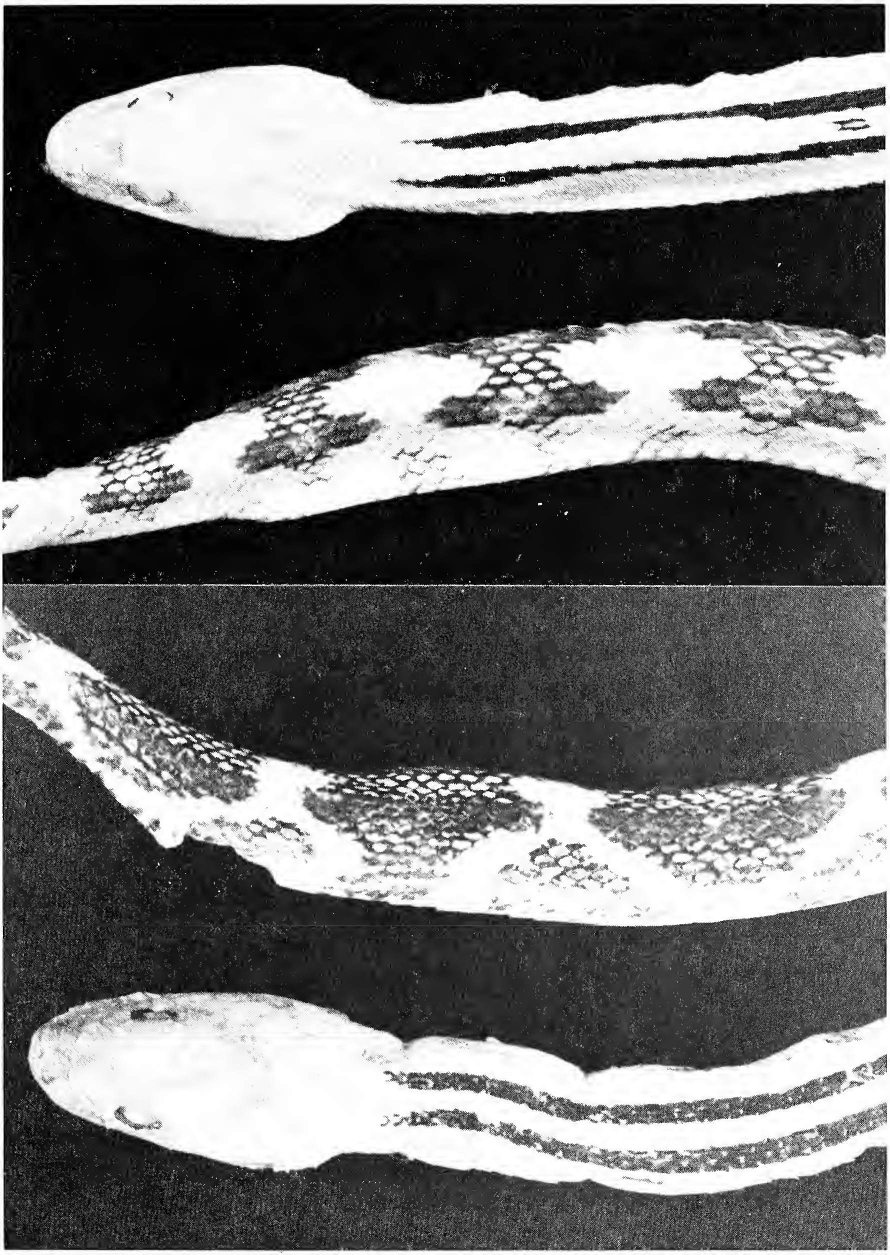

FIGURE 2. Black striping on neck, and blotching on posterior part of body and proximal part of tail (right side) of *Bogertophis subocularis subocularis* (above, UTEP 1825, Texas) and *B. s. amplinotus* (below, MSUM 2543, Durango) showing differences in pattern.

COMPARISONS

Variation in salient features of pattern and scutellation of *Bogertophis subocularis subocularis* is compared with that of *B. s. amplinotus*. Pattern differences, recognizable in both young and adults, are compared in Figures 1-3.

Black neck stripes.—In *Bogertophis subocularis subocularis*, each black paravertebral neck stripe has alternating wide (anteriormost) and narrow segments (usually two of each, prior to third expanded blotchlike segment with vertebral dark marks). Each expanded or widened segment usually covers 1/2-2-1/2 scale rows, whereas the narrowest intervening segments that often vary in width occupy either 1/2-1-1/2 or only 1/2-0-1/2 scale rows; occasionally this narrow segment is absent. The width of these narrow segments may vary in the same neck stripe. The wide and narrow segments are generally of corresponding length and position on each neck stripe, but lengths of each opposing segment may be variable. All opposing widened neck segments may have interconnecting pigment forming dorsal blotches (UTEP 2975). The anteriormost widened segment may cover only 1/2-1-1/2 scales on one (CM 59926, 61792) or both stripes (CM 59920, 59923); these opposing, anteriormost widened segments may be absent, with each stripe having lengthy segments of uniform width (1/2-1-1/2, CM 59918, 59922).

In *B. s. amplinotus*, alternating wide and narrow parts of the black neck stripes are usually absent. Stripes are wide and of uniform width (1/2-2-1/2) at least for a distance equal to about one and one-half head lengths; width of neck stripes may narrow to 1/2-1-1/2 for a short distance prior to first dorsal blotch. If widened segments are present (AMNH 96622), the narrowest part of black stripe is 1/2-2-1/2 (narrowest segment never this wide in *B. s. subocularis*).

Body pattern.—In *B. s. subocularis*, the primary dorsal body blotches on posterior fourth of body are usually rather prominently H-shaped with vertebral constrictions of blotches much shorter (three to five scales) than the longer vertebral parts of pale interspaces (six to nine scales—Table 1). Occasional specimens have only slightly biconcave blotches with the narrowest parts of the blotches about subequal in length to that of interspaces (for example, UTEP 3057, Presidio County, Texas; UTEP 10579, Terrell County, Texas). Also, the lateral black elongate parts of blotches have pale centers (opposite vertebral part of blotch), especially contrasting in juveniles (Fig. 3). Markings on side of body (vertical extensions of dorsal body blotches and intercalary blotches) are of varying distinctness, size, and configuration. Dorsal blotch extensions, usually broken, may reach ventral scales. All of these lateral body markings are usually indistinct or almost absent, with scales having little pigment and only partly dark, narrow margins.

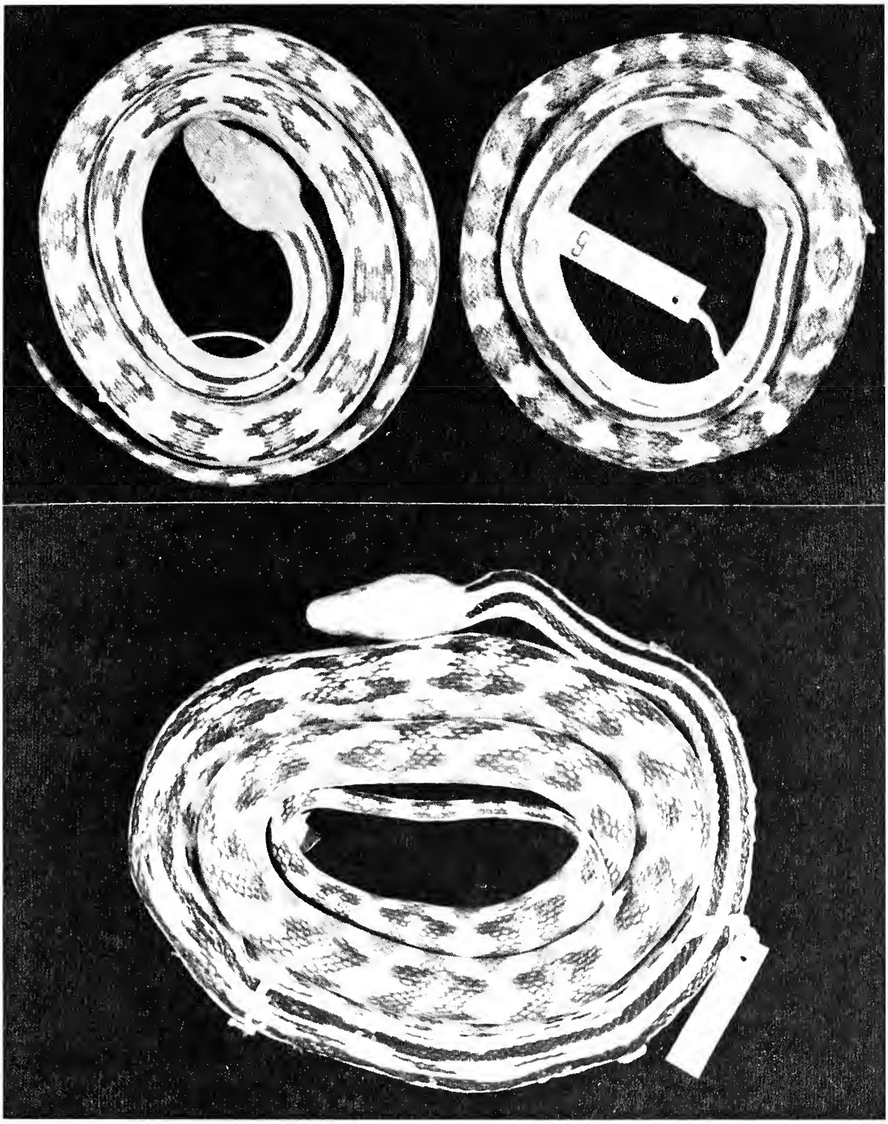

FIGURE 3. Above, juveniles of *Bogertophis subocularis* (left, *B. s. subocularis*, UTEP 11485, SVL 381 mm, Texas; right, *B. s. amplinotus*, UTEP 9596, SVL 343 mm, Durango) showing differences in pattern. Below, presumed intergrade specimen from Coahuila (CM 59924).

In *B. s. amplinotus*, the large posterior body blotches are relatively close together and only slightly biconcave with the length of the vertebral constriction of blotches about the same length as, but usually longer (five to nine scales) than, the maximal vertebral length of the pale interspaces (four or five scales—Table 1). The pale centers of the black lateral parts of dorsal blotches are indistinct. Markings on side of body are enlarged, dark, and with distinct borders. The vertical blotch extensions may taper to ventral scales forming inverted triangles. Intercalary blotches also may form large opposing triangular marks. Scales of these lateral markings generally are more uniformly pigmented and darker than those of *B. s. subocularis*.

Numbers of body and tail blotches differ between subspecies (Table 1). *B. s. subocularis* has more body blotches ($\bar{x}$ 24.9) and fewer tail blotches ($\bar{x}$ 8.6) than *B. s. amplinotus* ($\bar{x}$ 22.5 and 10.3).

Scutellation.—Chihuahuan specimens of *B. s. subocularis* are peculiar in having low numbers of ventral scales ($\bar{x}$ 263.4) and are treated separately (Table 1). The comparisons below (single values = means) are based on data derived from characters of the New Mexico-Texas sample of *B. s. subocularis*. Characters of diagnostic value (nonoverlap of two standard errors of means) include number of total subcaudals, dorsal scales at midbody, supralabials, and lorilabials (Table 1). Values for all characters are higher in *B. s. amplinotus* than in *B. s. subocularis*.

The number of ventrals (272.3) and subcaudals (75.4) in (at least) females (only one male) of *B. s. amplinotus* is higher than in females of *B. s. subocularis* (269.3 and 71.5). The number of dorsal scale rows at midbody is higher in *B. s. amplinotus* (35.1) than in *B. s. subocularis* (33.0); numbers of scale rows anteriorly and posteriorly seem not to differ between taxa. There are more supralabials and lorilabials in *B. s. amplinotus* than in *B. s. subocularis*. Differences are most pronounced when comparing the total number of scales on both sides of the head for both supralabials (22.7 in *B. s. amplinotus*, 21.1 in *B. s. subocularis*) and lorilabials (9.1 in *B. s. amplinotus*, 7.3 in *B. s. subocularis*). Data utilizing counts on one side of head also showcase the higher numbers of supralabials in *B. s. amplinotus* ($\bar{x}$ 11.4, 10-12, $N = 18$) than in *B. s. subocularis* ($\bar{x}$ 10.6, 10-12, $N = 146$). Differences in number of lorilabials is reflected in the greater number of anterior lorilabials in *B. s. amplinotus* ($\bar{x}$ 1.5, 0-3, $N = 18$, one side of head) than in *B. s. subocularis* ($\bar{x}$ 0.8, 0-2, $N = 144$); numbers of suboculars (two or three) and posterior lorilabials (usually none, rarely one) seem not to differ between taxa.

Distribution and Intergradation

Distribution

Bogertophis subocularis amplinotus occupies the southwesternmost part of the range of the species in the Mexican state of Durango (Fig. 5). All localities in Durango are west of the Río Aguanaval and most are south of the Río Nazas, and are associated with dissected terrain of dry rocky hills and low mountains. Specimens are from along either Highway 45 a short distance south of Rodeo, or Highway 40-49 between Lerdo

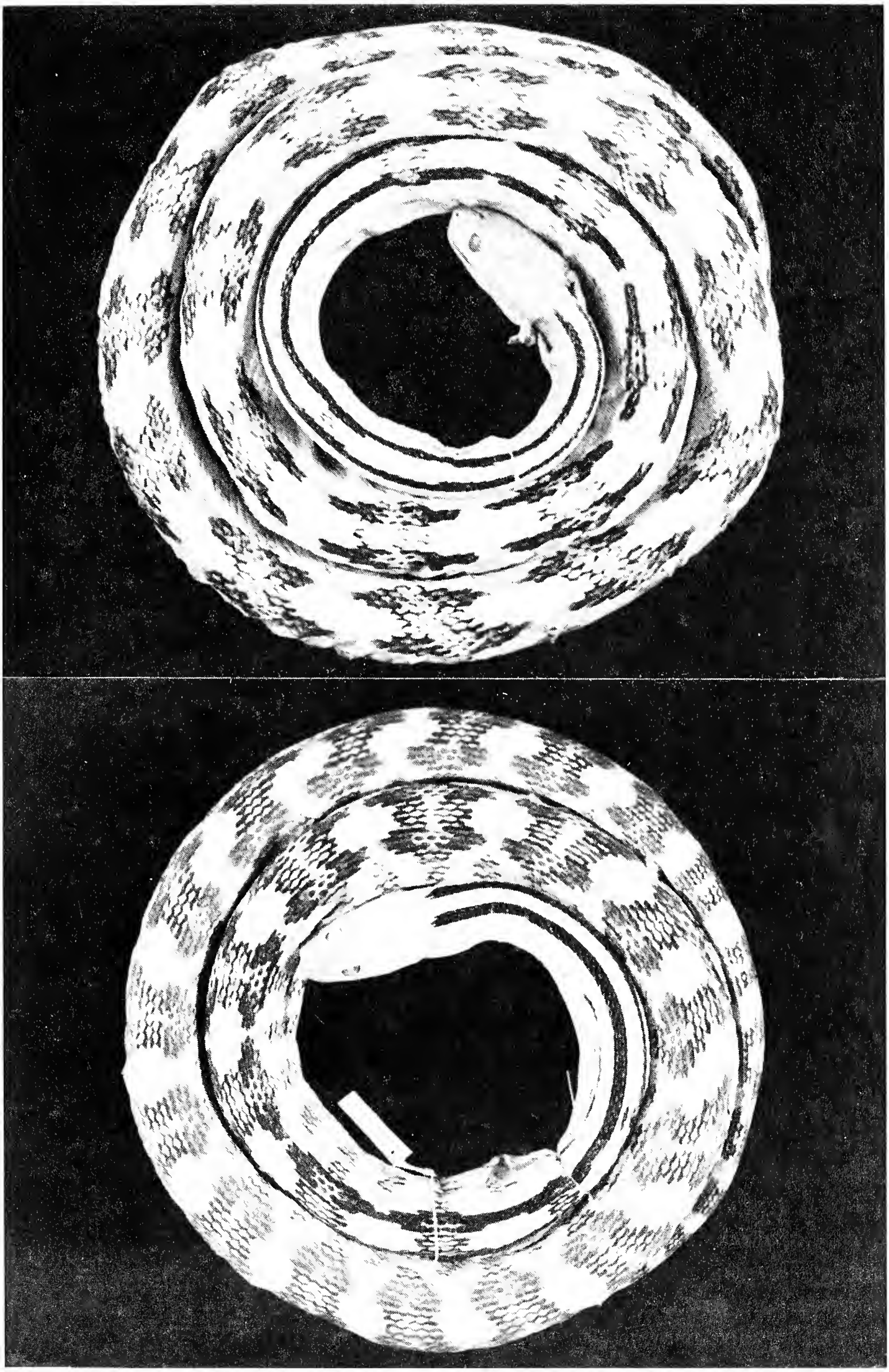

FIGURE 4. *Bogertophis subocularis* of presumed intergrade population from vicinity of Cuatro Ciénegas, Coahuila. Above, FMNH 47048 with patterns most like those of *B. s. subocularis*; below, CM 42767 with patterns most like those of *B. s. amplinotus*.

and Pedriceña. Three specimens are from just north of the Río Nazas a few miles east of Léon Guzmán. The southernmost record for the species in México is Ignacio López Rayón, Durango, near the Zacatecas state line (specimen not examined). Baker and Greer (1962) noted the Río Nazas as a north-south filter barrier affecting mammal distributions in Durango.

Intergradation

Material from the vicinity of Cuatro Ciénegas, Coahuila, is sufficient ($N = 16$) to indicate intergradation in features of pattern and scutellation. Some snakes have black neck stripes and pattern of body blotches most like those of *B. s. subocularis* (FMNH 47048, USNM 257962), although blotches are slightly wider than in most *B. s. subocularis*. Others (CM 42768-69) have neck striping similar to that in *B. s. amplinotus* (irregular in 42768) and body blotching resembling the pattern in *B. s. subocularis* (especially 42768). Others (CM 42770) have neck striping resembling that in *B. s. subocularis* and body blotching similar to the condition in *B. s. amplinotus*. Patterns of both neck stripes and body blotches in some snakes resemble those of *B. s. amplinotus* (CM 42766-67, 58121, 69053; SDSNH 57043). All body blotch patterns noted as similar to the pattern of *B. s. amplinotus* have vertebral lengths of blotches and interspaces subequal in length. Pattern extremes of snakes from the Cuatro Ciénegas area are compared in Figure 4.

The five snakes from eastern Coahuila and Nuevo León are rather uniform in pattern features, but also suggest intergrade status. The wide black neck stripes of uniform width (1/2-2-1/2) are not unlike those of *B. s. amplinotus*, whereas the character of the mostly equidistant blotches is generally intermediate between the patterns of the two subspecies (Fig. 3). The posterior body blotches of one Nuevo León specimen (AMNH 85283) are extremely irregular with the symmetrical blotches narrower (by one to three scales) than the pale interspaces (as in *B. s. subocularis*). The three Coahuilan specimens are from the Sierra de la Garia where this range is intersected by Highway 57. The two Nuevo León specimens are from the northern edge of the anticlinorum of Arteaga along Highway 40 (between Saltillo and Monterrey). These rat snakes seem to be limited southward by the high east-west trending arcs of the anticlinorum of Arteaga (Sierra Madre Oriental) and the east-west Sierra de Parras in southern Coahuila. Baker (1956), dealing with mammal distributions, noted a corresponding Southern Coahuila Filter Barrier.

In Coahuila, the most marked pattern disruption between the two subspecies of *Bogertophis subocularis* occurs in the Cuatro Ciénegas region, with other specimens of intergrade status to the south. This distribution generally corroborates the postulated historic route of the old Río Nazas system of pluvial lakes that exited to the Río Grande via a

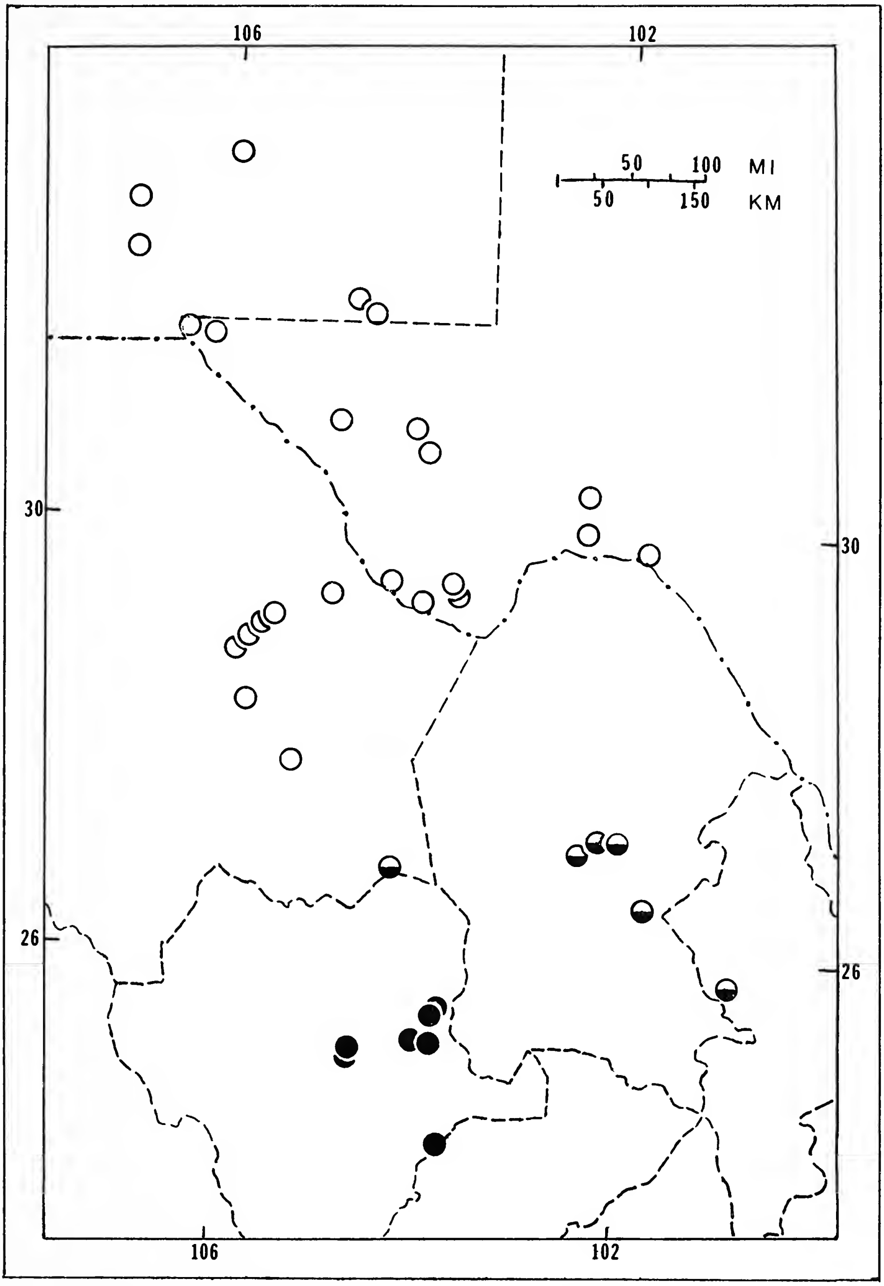

FIGURE 5. Map of north-central México and adjacent south-central United States showing localities for specimens examined of *Bogertophis subocularis amplinotus* (solid circles) and *B. s. subocularis* (open circles); presumed intergrades (*B. s. subocularis* × *B. s. amplinotus*) indicated by half-solid circles.

route toward Cuatro Ciénegas and perhaps the Río Salado (see comments in Conant, 1963:477-478, and Legler, 1990:96). This former extensive Río Nazas system posed a barrier to north-south dispersal and allowed for differentiation of *B. subocularis*; subsequent desiccation and removal of this barrier in Coahuila (but not in Durango) permitted amalgamation of the two subspecies.

Liner et al. (1982: figs. 1, 2) reported two specimens from western Nuevo León (34.5 km. SW and 28.3 km. W Bustamante) that appear to be intergrades (photographs only, no voucher specimens). The uniformly wide, black neck striping is similar to that of *B. s. amplinotus*. The pattern of wide interspaces between body blotches resembles that of *B. s. subocularis*. The body blotches of the snake depicted in Figure 1 are only slightly biconcave as are the blotches in some specimens of *B. s. amplinotus*.

The southernmost Chihuahuan specimen (E Escalón, UTEP 13659) also is assigned to intergrade status. The black neck stripes are of uniform width but only 1/2-1-1/2 scales wide (as in some *B. s. subocularis*); the dorsal blotches, however, are only slightly biconcave and about equidistant from each other (pattern similar to that of CM 42767 illustrated in Fig. 4).

Juveniles photographed in Campbell (1972: figs. 1, 2) that hatched in captivity (parent male of unknown origin, female from Brewster County, Texas) have features of *B. s. amplinotus*, namely, uniformly wide black neck stripes, and (Fig. 2) vertebral constrictions of some blotches longer than pale interspaces.

Integradation (*B. s. amplinotus* × *B. s. subocularis*) presumably occurs in the vicinity of Cuatro Ciénegas, to the east and south in Coahuila and Nuevo León, and in extreme southeastern Chihuahua (Fig. 5). Features of scutellation of these presumed intergrade specimens are compared with those of the two subspecies in Table 1. All characters show mean values intermediate between those of the two subspecies (except subcaudals).

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APPENDIX I

The localities listed below are based on specimens examined (one exception as noted) and are plotted on the distribution map (Fig. 5); distances (either miles or kilometers) are cited as originally transcribed. Museum codes follow Leviton et al. (1985), except EAL and RWA (see Acknowledgments).

Bogertophis subocularis amplinotus (*N* = 10).—DURANGO: just north of Km signpost 139, about 5 mi. from [S] Rodeo on Hwy 45 (UTEP 9596); 4 mi. S Rodeo (AMNH 96622); 90.5 mi. N Cd. Durango (via Hwy 45) [= *ca.* 10.5 road mi. S Rodeo] (UIMNH 62817; Webb and Ferguson, 1986); 50 mi. S La Zarca (vicinity of Rodeo) on Hwy 45 (CAS 169715); 2 mi. NE León Guzmán (MSUM 2543; Webb, 1960; Degenhardt and Degenhardt, 1965); 8.6 road mi. [Hwy 47] NW Pedriceña toward Emiliano Carranza (UMML 5525); 8 mi. W Torreón, Coahuila, Hwy 40-49 (UTA 7033); Los Rayos [= El Rayo, 4 road mi. E León Guzmán on Hwy 40-49] (KU 174802); 10.5 km. NE Pedriceña (MCZ 146391); Ignacio López Rayón [24°13′N, 103°43′W] (IBH 3884, not examined; taxonomic allocation based on geographic provenance).

Bogertophis subocularis amplinotus × *B. s. subocularis* (*N* = 21).—CHIHUAHUA: 13.3 road mi. E Escalón [= 0.8 mi. W Mercurio] (UTEP 13659). COAHUILA: Cuatro Ciénegas (FMNH 47048; Schmidt and Owens, 1944; ASU 5831); Hwy. 30 from 1-3 km. E (CM 48146), 3.2 mi. E (CM 42766), 4 mi. E (CM 42764), 9.2 mi. E (CM 42769), 10 mi. E (CM 58121), 13 mi. E (CM 42768), and 13.1 mi. E (CM 42770) Cuatro Ciénegas; 6.3 mi. E (EAL 2635), and 7.9 mi. E (EAL 2632) Cuatro Ciénegas; 3.9 mi. E Sacramento (CM 42767); 5 mi. E Sacramento on Hwy. B-3 (CM 69053); Poza la Becerra on Hwy. 30 S [14 km. SW] Cuatro Ciénegas (SDSNH 57043, USNM 257962); 42 mi. S Monclova on Hwy. 57 (CM 59925); 26 mi. N Saltillo on Hwy. 57 (CM 59924); 40.2 mi. S Monclova (AMNH 107278). NUEVO LEON: 11 mi. W Santa Catarina (AMNH 85283; Conant, 1965); 28 mi. E Saltillo, Coahuila (CM 9781; Smith, 1939; cataloged as in state of Coahuila, collecting site presumably road miles on Hwy 40 and thus in state of Nuevo León).

Bogertophis subocularis subocularis.—CHIHUAHUA (*N* = 16): Hwy. 16 from 10.2 mi. E (MSB 34227), 12 mi. or 19.3 km. NE (CM 59918, MSB 34234), 12-17 mi. NE (CM 59926), 19 mi. NE (CM 59919), 25.5 mi. E (MSB 34228), 27 mi. NE (CM 59921), 28 mi. NE (CM 59923, 61792), 30 mi. NE (CM 59917), 38 mi. NE (CM 59920), and 39 mi. NE (CM 59922) Aldama (Tanner, 1985:630); 17.7 mi. E Coyame (TCWC 44005; Tanner, 1985:630); 18 mi. SE Ciudad Chihuahua on Hwy. 45 (MSB 9307; Tanner, 1985:630); 19 mi. NW Meoquí on Hwy. 45 [= 3.5 mi. NW Est. Bachimba] (RWA 1089; Axtell and Webb, 1963; Degenhardt and Degenhardt, 1965); Microondas La Cruz, *ca.* 15 mi. N Camargo (UTEP 10610). Of 23 specimens collected along a 44-mile segment of Highway 16 between Aldama and Ojinaga (10.2 to 54.3 mi. NE Aldama), data have been recorded for only 12 (listed above). The other 11 specimens, all with patterns of *B. s. subocularis*, are MSB 34224 (42.7 km. E Presa Granero on Hwy. 16—mileage from signpost-turnoff to Presa, which is 27.8 mi. NE Aldama plaza, this site of collection is about 54.3 mi. NE Aldama on Hwy. 16), 34225 (15.2 mi.), 34226 (16.0 mi.), 34229 (26.4 mi.), 34230 (42.8 km.), 34231 (45.2 mi.), 34232 (25.4 mi.), 34233 (18.3 mi.), 34235 (17.9 km.), 34236 (15.9 mi.), and MSB 34237 (10.2 mi.) E [NE] Aldama. NEW MEXICO (*N* = 5). *Dona Aña County*: Rincón at Interstate 10 (UTEP 1520). *Eddy County*: Guadalupe Mts., about 5 mi. ENE Sitting Bull Falls (UTEP 2984); Carlsbad Caverns National Park (UTEP 9642). *Lincoln County*: 5 mi. W, 4 mi. N Carrizozo (MSB 4746). *Sierra County*: 1.5 km. S, 3.7 km. E jct. St. Hwys. 51-52 at Elephant Butte (RWA 6374). TEXAS (*N* = 69). *Brewster County*: 8.4 mi. N jct. with Hwy. 170 on Hwy. 118 (TCWC 65950); Christmas Mts., 0.8 mi. N Study Butte at Linda Vista Restaurant (UTEP 2976). *Culberson County*: 11.4 mi. N (on US Hwy. 54) jct. with US Hwy. 80 in Van Horn (UTEP 13637). *El Paso County*: Franklin Mts. (*N* = 46, UTEP numbers and specific localities in Webb and Ferguson, 1986); Franklin Mts., Trans-Mountain Road (Loop 375), 1.3 mi. E entrance Tom Mays Park (UTEP 11285), 1.9 mi. (UTEP 11123), 6.2 mi. (UTEP 11410), and

6.9 mi. (UTEP 10777) W jct. with US Hwy. 54; Hueco Mts., 1.5 mi. W Hudspeth County line on US Hwy. 62-180 (UTEP 809, 1825); Hueco Mts., 1.4 mi. SSE jct. with US Hwy. 62-180 on Gasline Road (UTEP 1823); Hueco Mts., 4 mi. W Pump Station (UTEP 5101); Hueco Mts., vicinity Hueco Tanks (UTEP 11589). *Hudspeth County* (all Hueco Mts.): 3/4 mi. E El Paso County line on US Hwy. 62-180 (UTEP 1821); 1.9 mi. SE Fabens cutoff on Gasline Road (UTEP 2404); 11.2 mi. S jct. with US Hwy. 62-180 on Gasline Road (UTEP 11457); 4.9 mi. E jct. with Farm Road 2775 on US Hwy. 62-180 (UTEP 11485). *Jeff Davis County*: Davis Mts., 1.9 road mi. W jct. with St. Hwy. 17 on Ranch Road 1832 (UTEP 3676). *Presidio County*: 10 mi. E Presidio on Hwy. 170 (UTEP 3057); 8.9 mi. W Lajitas, Brewster County (TCWC 65952). *Reeves County*: 14.3 mi. E Kent on Interstate 10 (UTEP 2862). *Terrell County*: 8.3 road mi. ESE Dryden on US Hwy. 90 (UTEP 10579); 2.5 road mi. S Big Canyon [bridge-arroyo] on St. Hwy. 349 (UTEP 12338). *Val Verde County*: about 4 air km. E Langtry (UTEP 9597).

SNAILS AS A FOOD SOURCE FOR *GAMBUSIA*

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ABSTRACT.—The six species of *Gambusia* tested consumed substantial numbers of young snails and some snail egg masses. Gastropodivory is most pronounced in females with a trend toward larger females as major consumers. *Key words*: mosquitofish; *Gambusia*; food habits; gastropodivory.

Fishes of the genus *Gambusia* are well known for their consumption of insect larvae. The widely distributed members of the *Gambusia affinis* complex are commonly known as mosquitofish because of their reputation as biological control agent for mosquito infestations. Almost all studies have focused on *G. affinis* (or close relatives) as an insectivore and a wide dietary opportunist (Hubbs, 1971; Hubbs et al., 1978; Reddy and Shahuatala, 1979; Harrington and Harrington, 1982; Meffe, 1985). Although Hubbs (1971) reported feeding differences between *G. affinis* and *G. heterochir*, Hubbs et al. (1978) reported dietary similarities between *G. affinis* and *G. nobilis*. The latter paper is the only reference available on mollusk feeding by *Gambusia*. Despite the scarcity of literature references, small snails readily were eaten by the six *Gambusia* species tested in this study.

My first suggestion that large number of snails may be eaten by *Gambusia* was the observation that aquaria with *Gambusia* adults did not recruit snails, whereas adjacent tanks with other fish frequently had numerous small snails. The following tests were performed to ascertain whether and to what extent *Gambusia* eats small snails.

MATERIALS AND METHODS

The experiments were in floating "breeding traps" approximately 16 centimeters long, five centimeters wide, and nine centimeters deep (one centimeter was above the water). Chambers that floated in a single aquarium at the same time intervals were contrasted. Some chambers included one fish of a given size, sex, and species and one or two that lacked fish (controls). Four adult snails (either Ramshorn or Physa) were placed in each chamber and the subsequent number of egg masses and young snails recorded. Some chambers had a partition separating the lower two centimeters from the upper six centimeters (of water) containing the fish. This provided a potential refugium for the snails. The experiments lasted about five weeks because after that interval surviving F_1 snails became mature and would have exponentially increased the number of egg masses and young snails present. Egg mass deposition occurred on the first day after introduction of adult snails and young snails were noted 10 days later. The animals in each chamber were fed daily—tetramin or *Drosophila* adults, or both, at about 25 percent of the largest fish biomass. Surplus food was removed from all chambers at the same time (usually just before feeding). Effectively, food was present in all test chambers. Both fish and snails grew rapidly in the test chambers and female fish often produced offspring. Individual aquarium conditions seemed to have a major impact on snail reproduction, thus comparisons are

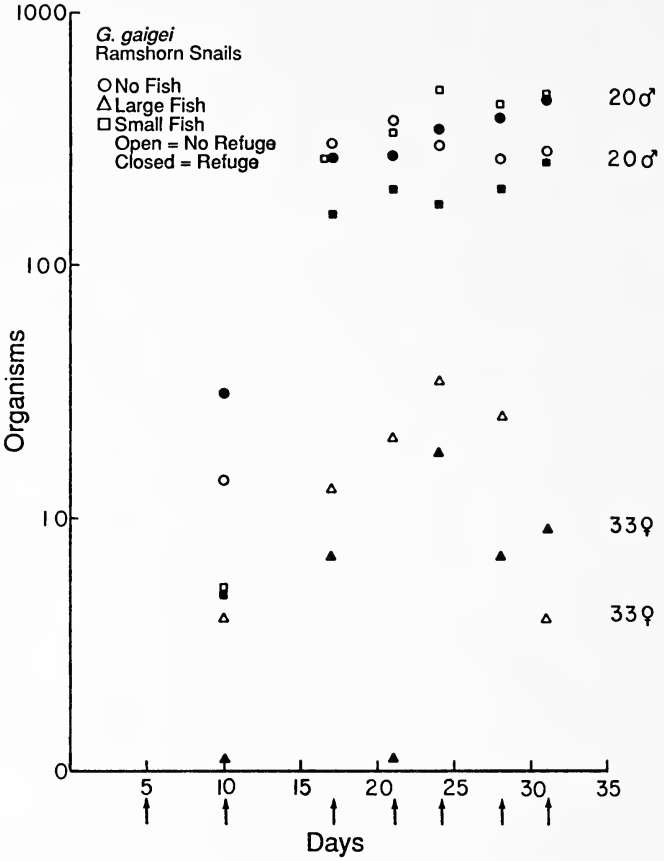

FIGURE 1. Example of the relative abundance of young Ramshorn snails in experimental chambers with or without *Gambusia gaigei* present. The fish sizes in millimeters are shown at right.

restricted to among the chambers floating in one aquarium at the same time interval. Snail reproduction was substantial, with up to 100 egg masses and 1000 young snails counted in a chamber.

The fishes used (and collection locations, all in Texas) were: *Gambusia gaigei* (Big Bend National Park); *Gambusia nobilis* and *G. geiseri* (Balmorhea Recreation Area); *Gambusia heterochir* (Clear Creek, Menard County); *Gambusia speciosa* (Devils River Recreation Area at Fawcett Springs); and *Gambusia affinis* (Big Bend National Park and Clear Creek). All fish had been maintained at the University of Texas for at least a month before being used in an experiment.

The number of egg masses and young snails were recorded for each test (see Figs. 1 and 2 for examples of abundance). The data are presented as indices of relative abundance. Indices were derived from the percent of egg masses (or snails) in a series of experiments floating in the same aquarium and multiplying that percent by the number of chambers. A score of 100 would be the average number of egg masses or snails present in both the control and experimental chambers and lower (or higher) numbers relative infrequency (or abundance) of mollusks. Contrasts with fewer than 25 egg masses or 75 snails were

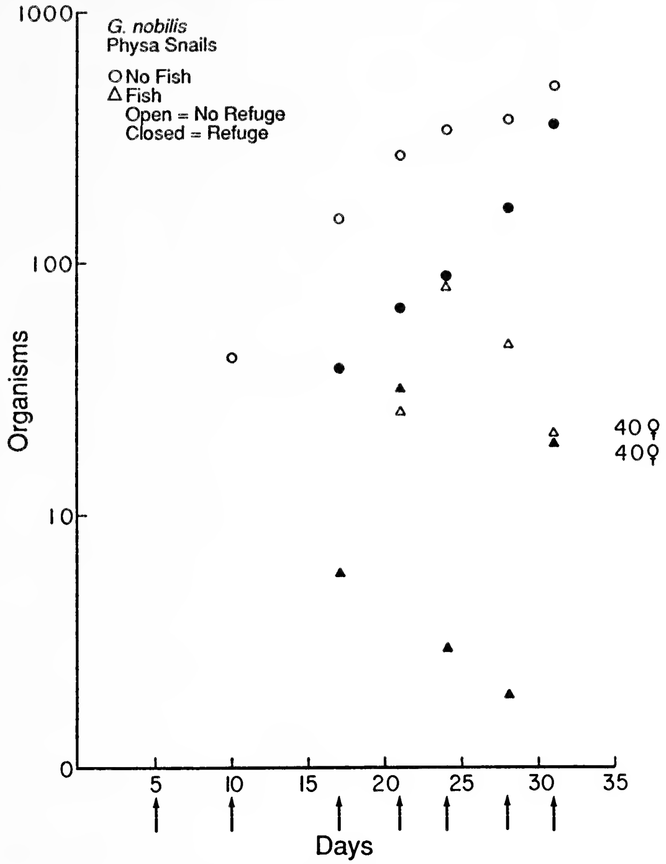

FIGURE. 2. Example of the relative abundance of young Physa snails in experimental chambers with or without *Gambusia nobilis* present. The fish. sizes in millimeters are shown at right.

excluded from the results presented. An index may be impacted by the success of a single chamber; that is, a chamber with unusual snail fecundity may cause the index number of an equivalent experiment to be artifically low (or vice versa). For example, one of two controls had a "population explosion" and the other control, although "better" than the experimentals, had an index value below 100.

RESULTS

The 50 Ramshorn experiments without fish had a median index value for egg masses of 111 ($\bar{x} = 113 \pm 3$), but for snails the median index value was 166 ($\bar{x}$ 181 ± 10). Both significantly ($P < 0.01$) more successful than the comparable tests with fish and the control snail number was significantly higher than that of the Ramshorn egg masses. These data show that the presence of a fish somewhat depressed the numbers of egg masses present and severely depressed the number of snails. The experiments with a refuge had an equivalent number of Ramshorn egg masses ($\overline{x} = 110$) as did those without refugia.

The 36 Physa experiments without fish had a median index value for egg masses of 109 ($\overline{x} = 109 \pm 4$), but for snails the median index value was 189 ($\overline{x} = 201 \pm 14$). The differences were marginally ($P = 0.01$) or much ($P < 0.01$) more successful than comparable tests with a fish. Again, snail number was significantly ($P < 0.01$) higher than that of Physa egg masses. These data show that the presence of a fish somewhat depressed the numbers of egg masses present and severely depressed the number of snails. The experiments with a refuge had fewer egg masses ($\overline{x} = 98$) than those without refugia. Presumably, Physa are inclined to avoid laying egg masses in the lower part of experimental chambers (they are pulmonates). The observation that egg masses laid on one side of an experimental chamber with female *Gambusia gaigei* present often lacked egg masses at that site the next day, prior to snail hatching, suggests the difference is due to consumption by fish more than to differences in egg deposition by snails.

The most pronounced depression in snail egg masses and young snails present occurred in chambers with *Gambusia gaigei* (Table 1). Only one Ramshorn egg mass index number (of 16) with female *G. gaigei* exceeded that of the controls (another had an equivalent value). There was no obvious correlation with female size or presence of refugia. The data on snails present were even more striking. None of the snail indices was as high as the controls and the only two with values above 100 were for experiments with refugia ($\overline{x} = 56$), whereas the highest index for tests without refugia was 38 ($\overline{x} = 19$). The results for males was quite different—four (of 12) had egg mass indices above the control and three more had indices above 100. There was no obvious association with refugia. Data on Ramshorn snails present suggest some consumption, with only one test above that of the controls and three more above 100. The data suggest that males have less impact on snail numbers than equivalent-sized females if no refuge is present (males with refuge $\overline{x} = 70$, females $\overline{x} = 83$; males without refuge $\overline{x} = 91$, females $\overline{x} = 29$).

Data on Physa experiments were even more indicative of depression in the presence of fish. Only two of 16 tests with females present had egg mass index values above the controls (or 100) and one of them was nearly the same as that of the controls. There was no obvious correlation with female size or presence of refugia in the egg mass comparisons. None of the snail contrasts had index values above 48. There was no obvious correlation with presence of refugia ($\overline{x} = 7$ refuge; $\overline{x} = 12$ without) but a suggestion of an effect of female size ($\overline{x} = 8$ for 30 mm or more in standard length; $\overline{x} = 16$ for females less than 25 mm long). Similar to the Ramshorn tests the presence of males seemed to have less impact. Four (of 12) had egg mass index values above those for the

TABLE 1. Abundance indices for snails in *Gambusia gaigei* experimental chambers. The control indices were: Ramshorn egg masses 113 ± 3, snails 181 ± 10; Physa egg masses 109 ± 4, snails 201 ± 14. An asterisk indicates tests with refugia.

Ramshorn			Physa		
	Eggs	Snails		Eggs	Snails
40-mm female*	51	21	40-mm female*	26	6
40-mm female	66	15	39-mm female	77	6
37-mm female*	89	140	37-mm female*	52	2
37-mm female*	46	2	37-mm female	74	3
37-mm female	96	30	37-mm female	133	21
37-mm female	98	2	35-mm female*	51	16
33-mm female*	66	4	34-mm female*	111	0
33-mm female	78	12	34-mm female	86	8
33-mm female	59	22	34-mm female	74	0
33-mm female	82	27	33-mm female	85	15
26-mm female	111	39	23-mm female*	86	9
23-mm female*	117	148	23-mm female	63	48
22-mm female*	71	18	22-mm female	76	32
22-mm female	86	22	22-mm female	69	4
22-mm female	88	38	22-mm female	87	0
21-mm female	78	18	22-mm female	61	0
20-mm male*	102	81	20-mm male*	93	106
20-mm male	142	203	20-mm male	146	73
21-mm male	92	60	22-mm male	113	58
22-mm male	103	118	22-mm male	146	21
22-mm male*	134	33	23-mm male	115	64
23-mm male*	74	56	23-mm male	104	12
23-mm male*	84	42	23-mm male*	96	114
23-mm male	105	42	24-mm male*	102	95
24-mm male	91	39	25-mm male*	77	30
25-mm male	141	57	25-mm male*	99	87
25-mm male	98	120	25-mm male	102	10
25-mm male*	128	139	25-mm male	93	46

controls and three more had indices above 100. There was no obvious correlation with refugia. None of the snail comparisons had index values similar to those for the controls and only two (both with refugia) had indices above 100. Indices for experiments with refugia had higher indices ($\bar{x} = 85$) than those without refugia ($\bar{x} = 41$). Both values are much higher than those for small females and there is virtually no overlap. In conclusion, egg mass numbers were depressed in female tests and snail numbers were depressed in the presence of both males and females. The presence of refugia reduced depression of egg mass and snail numbers. Tests with males have less depression than those using females of equivalent size.

Data on *Gambusia heterochir* were similar to those for *G. gaigei* but less pronounced (Table 2). Two of the nine female indices for Ramsborn

TABLE 2. Abundance indices for snails in *Gambusia heterochir* experimental chambers. The control indices were: Ramshorn egg masses 113 ± 3, snails 181 ± 10; Physa egg masses 109 ± 4, snails 201 ± 14. An Astrisk indicates tests with refugia.

Ramshorn			Physa		
	Eggs	Snails		Eggs	Snails
44-mm female*	105	192	42-mm female*	126	137
42-mm female	75	109	39-mm female	79	23
38-mm female*	49	13	38-mm female*	117	35
33-mm female*	116	6	36-mm female*	60	33
32-mm female*	92	20	35-mm female*	63	1
32-mm female	117	3	35-mm female	70	6
32-mm female*	72	12	24-mm female	134	178
32-mm female	96	2	22-mm female*	109	32
21-mm female	83	90			
18-mm male*	119	91	23-mm male	85	63
22-mm male	92	120	23-mm male*	118	106
23-mm male	101	133	24-mm male*	104	50
			24-mm male	125	101

egg masses were higher than those for the controls and there was no obvious association with refugia or female size. Only one of the comparions with snails ($\bar{x} = 49$) was above that of the controls and another was above 100. Both were for the two largest females. The other relatively high index value was for the smallest female. The male comparisons had one of three with an egg mass index above the controls and one more above 100. None of the male tests had snail index values nearly as high as the controls but two were above 100. All three male tests had index values higher (one was only marginally so) than that for the one test with a female of equivalent size. The Physa comparisons had three (of eight) with egg mass index values higher than the controls and another was equivalent. There was no association with refugia and only a suggestion of an impact of fish size (the largest and smallest females had relatively high index values). The snail index values ($\bar{x} = 56$) were all below that of the controls and only two (one large and one small) above 100. There was no clear indication of association with size or presence of refugia. Two of the four male egg mass chambers had indices above that of the controls and one more was above 100. None of the snail tests had an index as high as the controls but two were above 100. The mean value for male snail indices was slightly lower than that for the two equivalent sized females but the small sample size makes any conclusion premature. In conclusion, all comparisons of males and females with Ramshorn or Physa showed reduced numbers of snails and there was a suggestion that the largest and smallest females are less inclined to eat snails. Females vary widely in snail depression with all five tests of those in the 30 to 39

TABLE 3. Abundance indices for snails in *Gambusia nobilis* experimental chambers. The control indices were: Ramshorn egg masses 113 ± 3, snails 181 ± 10; Physa egg masses 109 ± 4, snails 201 ± 14. An asterisk indicates tests with refugia.

Ramshorn			Physa		
	Eggs	Snails		Eggs	Snails
42-mm female*	68	7	40-mm female*	74	14
42-mm female*	87	11	40-mm female	106	17
42-mm female	66	4			
40-mm female*	67	63			
40-mm female*	49	122			
40-mm female	92	16			
40-mm female	95	33			
38-mm female	90	9			
27-mm female*	95	61			
23-mm female	150	6			
22-mm female	136	20			
22-mm female	75	4			
22-mm female*	91	135			
20-mm female*	125	120			
23-mm male	129	21			
25-mm male*	133	130			

mm range having index values of 35 or lower, whereas all tests with the three larger or smaller fish had index values of 32 or higher.

A similar pattern to that of the previous two species prevailed in the *Gambusia nobilis* tests (Table 3). Only three of the comparisons with females and Ramshorn egg masses had indices above those for the controls and all three were for small (of six) females. There was no obvious association with refugia. None of the indices for snail abundance was equivalent to those of the controls and only three were above 100. All were among the seven tests with refugia. The tests with refugia ($\bar{x} = 74$) had much higher index values than those without ($\bar{x} = 13$). The two tests with males had both indices for egg mass above those for controls but both snail indices below those of controls. The test with a refugium had a much higher index value (139) than that of the one without (21). The tests with females and Physa (none was run using male fish) had indices below those of controls with the snail indices much lower than those for the egg masses. In conclusion, the indices for *G. nobilis* showed depression in egg mass numbers for females but not for males and the snail indices were drastically reduced for both sexes with the reduction most pronounced when refuges were absent.

The results of *Gambusia speciosa* tests were similar to those found in the previous three species (Table 4). Four of the 22 Ramshorn egg mass indices for females were above those of the controls and five more were above 100. There was no obvious association with female size or presence

TABLE 4. Abundance indices for snails in *Gambusia speciosa* experimental chambers. The control indices were: Ramshorn egg masses 113 ± 3, snails 181 ± 10; Physa egg masses 109 ± 4, snails 201 ± 14. An asterisk indicates tests with refugia.

Ramshorn			Physa		
	Eggs	Snails		Eggs	Snails
42-mm female*	124	103	42-mm female	113	147
42-mm female	103	144	42-mm female	99	68
42-mm female*	77	69	42-mm female*	50	20
40-mm female*	72	40	41-mm female*	134	83
40-mm female	86	37	41-mm female	138	18
40-mm female	87	12	40-mm female*	134	95
40-mm female*	87	74	38-mm female*	106	17
36-mm female*	106	43	38-mm female*	111	76
36-mm female	111	71	28-mm female*	133	111
35-mm female	54	48	27-mm female	87	27
35-mm female	86	12	25-mm female*	65	37
35-mm female*	114	56	25-mm female	93	180
33-mm female*	96	45	20-mm female*	59	29
33-mm female	100	14	20-mm female	88	10
32-mm female*	96	76			
32-mm female*	109	119			
31-mm female	79	26			
30-mm female	117	46			
25-mm female*	81	24			
24-mm female	44	52			
23-mm female	125	186			
23-mm female	89	8			
23-mm male	128	242			
25-mm male	153	220			

of refugia. The snail comparisons showed considerable depression with only one index above those of the controls and three more above 100. The indices for eight tests using large females with refugia had less depression ($\bar{x} = 82$) than for the 10 without refuges ($\bar{x} = 38$). Comparisons for the four small females were less distinctive in large part because only one had a refuge. The data for males do not indicate depression; all four indices were above those for the controls and well above those for females of equivalent size. The results of the 14 Physa egg mass tests with female fish (none was run with males) showed four indices above those for the controsl, two equivalent, and one more above 100. Seven of the indices were below 100. There was no obvious correlation with refugia and at most a minor suggestion that chambers with small females have fewer egg masses. None of the 14 snail indices was above those for the controls and only three were above 100. Again, the tests with refuges tended to have higher index values ($\bar{x} = 81$) than those without ($\bar{x} = 50$). In summary, there was a minor suggestion of egg

TABLE 5. Abundance indices for snails in *Gambusia affinis* experimental chambers. The control indices were: Ramshorn egg masses 113 ± 3, snails 181 ± 10; Physa egg masses 109 ± 4, snails 201 ± 14. An asterisk indicates tests with refugia.

Ramshorn			Physa		
	Eggs	Snails		Eggs	Snails
			Clear Creek		
40-mm female*	90	31	37-mm female*	111	37
40-mm female	106	75	36-mm female	98	3
39-mm female	84	28			
39-mm female	88	66			
			Big Bend		
38-mm female*	109	96	36-mm female	113	20
38-mm female*	101	130	35-mm female*	68	51
38-mm female	52	6	33-mm female*	125	36
36-mm female	51	1	33-mm female	86	8
27-mm female	99	21	19-mm female*	131	92
27-mm female*	58	59	17-mm female	112	18
16-mm male	93	67	18-mm male	126	113
17-mm male*	103	143	18-mm male*	76	140

mass depression and a clear demonstration of a reduction in snail numbers in female tests. The depression was most pronounced in tests without refuges. The two tests using males had higher snail index values than any (of 36) using females.

Data from the *Gambusia affinis* experiments were similar to those obtained for the other four fishes (Table 5). No obvious differences occurred that could be attributed to the population of *G. affinis* used, thus the results were combined. None of the 10 Ramshorn egg mass numbers using females was above those for the controls and only three were above 100. There was no indication of an association with female size or presence of refugia. None of the snail indices was above those for controls and only one above 100 (it was a test with a refuge). The four tests with refugia had much higher indices ($\bar{x} = 79$) than those without ($\bar{x} = 33$). The two tests with males had no indices as high as those of the controls although the one with a refuge had a snail index (143) well above 100. This test had a higher index than that without a refuge (67). The Ramshorn snail index values for tests using males had index values almost twice those of females. The eight Physa egg mass tests using females had indices similar to those for the controls (two above, three equivalent and three below). There was no obvious correlation with female size or presence of refugia. All snail index values were well below 100 and those four with refugia ($\bar{x} = 54$) were above any of the four without refugia ($\bar{x} = 12$). The two tests using males had one egg mass index above that of the controls and one below. The snail indices were

TABLE 6. Abundance indices for snails in *Gambusia geiseri* experimental chambers. The control indices were: Ramshorn egg masses 113 ± 3, snails 181 ± 10; Physa egg masses 109 ± 4, snails 201 ± 14. An asterisk indicates tests with refugia.

Ramshorn			Physa		
	Eggs	Snails		Eggs	Snails
40-mm female	81	13	38-mm female	80	37
40-mm female*	92	19	34-mm female	81	90
37-mm female*	80	30	24-mm female	115	105
36-mm female	78	20	23-mm female	91	92
20-mm male*	100	15			
20-mm male	90	34			

below that of the controls and the one with a refuge higher than the one without. Both were higher than the comparable values for females. In conclusion, there was an indication of reduced Ramshorn egg mass numbers and a clear demonstration in reduction in numbers of snails in all tests. The reduction was associated with absence of refuges and females seemed to have more impact than males.

Results of the 10 experiments using *Gambusia geiseri* were similar to results in the other five series (Table 6). All but one (an egg mass contrast) were below the controls. There was a suggestion that small females have less impact on snail numbers than do large females but otherwise there was no association with refugia, sex, or size. The Ramshorn tests showed substantially lower snail indices than egg mass indices.

DISCUSSION

The data demonstrate that chambers with fish commonly have fewer snail egg masses and young snails than similar chambers without fish. It is presumed that the difference results from the fish eating the egg masses and snails. The reduction in numbers could have resulted from fish eating so much food that egg deposition by snails was reduced. This is unlikely, however, because food was consistently present and available for the snails to eat. Similarly, the fish may have "harassed" the snails sufficiently that they did not lay eggs. This is unlikely for Ramshorn experiments because the chambers with refugia had the same number of egg masses in the refuge area as in the same regions of chambers without refugia. More critically, the most pronounced results were with young snails. If egg deposition was impacted, the number of young snails would be equivalent to the number of egg masses. The results uniformly show more snail impact than egg mass impact by fish in the test chamber. Finally, when an experiment was terminated, the snails and egg masses were put into stock aquaria. In each of those instances, the fish fed avidly on both small snails and egg masses. This prevailed when alternate foods (tetramin and *Drosophila* adults) also were present in the aquarium. Consequently, the parsimonious conclusion is that *Gambusia* ate the snails and egg masses in tests that had reduced numbers of the mollusks.

A number of patterns are readily apparent. 1) The number of snails in the experimental chambers was impacted by the presence of a refugium but not so in the controls. Commonly an experimental chamber with a refugium would have twice as many snails as a similar one without a refugium. There was essentially no difference in egg mass numbers associated with the presence of a refugium. It is likely that small snails moved at random into the refugia and did not seek refuge because chambers with refugia had the reduction of snail numbers delayed. Presumably the snails also moved out of the refugia at random. 2) Males ate fewer snails than did females. This difference was maintained when the contrast was between males and equal-sized females. It is likely that males have lower feeding needs as poeciliid male growth is slow after maturity (Snelson, 1982). Thus an adult male does not have to allocate as much of its ingestate to growth. Similarly, males seldom ate egg masses in the tests (although they were seen to avidly feed on the egg masses from a terminated experiment). 3) Some size classes of females ate more mollusks than others. Large females of *Gambusia gaigei* and *G. nobilis* were substantial predators on snails as were intermediate-sized classes of *Gambusia heterochir* and *G. speciosa.* 4) Most fishes tested seem to have impacted Physa more than Ramshorn; however, the converse seems to apply to *G. geiseri.* 5) *Gambusia gaigei* females were major snail predators as contrasted with *Gambusia speciosa.* It is likely that *G. heterochir* and *G. nobilis* resemble *G. gaigei* in snail consumption, and *G. geiseri* and *G. affinis* resemble *G. speciosa.* The first group have blunt heads and relatively massive jaws, whereas the other three species have a more pointed snout and less massive jaws.

Use of indices obscures the magnitude of the consumption of small snails. A common difference was that a control experiment contained 400 to 500 more snails at the end of a test series than did an experimental series. The difference suggests individual females ate that number of snails during the experiment. Because the experiments ran 30 to 35 days and the first snail hatching (usually in controls) was after 10 days, they ate that number of young snails in 20 to 25 days (or a consumption of 20 per day). Virtually no dead snail shells were found in the chambers, leading to the conclusion that the fish also digested the thin shell. This would virtually eliminate the possibility that stomach analyses would record consumption of snails.

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ON IMPROVING CONVERGENCE RATES IN NON-NEGATIVE KERNEL HAZARD-RATE ESTIMATION FOR CENSORED DATA USING A STRONG REPRESENTATION OF THE KAPLAN-MEIER ESTIMATOR

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Abstract.—The generalized jackknife is used to obtain bias reduction in the logarithm of the kernel estimator of the hazard-rate function based on censored data. The resulting estimator has an improved rate of convergence of the bias and mean-squared error. The desirable property of non-negativity of the estimator is also preserved. *Key words*: hazard-rate function estimation; density estimation; kernel estimator; generalized jackknife; censored data.

Lo et al. (1989) employed the kernel smoothing method to obtain a hazard-rate function estimator based on a modified form of the Kaplan-Meier estimator. They obtained expressions that yield the rate of convergence of the bias, variance, and mean-squared error of their estimator. In their concluding comments, they alluded to the fact that the rate of convergence of the bias to zero could be made faster by using the jackknifing method of Singpurwalla and Wong (1983); however, they avoided this approach because it yielded an estimator that can assume negative values.

This paper introduces a modified form of the Lo, Mack, and Wang estimator that maintains non-negativity. The technique applies the generalized jackknife (Gray and Shucany, 1972) to reduce the bias in the logarithm of the bias expansion of the Lo, Mack, and Wang estimator. Improved rates of convergence for the bias and mean-squared error are demonstrated. The method is analogous to that used by McCune and McCune (1987) where an estimator of the failure-rate (hazard-rate) function on noncensored data was obtained.

Preliminaries

Let $T_1,\ldots,T_n$ be the lifetimes of the n items under study, and let $C_1,\ldots,C_n$ be the corresponding censoring times. In the setting of survival analysis with right-censored data, we only observe $X_i = \min(T_i, C_i)$ and $\delta_i = I_{[T_i \leq C_i]}$ where I_A denotes the indicator function of the event A. Furthermore, we assume the random censorship model: $T_1,\ldots,T_n$ are independent and identically distributed (iid) with continuous distribution function F, independent of $C_1,\ldots,C_n$, which are iid with continuous distribution function G. The object of estimation is the hazard-rate function h, defined

$$h(x) = \frac{f(x)}{1 - F(x)}, \tag{1}$$

where $F(x) < 1$ and f is the corresponding density function of F. We assume throughout that f is continuous at x, $f(x) > 0$, G is continuous at x, and the condition $[1 - F(x)][1 - G(x)] < 1$ holds for a given point x under consideration.

Lo et al. (1989) proposed an estimator of $h(x)$, namely

$$h[x; K, b(n)] = \frac{f_n(x)}{1 - \Gamma_n(x)}, \tag{2}$$

where the nonparametric kernel density estimator of $f(x)$ is

$$f_n(x) = \frac{1}{b(n)} \int K\left[\frac{x-u}{b(n)}\right] d\Gamma_n(u) \tag{3}$$

with specified kernel function K, positive bandwidth $b(n)$, and Γ_n is defined by

$$\Gamma_n(x) = \begin{cases} 1 - \Pi^{n}_{X_{(i)} \le x} \left[\frac{n-i+1}{n-i+2}\right]^{\delta_{(i)}}, & x \le X_{(n)} \\ \Gamma_n(X_{(n)}), & \text{if } x > X_{(n)} \text{ and the largest observation is uncensored.} \end{cases} \tag{4}$$

Note that $\delta_{(i)}$ is the induced statistic corresponding to the order statistic $X_{(i)}$. Furthermore, the assumptions to be made about the kernel function K are:

(A1) K is a symmetric probability density function;
(A2) K has compact support $[-c,c]$, $c > 0$;
(A3) K is continuous;
(A4) K is of bounded variation.

The sequence of bandwidths $\{b(n)\}$ also will be required to satisfy (B1) $b(n) \rightarrow 0$ as $n \rightarrow \infty$; (B2) $(\log n)^2 [n \cdot b(n)]^{-1} \rightarrow 0$ as $n \rightarrow \infty$.

RESULTS

The bias and variance theorem of Lo et al. (1989) was expanded further by using higher order terms of the Taylor series representation of the bias. The following representation of the mean-squared error was obtained.

Theorem 3.1.—Suppose K satisfies (A1)-(A4) with the first 2t moments finite, $\{b(n)\}$ satisfies (B1)-(B2), $f(x) > 0$, and f is $2t+1$ times continuously differentiable at x, then

$$E\{h[x; K, b(n)]\} = h(x) + \sum_{p=1}^{t} Q_{2p}\, I(K,2p)\, [b(n)]^{2p} + o\{[b(n)]^{2t} + [n\, b(n)]^{-1/2}\}, \tag{5}$$

$$Var\{h[x; K, b(n)]\} = \left\{\frac{h(x)}{[1-F(x)][1-G(x)]} \cdot I(K^2,0)\right\}[nb(n)]^{-1} + o\{[nb(n)]^{-1}\}, \tag{6}$$

and hence

$$MSE\{h[x; K, b(n)]\} = \left\{\frac{f^{(2)}(x)}{2[1-F(x)]} \cdot I(K,2)\right\}^2 [b(n)]^4 + \left\{\frac{h(x)}{[1-F(x)][1-G(x)]} \cdot I(K^2,0)\right\}[nb(n)]^{-1} + o\{[b(n)]^4 + [nb(n)]^{-1}\}, \tag{7}$$

where

$$Q_j = \frac{f^{(j)}(x)}{j![1-F(x)]} \tag{8}$$

and

$$I(K,j) = \int v^j K(v)dv. \tag{9}$$

Furthermore, if b(n) $= O(n^{-1/5})$, it follows immediately from (7) that

$$MSE_{opt}\, h[x; K, b(n)] = O(n^{-4/5}). \tag{10}$$

We are interested in improving the rate of convergence of (5) and (10). We next defined a new estimator of $h(x)$ as a product of the Lo, Mack, and Wang estimators.

Definition 3.1.—An estimator M_n of $h(x)$ is defined as

$$M_n(x) = M_n\{h[x; K_1, b_1(n)]; h[x; K_2, b_2(n)]\} = \{h[x; K_1, b_1(n)]\}^{1/(1-R)} \cdot h[x; K_2, b_2(n)]^{-R/(1-R)} \tag{11}$$

where

$$R = \frac{I(K_1, 2)\,[b_1(n)]^2}{I(K_2, 2)\,[b_2(n)]^2}. \tag{12}$$

Note that (11) is the product form of the generalized jackknife (Gray and Shucany, 1972) and is always nonnegative. We select any kernels K_1 and K_2 satisfying (A1)-(A4); bandwidth sequences $\{b_1(n)\}$ and $\{b_2(n)\}$ are selected to satisfy (B1)-(B2) provided $R \neq 1$ in (12).

Convergence rates for the bias and mean-squared error of M_n are established by the following theorem.

Theorem 3.2.—If the assumptions of Theorem 3.1 hold and if

$$b_1(n) = Ab_2(n), \tag{13}$$

where A is a positive real number and $R \neq 1$, then

$$\begin{aligned} &(i)\ \mathit{Bias}\ M_n(x) = o\{\,[b_1(n)]^4 + [nb_1(n)]^{-1/2}\} \\ &(ii)\ \mathit{MSE}\,[M_n(x)] = O(n^{-8/9}) \text{ for } b_1(n) = O(n^{-1/9}). \end{aligned} \tag{14}$$

Proof: Let

$$Y_1 = h\,[x;\, K_1,\, b_1(n)] - E\{h\,[x;\, K_1,\, b_1(n)]\} \tag{15}$$

and

$$Y_2 = h\,[x;\, K_2,\, b_2(n)] - E\{h\,[x;\, K_2,\, b_2(n)]\,\}. \tag{16}$$

It follows from (5) and (6) that the random variables Y_1 and Y_2 have expection zero while variances and thus covariances of Y_1 and Y_2 are of orders $[n\ b_1(n)]^{-1}$ and $[nb_2(n)]^{-1}$, respectively. Application of the series expansion for natural logarithms to (5), followed by application of the generalized jackknife to the resulting bias expansion, allows us to write (11) as follows:

$$\begin{aligned} M_n(x) = h\,(x) + \frac{1}{1-R} \cdot Y_1 \cdot \left(\frac{E\{h[x;\, K_1,\, b_1\,(n)]\,\}}{E\{h[x;\, K_2,\, b_2\,(n)]\,\}}\right)^{R/(1-R)} \\ - \frac{R}{1-R} \cdot Y_2 \cdot \left(\frac{E\{h[x;\, K_1,\, b_1\,(n)]\,\}}{E\{h[x;\, K_2,\, b_2\,(n)]\,\}}\right)^{1/(1-R)} \\ + \frac{[Q_4 \mathrm{I}(K_1,4)\,h\,(x) - \frac{1}{2}\,Q_{2}^{2}\,I^2\,(K_1,2)]\,.\,[b_1(n)]^4}{(1-R)\,h\,(x)} \\ - \frac{R\,[Q_4 \mathrm{I}(K_2,4)\,h\,(x) - \frac{1}{2}\,Q_{2}^{2}\,I^2\,(K_2,2)]\,.\,[b_2(n)]^4}{(1-R)\,h\,(x)} \\ + o\,[(Y_1 + Y_2)^2] + o\,\{[b_1(n)]^4\} + o\{[b_2(n)]^4\} \\ + o\{nb_1(n)]^{-1}\} + o\,\{[nb_2(n)]^{-1}\}. \end{aligned} \tag{17}$$

The proof of (i) follows from (1·3), (17) and the properties of the order function. For the proof of (ii) we have

$$\frac{1}{1-\Gamma_n(x)} \cdot \frac{\frac{1}{b_1(n)} \int K_1 \left[\frac{x-u}{b_1(n)}\right] d\Gamma_n(u) - \frac{R}{b_2(n)} \int K_2 \left[\frac{x-u}{b_2(n)}\right] d\Gamma_n(u)}{1-R}$$

$$= \frac{1}{[1-\Gamma_n(x)]b_1(n)} \int \tilde{K} \left[\frac{x-u}{b_1(n)}\right] d\Gamma_n(u), \tag{18}$$

where

$$\tilde{K}(w) = \frac{K_1(w) - A^3 . \frac{I(K_1,2)}{I(K_2,2)} . K_2(Aw)}{1 - A^2 . \frac{I(K_1,2)}{I(K_2,2)}} . \tag{19}$$

Hence (11), (17), and (18) yield

$$Var[M_n(x)] = E\left(\frac{1}{1-R} . Y_1 - \frac{R}{1-R} . Y_2\right)^2 + o\{[nb_1(n)]^{-1}\}$$

$$= \frac{H}{nb_1(n)} + o\,\{[nb_1(n)]^{-1}\}, \tag{20}$$

where

$$H = \frac{h(x)}{[1-F(x)]\,[1-G(x)]} \int \tilde{K}^2(w)\, dw\, . \tag{21}$$

Using (17) and (20) we have

$$MSE\,[M_n(x)] \sim B^2 . [b_1(n)]^8 + \frac{H}{nb_1(n)}, \tag{22}$$

where

$$B = \frac{Q_4 \mathrm{I}(K_1,4)\, h\,(x) - \frac{1}{2}\, Q_2^2\, I^2\,(K_1,2)}{(1-R)\, h\,(x)} - \frac{R\, Q_4 \mathrm{I}(K_2,4)\, h\,(x) - \frac{1}{2}\, Q_2^2\, I^2\,(K_2,2)}{A^4\,(1-R)\, h\,(x)} .$$

Minimizing (22) with respect to $b_1\,(n)$ yields

$$b_1(n) \sim \left(\frac{H}{8\,B^2}\right)^{1/9} . \, n^{-1/9}$$

from which (ii) follows. The proof is therefore complete.

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INTRASPECIFIC COMPARISONS OF DIET OF *CNEMIDOPHORUS GULARIS* (SAURIA:TEIIDAE) IN CENTRAL TEXAS

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ABSTRACT.—Aspects of the diet of *Cnemidophorus gularis* were examined in two dominant habitats (mesquite and juniper woodlands) of central Texas. One hundred thirty-two lizards were categorized into groups based upon age and sex. Morphometric data of individual *C. gularis* were collected to characterize the relationship between body size and food size for age-sex groups within each habitat. Diet composition was determined from stomach contents, which were quantified by number and volume of each prey taxon present for each lizard. The distribution of prey categories within age-sex groups then were compared via a log-linear model of three-way contingency tables within each habitat. Isoptera (termites) were the numerically dominant prey category for all groups of lizards, whereas Orthoptera were dominant based on volumetric contribution to the diet. No differences in the proportional contribution of prey taxa to the diet of different age-sex groups were detected in the juniper habitat. A significant three-way interaction among prey taxa and age and sex of lizards was detected in the mesquite habitats, but the observed difference is probably an artifact of small sample size of juveniles. Consistent secondary sexual dimorphism was found regardless of age or habitat. Similarly, significant differences in size of prey between lizard age groups were detected regardless of sex or habitat. Nonetheless, variation in diet among individuals could not be ascribed to differences in age, sex, habitat, or their interactions, when number, volume, or proportional volume of prey were considered as dependent variables using multivariate analyses of variance. Dietary differences in prey size regardless of taxon were detected for maximum prey size (but not minimum or mean prey size) using analysis of covariance. However, only the covariate (lizard size) was significant and the magnitude of variation accounted for was small. *Key words*: ecology; niche; whiptail lizard; *Cnemidophorus.*

Body size is an important attribute of an organism from both ecological and evolutionary perspectives. Differences in body size appear to be a major mechanism by which various species avoid competition for resources (Wilson, 1975; Brown et al., 1979; Werner and Gilliam, 1984), and in some situations, it is an important reflection of community structure (Schoener, 1977). Nonetheless, the range of individual body sizes within a species, particularly in those taxa with indeterminate growth, commonly spans one or more orders of magnitude, and ontogenetic changes in body size often transcend size differences among strongly competing species (Werner and Gilliam, 1984). Given such circumstances, differences in resource utilization among size classes of a single species might be greater than those among different competing species. This assumes predator size constrains prey choice either directly through trophic limitations or indirectly through other factors (for example, habitat selection) that may impinge upon prey selection. In addition to dietary differences associated with age due to size, modifications in foraging strategy associated with habitat selection, or the physiological requirements associated with reproductive status, reproductive potential, or sexual maturity, could produce diet shifts between age classes. Thus, intraspecific differences in size or physiology could produce considerable dietary variation within a population.

Ontogenetic niche shifts are defined as changes in the pattern of resource utilization by an organism as it increases in size with age. Ontogenetic diet shifts have been well documented for many invertebrates (Wilson, 1973; Maly, 1976; Sebens, 1981; Hines, 1982) and vertebrates, including fish (Ross, 1978; Grossman, 1980), amphibians (Townsend, 1985; Southerland, 1986), and reptiles (Schoener and Gorman, 1968; Pough, 1973; Ballinger et al., 1977; Schoener, 1977; Mushinsky et al., 1982). Size differences among age groups or between sexes may separately or in combination reduce intraspecific competition for resources (see Selander, 1966, 1972), regardless of the selective forces responsible for the size differences.

Food habits of a variety of species of whiptail lizards (*Cnemidophorus*) have been studied in several areas of the southwestern United States (Pack, 1923; Milstead, 1957*a*; 1957*b*; 1958; 1965; Johnson, 1966; Milstead and Tinkle, 1966, 1969; Pianka, 1970; Bickham and MacMahon, 1972; Scudday and Dixon, 1973; Mitchell, 1979; Best and Polechla, 1983; Best and Gennaro, 1985). The overall diet composition of *Cnemidophorus* in similar habitats has been reported by several authors. Milstead and Tinkle (1969) found Orthoptera, Coleoptera, and Isoptera to be the major foods of *C. tigris* in southwestern Texas. The diet of *C. tigris* in an oak-mesquite habitat of southeastern New Mexico consisted mainly of Orthoptera, Isoptera, Coleoptera, and Araneae, whereas *C. gularis* from New Mexico consumed Orthoptera, Isoptera, and Araneae (Best and Gennaro, 1985).

Milstead (1958) examined the diet of four species of *Cnemidophorus*. He found that although variation occurred between species, termites formed the largest portion of the diet, with orthopterans, coleopterans, and lepidopterans ranking second, third, and fourth, respectively. Smith (1989) found the consumption of termites by *C. gularis* and *C. exsanguis* in western Texas to vary with rainfall and suggested that the use of termites as food is associated with dry or drought conditions. These studies documented that whiptails are opportunistic feeders and that different species eat similar foods. Although intraspecific dietary differences between the sexes have been documented in several studies of *C. tigris* (Johnson, 1966; Pianka, 1970; Karasov and Anderson, 1984; Best and Gennaro, 1985), no dietary differences associated with age have been demonstrated. Paulissen (1987) has stated that juvenile *C. sexlineatus* eat smaller prey items than do adults, but adults and juveniles of this species show a pronounced separation in their seasons of activity. They are, therefore, not competing for the same prey resources. In contrast, Anderson and Karasov (1988) found no evidence for dietary differences between sexes of *C. tigris* in California. Simiarly, Best and Polechla (1985) found no differences in diet between sexes of *C. gularis* in New Mexico, but their study was conducted in habitats where other closely related and possibly competing lizard species were present. In speciose assemblages, interspecific competition may result in intraspecific niche compression, thereby making differences in diet between the sexes less pronounced than in situations where a species niche is not affected by closely related competitors.

We investigated intraspecific resource partitioning among age-sex classes of *Cnemidophorus gularis*, a large, common, teiid lizard that ranges widely from the prairies, grasslands, and rocky hillsides of Texas and northern México, into southern Oklahoma and the eastern edge of New Mexico. These whiptails are slow-moving, methodical foragers that turn small rocks and sticks in search of food; they actively stalk moving objects as well (Scudday and Dixon, 1973). Most feeding occurs on lower branches of shrubs or under ground litter, whereby a variety of burrowing and surface prey may be discovered.

MATERIALS AND METHODS

We selected sites at The Junction Center of Texas Tech University, 1 mi. S Junction, Kimble County, Texas (30°30′N, 99°45′W), to study whiptail ecology because this area provided both diverse habitats and an abundant whiptail population. Moreover, *C. gularis* represents an appreciable portion of the herpetofauna and is virtually free of other lizard competitors in this area. Only two other lizard species (*Sceloporus undulatus* and *Phrynosoma cornutum*) were observed in the area, and each was present in extremely low numbers in both habitats.

Lizards were collected over an 18-day period in late June and early July of 1986 in each of two distinct habitats. The first, dominated by mesquite and prickly pear, was flat and sandy, with sparse shrub and ground cover (approximately 20 percent) occurring in small patches. The second habitat comprised mostly juniper with some mesquite. The terrain was rocky and broken; both shrub and ground cover were dense and pervasive (approximately 40 percent).

Individual lizards were characterized as to sex, age (reproductively mature adult or juvenile), and habitat affinity (mesquite or juniper sites), and body measurements including snout-vent length, head length, and head width were taken to the nearest 0.1 millimeter using ruler and digital caliper. Weight was recorded to the nearest 0.01 gram using a Pesola balance. Specimens were dissected and stomach contents were removed immediately after collection, placed in vials, and preserved in 70 percent ethanol. They were identified to the ordinal or familial level and quantified as to the total number of individuals of each taxon, the volume (by displacement) of each individual prey item, and the total volume (to the nearest 0.1 milliliter) of each taxon. Data were analyzed by multivariate analysis of variance (MANOVA), analysis of covariance (ANCOVA), and regression procedures (SPSS-X Inc., 1988).

The diet of an organism can be characterized in a variety of ways, each elucidating particular aspects of foraging ecology. One approach is to categorize prey into discrete taxa and evaluate if different main treatment factors (age, sex, and habitat, for example) affect diet composition based on results from MANOVA. With this approach, the dependent variable can be quantified according to the number of individual items within each prey category or according to volume (either total volume of each prey category within a stomach or the proportional volume of each prey category within a stomach). A second approach, especially useful for opportunisitic or eurytopic consumers, is to categorize prey items by size without regard to their taxonomic identity. Two-way ANCOVA (age versus sex) then can be used to evaluate the degree to which age- or sex-associated differences in diet (that is, minimum, maximum, or mean prey size) are a product of the size of the lizards within age-sex groups or are emergent properties related to physiological and behavioral correlates of sex and age.

Pooling counts of prey taxa from all individuals within age-sex group produces a prey taxon frequency distribution. Log-linear model approaches to contingency tables then can be evaluated by G-tests (Sokal and Rohlf, 1981) in order to ascertain if the proportional distribution of prey categories is affected by the age or sex of the consumer (analyses were conducted separately for mesquite and juniper habitats).

Results and Discussion

A total of 140 lizards was collected, of which eight had empty stomachs and were excluded from analyses. Approximately twice as many males as females, and four to five times as many adults as juveniles were collected. Sample sizes categorized by age, sex and habitat are: 73 adult males (34 mesquite, 39 juniper); 37 adult females (16 mesquite, 21 juniper); 12 juvenile males (two mesquite, 10 juniper); 10 juvenile females (one mesquite, nine juniper). Body measurements were analyzed by three-way MANOVA with habitat, sex, and age as treatment factors (Table 1). Significant differences in body size were detected between age groups and sex groups, but not between habitats. The absence of significant two- or three-way interactions indicated that each of the significant main factors had consistent effects, regardless of the levels of the other factors. Subsequent univariate analyses demonstrated that *C. gularis* exhibited consistent significant size variation between age and between sex groups for snout-vent length, as well as head length and width (feeding parts). Adults were 10 to 35 percent larger than juveniles, whereas males were eight to 14 percent larger than females, depending on the morphometric variable.

Stomach contents were classified into eight orders (Table 2). Orthoptera (grasshoppers), Isoptera (termites), and Araneida (spiders) were the only three categories that occurred in sufficient frequency (at least one percent based upon the numbers of individual items) to be considered common. The remaining five categories, Scorpionida (scorpions), Lepidoptera larvae (butterflies), Coleoptera (beetles), Dictyoptera (roaches), and Isopoda (isopods) were considered rare and were pooled into a single prey category for subsequent analyses.

TABLE 1. Three-way MANOVA (age × sex × habitat) results for *Cnemidophorus gularis* using snout-vent length, head length, and head width as variables. Pillias', Hotellings', and Wilks' criteria yielded identical F-values and significance.

Source	DF	Pillias'	F	Significance
Age (A)	3	0.924	4.347	0.01
Sex (S)	3	0.087	4.042	0.01
Habitat (H)	3	0.484	2.171	0.10
H × A	3	0.165	0.716	0.54
H × S	3	0.040	1.791	0.15
A × S	3	0.028	1.241	0.30
H × A × S	3	0.013	0.545	0.65
Error	128			

Because significant size differences existed between lizard sex groups as well as between age groups, we examined diets for both intersexual resource partitioning and ontogenetic niche shifts. Because dietary differences could be manifested in a vareity of ways, we analyzed data using a number of approaches. We first evaluated dietary differences associated with age, sex, or habitat using three-way MANOVA on numbers of each prey category. However, because prey items from one category to the next can vary greatly in size (grasshoppers are larger than termites, for example), we additionally used both total volume and proportional volume of prey categories as dependent variables in subsequent three-way MANOVA analyses. Regardless of the analysis, no significant differences were detected for any main treatment or their interactions for Pillias', Hotellings', or Wilks' criteria (Table 1). This indicates indistinguishable diets, regardless of age, sex, or habitat. High within-group variability makes differences between groups difficult to detect with this parametric test. Therefore, we pooled data on stomach contents from individuals to make a composite diet for each age-sex group within each habitat. Four prey categories, each of the three common prey taxa and a category comprising all rare prey, were used to define diets (rare taxa had to be pooled into a single category in order to meet the requirements of the Goodness of Fit Test). These prey categories were evaluated via G-tests to examine whether proportional dietary composition was independent within each habitat for each age-sex group. In the juniper habitat, significance was not detected for any main effect or interaction, whereas a significant three-way interaction was detected in the mesquite habitat ($G = 26.974$, $df = 3$, $P < 0.001$). Significance was attributable to juvenile females, which consumed a higher proportion of Orthoptera, by numbers, than any other age-sex group. All other groups exhibited virtually identical diets dominated by Isoptera (for numbers) and Orthoptera (for volume). Although these results may reveal an actual group preference, it is more likely to be an artifact. The number of

TABLE 2. Number of prey items, followed by total volume (milliliters) consumed (in parentheses) by age and sex groups of *Cnemidophorus gularis* in mesquite and juniper habitats (A, adults; J, juveniles; sample size in parentheses).

	Mesquite				Juniper			
	Males		Females		Males		Females	
Taxa	A(34)	J(2)	A(16)	J(1)	A(39)	J(10)	A(21)	J(9)
Orthoptera								
Acrididae	32(57.1)	3(7.0)	9(18.6)	4(6.0)	40(75.1)	12(16.1)	17(20.8)	10(9.6)
Isoptera								
Kalotermidae	1300(26.4)	191(3.0)	869(27.0)	7(0.1)	1395(31.4)	514(9.7)	886(21.9)	27(6.2)
Araneida								
Araneae	11(11.3)	1(0.1)	6(6.1)	0	16(7.4)	7(0.5)	16(8.5)	5(1.7)
Scorpionida								
Scorpionidae	2(5.0)	0	0	0	1(0.1)	0	1(1.0)	0
Lepidoptera								
Larvae	1(2.0)	0	0	0	0	2(2.5)	2(1.1)	0
Dictyoptera								
Blattidae	0	0	2(0.5)	0	5(2.1)	0	3(2.0)	0
Isopoda	0	0	0	0	2(0.2)	0	0	0
Coleoptera								
Carabidae	4(3.5)	0	2(1.0)	0	1(1.1)	2(2.0)	0	1(0.5)

juveniles in our sample was small in each habitat; moreover, the diet for juvenile females in mesquite was determined from only one individual. Thus, the difference between adults and juveniles may represent individual differences rather than group differences.

Additionally, we examined diet by prey size regardless of taxonomic identity. Maximum, minimum, and mean size prey size (volume) in each stomach were used to evaluate differences between groups (Table 3). We used ANCOVA to examine whether differences in predator size obscured dietary differences related to age and sex. Using lizard size (head width) as a covariate, no significant differences in maximum, minimum, or mean prey size could be attributed to age or sex. Head width was chosen as the covariate measurement because differences in mouth size, as indicated by head width, would more likely reflect differences in the size of prey consumed. A significant relationship existed between predator size and maximum size of prey ($P < 0.005$); in contrast, no significant relationship existed between predator size and either minimum or mean prey size (Fig. 1). Nonetheless, consumption of larger prey must be infrequent as mean prey size does not increase significantly with body size. Ontogenetic diet shifts in prey size do occur to some extent in *C. gularis* (Table 3). Diet differences are attributable only to lizard size (the covariate in the ANCOVA) and not to other physiological or behavioral differences between adults and juveniles, which per se are uncorrelated with size. Even so, only a small percentage of the variation in maximum prey size was accounted for by lizard size (four percent). This suggests that larger lizards, although able to consume large prey, either do not specialize on

TABLE 3. Maximum and minimum prey sizes for each age-sex group of *Cnemidophorus gularis*. Only individuals with stomachs containing two or more prey items are included. Range is followed by mean and standard deviation (in parentheses).

Age and sex	N	Head width	Maximum prey	Minimum prey
Adult males	(45)	7.8-13.2 (9.53, 1.17)	0.1-14.0 (2.18, 2.48)	0.1-13.2 (1.04, 2.36)
Adult females	(22)	7.0-10.3 (8.69, 0.53)	0.1- 8.0 (1.93, 2.01)	0.1- 4.0 (0.29, 0.72)
Juvenile males	(9)	7.7- 8.8 (8.31, 0.33)	0.5- 4.0 (1.82, 1.01)	0.1- 3.0 (0.53, 0.99)
Juveniles females	(7)	7.5- 8.8 (8.05, 0.40)	0.5- 4.0 (1.36, 1.07)	0.1- 3.8 (0.92, 1.27)

larger taxa or encounter them too infrequently to have an appreciable impact on the diet.

C. gularis appeared to be an ideal candidate for exhibiting ontogenetic diet shifts. Although we found significant intraspecific differences in body size between age and sex classes, no intraspecific differences in diet composition were detected. As other lizard competitors were absent from these habitats, we expected to see intraspecific differences maximized. *C. gularis* is an active and methodical predator. It thus has the potential to encounter a greater number and variety of prey items from which it can be selective than would a sit-and-wait predator (Anderson and Karasov, 1988). However, prey that are sedentary and distributed in a patchy fashion (for example, termites) are more likely to be discovered and eaten by active foragers (Eckhardt, 1979; Krebs, 1978). Other studies of lizards with foraging modes similar to those of *C. gularis* (Pianka, 1966; Wilson and Clark, 1977; Huey and Pianka, 1981; Anderson and Karasov, 1988) have demonstrated that these predators have substantial numbers of termites in their diets. In both of our study sites, termites were abundant and individuals were distributed in a clumped fashion. It may be more energetically economical to wait for larger prey than to consume a single termite; however, their clumped distribution may result in a more attractive packaging with a total energetic payoff equal to or greater than that of larger prey items.

Our study on the feeding ecology of *C. gularis* has shown that although morphological variation exists between groups, diets of these groups are indistinguishable. Sex and age differences, at least at the levels we investigated, do not act to reduce intraspecific competition for food. It is possible that dietary differences exist but are obscured by other factors. Because of the abundance of small prey in the diet of *C. gularis*, it is difficult to detect an effect by occasional large items. Also, prey seldom could be identified below the familial level; categorization at such taxonomic levels may obscure differences that would otherwise be detectable at lower levels (Krzysic, 1979). For example, groups may consume different species of Orthoptera, and preferences detectable at the generic or specific level may not be detected at the ordinal level.

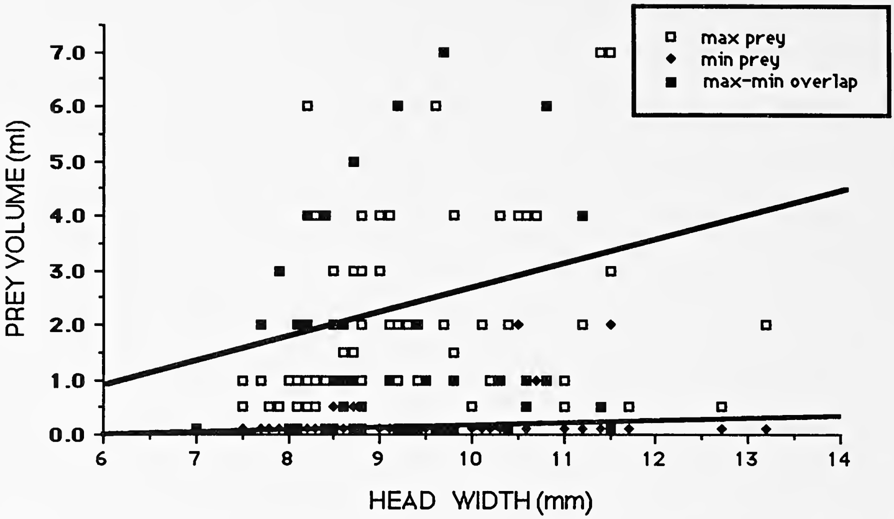

FIGURE 1. Relationship between predator size (head width) and diet (prey volume) for maximum and minimum prey from lizards that had consumed two or more prey items. The regression equations, plotted as solid lines, are: minimum prey and head width, $Y = -0.227 + 0.041X$, $r^2 = 0.04$; maximum prey and head width, $Y = -1.091 + 0.303X$, $r^2 = 0.02$.

Moreover, our size categories were discrete, corresponding to adult and juvenile. In actuality, lizards are characterized by indeterminate growth and continue to grow larger as they get older. There is a continuum of body sizes present throughout the population. Analysis using only two body sizes (effectively large and small), though related to sexual maturity, may serve to mask diet shifts that occur.

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MACROBENTHOS IN EARTHEN SHRIMP PONDS IN SOUTHERN TEXAS

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Abstract.—During the summer of 1985, macrobenthic infauna were sampled from 0.1-hectare earthen ponds in both the presence and absence of shrimp. In Experiments 1 and 2, either *Penaeus schmitti* or *P. setiferus* were stocked at 25 per square meter in outside exclosures. In Experiment 3, *P. vannamei* were stocked at 15 per square meter in enclosures.

In Experiments 1 and 2, 15 benthic species were collected. Polychaetes (97 percent) predominated. *Polydora ligni, Prionospio heterobranchia* (Spionidae), and *Capitomastus aciculatus* (Capitellidae) represented 99 percent of all polychaetes. Polychaete abundance declined dramatically after the third week in the presence of shrimp.

In Experiment 3, 13 benthic species were collected. Polychaetes (83 percent) and ostracods (14 percent) were the most numerous with shrimp present. In the absence of shrimp, polychaetes (58 percent), bivalves (22 percent), and ostracods (14 percent) were the most numerous. Supplemental feeding did not significantly increase survival or biomass of shrimp, nor did it increase the benthic population compared to nonfed cages.

Data from all experiments indicated that shrimp consumed polychaetes and bivalves when they were available. Delayed stocking of shrimp by two or three weeks after filling the pond would best exploit the available benthos as food organisms. After the first shrimp crop is harvested, the pond may be restocked in one week if the pond bottom is not allowed to dry. *Key words*: polychaetes; food web; benthos; shrimp culture; *Penaeus*; Texas.

Benthic meiofauna were found to be important to the sustenance of the macrofaunal community in natural systems (Gerlach, 1971). Boyd (1973) and Stahl (1979) were the first to stress the role of natural production in ponds. Nutrients needed for growth and survival of shrimp in semiintensive ponds come from two sources; supplemental feeds and natural production of the pond system. Added feeds may be consumed directly by shrimp, or by benthic organisms that may then be fed upon by shrimp. Natural production satisfied all the nutritional needs of shrimp during the first four weeks of pond culture (Rubright et al., 1981), and the net productivity contribution to shrimp growth was 53 to 77 percent (Anderson et al., 1987).

Natural producers that contribute to the nutritional requirements of shrimp include both plankton and benthos. Planktonic larvae are introduced from the water source and are important in determining which benthic organisms will colonize shrimp ponds. The water source for the earthen ponds used in this study was the Laguna Madre, a shallow coastal lagoon located south of Corpus Christi Bay and separated from the Gulf of Mexico by Padre Island. The nekton, plankton, and benthos have been catalogued by Simmons (1957) and were extensively studied by Hildebrand and King (1979).

The objectives of this study were 1) to determine which species of benthic organisms would colonize earthen ponds in southern Texas, and 2) to assess the effect of grazing pressure from shrimp on the standing crop of those benthos.

MATERIALS AND METHODS

The Texas A&M University (TAMU) Shrimp Mariculture earthen ponds have been described by McKee (1986). Ponds were partially filled with Laguna Madre water filtered through two 0.54-mm mesh bags, and fertilized using a 3:1 ratio of phosphoric acid (0-54-0) and urea (46-0-0) to stimulate plankton production. They were filled slowly over a one-week period and then stocked with juvenile shrimp. Hydrological parameters were monitored at the deep end of the pond near the bottom. Dissolved oxygen and temperature were recorded twice daily, 30 minutes after sunrise and midafternoon. Salinity was recorded in the morning only.

In the summer of 1985, benthic data were collected from three separate experiments. In Experiment 1, conducted from 6 June to 12 September, and Experiment 2, conducted from 26 July to 23 August, two exclosures were used to monitor growth and composition of the benthos in the absence of shrimp. The multilayered exclosures were made by wrapping successively smaller meshed plastic screens around a PVC pipe frame. As the shrimp grew, outer screen layers were removed to allow better water flow through the exclosures. Two unmeshed cage frames were used to mark open pond sample areas where the benthos could be grazed upon by shrimp.

In Experiment 1, a pond was stocked with *Penaeus schmitti* (25 per square meter; mean weight 0.05 grams). One hundred-eighty benthic samples were collected over 15 weeks. An enclosure placed at mid-depth and stocked with shrimp at pond density was additionally included in Experiment 2 to quantify the "cage effect" on the benthos (Virstein, 1977). This pond was stocked with *P. setiferus* (25 per square meter; mean weight 0.35 grams). Sixty benthic samples were collected over four weeks.

In Experiment 3, *Penaeus vannamei* were stocked inside circular enclosures with a bottom area of one square meter (McKee et al., 1989). No shrimp were stocked in the open pond. Fifteen juveniles (mean weight 1.3 grams) were placed into each enclosure. Benthic samples were collected from five replicates of the following treatments: 1) cages fed an all animal protein diet; 2) cages fed an all plant protein diet; 3) cages receiving no supplemental feed; and 4) five random sites outside the cages. A single sample was collected from each site at the end of the five-week experiment.

Disturbance to the pond bottom was minimized by collecting samples from a portable barge with an Ekman dredge of 15.24 square centimeters. Each sample was washed into a 9.5-liter bucket. Most of the fine sediment was removed by washing through a 425-millimeter mesh sieve. Specimens were narcotized with a 0.15 percent propylene phenoxetol-salt water emulsion (McKay and Hartzband, 1967). A five percent formalin solution containing rose bengal was added as a preservative and to aid sorting (Mason and Yevich, 1967). Samples remained in the preservative for two weeks, then were rinsed and stored in 45 percent isopropyl alcohol. Organisms were sorted, identified to species, and counted. Voucher specimens were sent to appropriate authorities for verification. All polychaetes from each sample were oven dried at 95°C in preweighed aluminum pans for 24 hours (Winberg, 1971). Their biomass was determined using an analytical balance that was accurate to 0.0001 of a gram.

Statistical analysis of data was performed using the SPSS^x Statistical Package (SPSS^x, 1983). The Kruskal-Wallis one-way ANOVA was used to test for significant differences ($P <$

TABLE 1. Checklist of macrobenthic organisms collected during the experiments in 1985.

	Experiment		
Species	1	2	3
Amygdalum papyrum	x		x
Balanus eburneus	x	x	
Bulla striata	x	x	x
Caecum pulchellum	x	x	x
Calanoid copepodes	x	x	
Capitomastus aciculatus	x	x	x
Chione cancellata			x
Eupomatus dianthus		x	
Grandidierella bonnierodes	x	x	
Harpacticoid copepodes	x		
Laevicardium mortoni	x	x	x
Notonectidae	x	x	x
Mitrella lunata	x		
Ostracods			x
Penaeus setiferus		x	
Polydora ligni	x	x	x
Prionospio heterobranchia	x	x	x
Sagitella sp.			x
Tellina sp.	x	x	x
Turbellarians	x	x	

0.05) in the number of individuals of the dominant taxa collected from shallow and deep pond stations and exclosures, and between pond stations and exclosures in experiments 1 and 2. A parametric one-way ANOVA was used to test for significant differences ($P < 0.05$) within and between treatments in Experiment 3. Shannon-Weiner Diversity Indices (Smith, 1980) were calculated to ascertain how feeding treatments affected the diversity of the benthos in Experiment 3.

RESULTS

Water quality in all experiments was within desired ranges. Although dissolved oxygen levels (mean, 6.4 milligrams per liter, S.D. 2.7) reached a one-day low of 1.5 milligrams per liter in Experiment 2, this condition did not persist. Salinities fluctuated from 29 to 40 parts per thousand in the ponds (mean, 34.2 parts per thousand, S.D. 3.6). Temperatures ranged from 25 to 34° C (mean, 29.8° C, S.D. 3.6).

Twenty-one species from the phyla Annelida, Mollusca, Arthropoda, Platyhelminthes, and Chaetognatha were identified from the experiments (Table 1). Fifteen species were collected from experiments 1 and 2. Thirteen benthic species were collected in Experiment 3.

Experiment 1.—In the open pond, 55 percent of the total number of organisms collected were polychaetes and 35 percent were tentatively identified as a turbellarian flatworm (William J. Wardle, written communication). Polychaetes (97 percent) were the dominant taxa in the exclosures. Ninety-nine percent of the polychaetes collected were either

TABLE 2. Polychaetes per square meter collected from pond stations and exclosures during Experiment 1. *Penaeus schmitti* were stocked at 25 per square meter outside the exclosures.

	Polydora		*Prionospio*		*Capitomastus*	
Week	Pond	Exclosure	Pond	Exclosure	Pond	Exclosure
1	30	15	0	15	0	0
2	60	83	60	150	0	0
3	360	2393	1050	713	0	0
4	23	10500	8	2528	0	8
5	143	28905	8	1305	0	180
6	8	7868	8	2123	0	113
7	38	14355	15	1380	0	630
8	83	7403	0	435	15	908
9	156	40305	15	3080	0	1193
10	8	62468	8	2025	15	3158
11	0	1793	8	360	15	1710
12	0	2040	0	203	30	758
13	0	1125	0	105	60	4553
14	8	135	0	38	30	2468
15	0	23	0	0	0	1155

Polydora ligni, Prionospio heterobranchia (Spionidae), or *Capitomastus aciculatus* (Capitellidae). The amphipod, *Grandidierella bonnierodes*, was abundant toward the end of Experiment 1. Less common taxa included the bivalves *Laevicardium mortoni, Amygdalum papyrium*, and *Tellina* sp.

No significant differences ($P > 0.05$) were found in the number of polychaetes collected from either deep or shallow exclosures, so these data were combined. Data from the open pond stations also were combined.

Prionospio heterobranchia was the most abundant polychaete in the open pond. *Polydora ligni* occurred at lower densities in the open pond, but persisted through the entire experiment. *Capitomastus aciculatus* began to occur in low numbers toward the end of the experiment. In exclosures, *Polydora* was dominant, whereas *Prionospio* and *Capitomastus* occurred at similar densities (Table 2).

Biomass of polychaetes from the pond and exclosures was compared with shrimp growth and feeding rate (Table 3). Biomass within the exclosures lagged behind the open pond for the first two weeks. By the fourth week, exclosure biomass exceeded supplemental feeding rate. Open pond biomass dropped rapidly after the sixth week.

Experiment 2.—After the second week, an inadvertent tear in the screens surrounding the deep exclosure allowed shrimp to enter the cage. Significant differences ($P < 0.05$) in the total number of polychaetes collected in the deep and shallow exclosures did not allow these data to be combined as in Experiment 1.

TABLE 3. Dry biomass of polychaetes collected during Experiment 1 from pond stations and exclosures compared with wet weight of shrimp and feeding rate. *Penaeus schmitti* was stocked at 25 per square meter.

Week	Polychaetes (g/m^2)		Shrimp (g/m^2)-	Feeding rate ($g/m^2/day$)
	Exclosures	Open		
1	0.0044	0.0059	1.25	1.36
2	0.0155	0.0303	2.71	1.36
3	0.4967	0.2308	14.79	1.36
4	3.3651	0.0103	33.87	2.27
5	6.5490	0.0488	62.07	5.45
6	2.9983	0.0022	81.16	4.67
7	4.6325	0.0103	93.68	4.71
8	1.4466	0.0303	103.24	5.90
9	4.8467	0.0325	112.75	5.37
10	8.1229	0.0059	123.87	4.54
11	1.5434	0.0022	134.11	5.30
12	1.0262	0.0022	143.10	8.90
13	3.5290	0.0569	138.38	5.56
14	2.0607	0.0118	149.48	8.17
15	0.9982	0.0000	162.00	6.56

At the open pond stations, both *Prionospio heterobranchia* and *Polydora ligni* occurred in greatest numbers the first two weeks. *Capitomastus aciculatus* seemed unaffected by shrimp grazing. Polychaete densities in the enclosure were slightly higher than the open pond. Deep and shallow exclosures had similar populations for the first two weeks, after which numbers in the deep exclosure dropped off dramatically, probably because shrimp entered the exclosure. *Polydora ligni* was numerically dominant when shrimp were absent (Table 4).

Polychaete biomass was similar to that found in Experiment 1, except that it was lower in the open pond. Biomass inside the enclosure was the same as in the open pond except during the third week. Exclosure biomass (Table 5) increased until the third week, after which the deep exclosure biomass fell until it was near that of the open pond by the fourth week.

Experiment 3.—In the enclosures, polychaetes (83 percent) and ostracods (14 percent) were dominant. Outside the cages, polychaetes (58 percent), ostracods (14 percent), and the bivalves *Laevicardium mortoni* (11 percent) and *Chione cancellata* (11 percent) were dominant. Polychaetes, bivalves, and ostracods were dominant in all treatments as well as outside the cages (Table 6). No significant differences ($P > 0.05$) were found in the number of individuals within or between cage treatments. Neither were there any significant differences when all fed treatments were tested against the nonfed treatment. *Prionospio heterobranchia, Laevicardium mortoni*, and *Chione cancellata* were significantly higher ($P < 0.05$) in samples collected outside the cages.

TABLE 4. Number of polychaetes per square meter from pond stations, shallow and deep exclosures, and shrimp enclosure during Experiment 2. *Penaeus setiferus* were stocked at 25 per square meter in the pond and the enclosure, but not in exclosures.

Week	Pond station	Shallow exclosure	Deep exclosure[a]	Enclosure
		Polydora ligni		
1	8	45	8	0
2	15	300	1005	0
3	0	2126	60	8
4	0	14505	0	8
		Prionospio heterobranchia		
1	68	60	8	60
2	8	1740	5850	60
3	0	1350	0	75
4	15	7200	0	75
		Capitomastus aciculatus		
1	0	90	8	0
2	0	360	285	0
3	15	1037	0	0
4	30	3855	15	315

[a] Due to a tear in screens, shrimp had access inside deep exclosure after second week.

Shannon-Weiner diversity indices were calculated for each treatment. The lowest diversity (0.6) was found in the nonfed treatment. Both all-plant (1.3) and all-animal (1.2) treatments were similar. The greatest diversity (2.2) was found outside the cages, where no shrimp were present.

Although survival of shrimp in all treatments was above 82 percent (Table 7), there was not significant difference ($P > 0.05$) in shrimp biomass between fed and nonfed treatments. Polychaete biomass was significantly higher ($P < 0.05$) outside the cages than in any of the cage treatments. No differences ($P > 0.05$) were found in polychaete biomass within or between cage treatments.

DISCUSSION

Many species of organisms were introduced into the ponds via the water supply from the Laguna Madre. Spionidae are the dominant polychaetes in the Laguna Madre grass beds near Pita Island (Hildebrand and King, 1979), and their larvae adapt well to the pond environment (Kindinger, 1980; Rubright et al., 1981). This is reflected in their ability to quickly establish a population. During the time when the ponds were filled, many polychaete larvae were available for recruitment (Hildebrand and King, 1979).

The number of benthic organisms decreases as predator pressure increases above the carrying capacity (Virnstein, 1977; Commito, 1982).

TABLE 5. Polychaete biomass (grams per square meter) collected from the enclosure, pond stations, and shallow and deep exclosure for Experiment 2. *Penaeus setiferus* were stocked inside the enclosure and open pond at 25 per square meter.

Week	Enclosure	Pond station	Shallow exclosure	Deep exclosure
1	0.0030	0.0030	0.2889	0.0030
2	0.0001	0.0015	0.2711	0.7007
3	0.0133	0.0015	0.4800	0.2670
4	0.0015	0.0015	7.5674	0.0015

As the management of Texas shrimp ponds becomes more intensive, pressure on the pond benthos also increases. This becomes obvious when the number of benthic species collected from a natural source, the Laguna Madre (Hildebrand and King, 1979) and a pond with lower shrimp density (Kindinger, 1980), is compared to the results of this study (Table 8). Species richness in the Laguna Madre reflects the abundance of niches found in a natural system, but differences in species richness between that reported by Kindinger (1980) and richness found in this study are best explained by differing management techniques. The age of shrimp and stocking densities used in the experiments were different. Subadult or mature shrimp and a lower stocking density were used by Kindinger (1980), whereas juveniles and higher stocking densities were used in this study.

Although the total number of benthic species in ponds may decrease as shrimp densities increase, certain opportunistic organisms such as polychaetes and bivalves can exhibit "population blooms" only days after water is added to the pond (Rubright et al., 1981). Because spionids are small, sessile, and abundant in the Laguna Madre, they are probably easy

TABLE 6. Number of dominant benthic organisms per square meter collected from Experiment 3. *Penaeus vannamei* was stocked inside cages at 15 per square meter and fed either an all animal or all plant protein diet, or no supplemental feed. No shrimp were stocked outside the cages.

Organism	Shrimp diet fed: Animal	Plant	Nonfed	Outside cages
Polychaetes				
Polydora ligni	9	45	0	36
Prionospio heterobranchia	45	18	36	285
Capitomastus aciculatus	871	240	89	169
Bivalves				
Laevicardium mortoni	9	9	0	231
Chione cancellata	0	0	9	125
Ostracods	1305	605	1200	729

TABLE 7. Percent survival and wet weight biomass (grams per square meter) of *Penaeus vannamei* stocked at 15 per square meter in enclosures compared with polychaete dry weight biomass (grams per square meter) at the end of Experiment 3. No shrimp were stocked outside the cages.

	Shrimp		Polychaetes
Treatment	Survival	Biomass	Biomass
Outside cages	—	—	0.1208
Animal diet	82.2	62.11	0.0693
Plant diet	82.8	61.34	0.0391
Nonfed	82.6	54.07	0.0400

prey for shrimp. Filling and fertilizing ponds two to three weeks before stocking shrimp would give the benthos time to increase the standing stock before the onset of predation. Transferring shrimp into the ponds is always critical, and the assurance of an abundant benthic population could stimulate shrimp growth and survival at the start of the season.

There were also differences in experimental design within this study. In Experiment 3, shrimp biomass and amount of supplemental feed were low when compared to experiments 1 and 2. Because less of the pond bottom received feed in Experiment 3, exclusion of shrimp from the benthos was emphasized, whereas shrimp predation was emphasized in the first two experiments.

Experiment 1.—The number of *Polydora ligni* within the exclosures may be influenced by the increased surface area provided by the cage screens. The *Polydora* population within exclosures would be limited only by space or interspecific competition because there was no shrimp predation. The other two polychaete species appeared to be more stenobenthic, and did not colonize on screens as did *Polydora*.

Shrimp weight increased dramatically the third week, and doubled each week until the fifth week. Spionid generation time is about five weeks (Rice, 1975), so the increase in polychaete biomass for the first five weeks in exclosures had to come from recruitment and growth only. The open

TABLE 8. Number of polychaetes and molluscs collected from Laguna Madre by Hildebrand and King (1979), and in ponds by Kindinger (1980), and in present studies under varying shrimp densities.

	Benthos			Shrimp density
Study	Polychaetes	Bivalves	Gastropods	
Hildebrand and King	48	20	12	—
Kindinger	22	14	6	1/m^2
Experiment 3	4	3	2	15/m^2
Experiments 1 and 2	4	3	3	25/m^2

pond had the same recruitment rate, so the rapid growth of shrimp was influenced by the benthos for up to two weeks past the biomass peak in the open pond. This can be explained by the concept of maximum sustainable yield (Chesney, 1985). Shrimp growth rate slowed after the fifth week, and was probably influenced more by supplemental feed than by benthic secondary production.

Experiment 2.—Inasmuch as the bottom of the pond was not completely dry at the start of Experiment 2 (a second crop pond), the benthic community was already partially established. The open pond was dominated by *Prionospio heterobranchia* by the first week. *Polydora ligni* was dominant only in the shallow exclosure, exhibiting its propensity for structures in the pond. Experiment 2 started six weeks after Experiment 1, which could account for the increased number of *Capitomastus aciculatus* collected. At the time the pond was filled, the *Capitomastus* larvae may have been the dominant polychaete in the plankton. These larvae would be in direct competition with the established spionids in the pond.

The strongest evidence that shrimp were feeding directly on polychaetes came from data collected from the deep exclosure after a tear in the screens. Until the second week of the experiment, samples from both deep and shallow exclosures were similar in number and biomass of polychaetes. The polychaete population increased in the shallow exclosure during the third week, but in the deep exclosure numbers dropped off, and the presence of shrimp was the only apparent change. By the fourth week, the polychaete population in the deep exclosure more closely resembled that of the open pond than that in the shallow exclosure.

Experiment 3.—Differences in experimental design between the first two experiments and Experiment 3 may explain the abundance of bivalves collected in Experiment 3. Because large areas of the pond bottom lacked both supplemental feed and shrimp, the benthic community found should parallel that in nonstocked, fertilized ponds. The high numbers of total individuals collected reflects the high densities of ostracods found in all treatments. *Prionospio heterobranchia* apparently was affected by shrimp predation, as were the bivalves *Laevicardium mortoni* and *Chione cancellata*. *Polydora ligni* and *Capitomastus aciculatus* appeared to be unaffected. This suggests that *Prionospio, Laevicardium*, and *Chione* are preferred natural foods. Low numbers of polychaetes outside the cages probably was due to the lack of supplemental feed as well as increased interspecific competition associated with greater species diversity.

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OBSERVATIONS OF SATURN IN THE SPRING AND SUMMER OF 1989

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ABSTRACT.—Saturn had two prominent belts and a dusky polar hood in 1989. These features along with smaller irregularities were studied and a map of them is presented in this report. More than 200 intensity estimates of disc features were made through integrated light as well as in red and green light. No major differences in intensity through the different colors were observed. The latitudes of major disc features were determined from micrometer measurements, photographs, and visual estimates; all three methods gave similar results. The mean values determined here are consistent with previous measurements, but also may suggest a tendancy of the observer to underestimate the distance between Saturn's north pole and north equatorial belt. *Key words*: Saturn; Saturnicentric; map of Saturn.

Saturn reached opposition on 2 July 1989 and was visible during the spring and summer of that year. Unfortunately, that planet had a declination of between 22°-23°S and thus was at a relatively low latitude for viewers in the Northern Hemisphere. Reasonable views of Saturn, however, were possible from the Texas A&M University (TAMU) Observatory (latitude, 30.6°N) because of its relatively southerly latitude. This observatory is equipped with a 35.5-centimeter, Schmidt-Cassegrain telescope having a focal length of 3900 mm. In this report, I summarize observations made of Saturn during the spring and summer months of 1989.

Saturn was studied in several different colors of light. In this report, integrated light refers to that which is not filtered and includes all colors visible to the naked eye; red light refers to that seen through a Kodak #25A filter, green light to that seen through a Kodak #58 filter, and blue light to that seen through a Kodak #47 filter.

APPEARANCE

A map of Saturn covering 360° of system I longitude was constructed during the nights of 6-8 May 1989. Most of the Southern Hemisphere of that planet was blocked by the rings during this time; the map (Fig. 1) covers only a small amount of that hemisphere, but covers all of the Northern Hemisphere. The 35.5-centimeter telescope at TAMU observatory along with a 12-millimeter orthoscopic eyepiece (giving a magnification of 325×) was used in making the map. Most of the detail shown was faint and has been enhanced.

The equatorial zone was the brightest region on Saturn, whereas the Crape band followed by the north equatorial belt were the darkest features on the planet. The north equatorial belt appeared as one solid feature instead of two closely spaced belts. A few faint, bright ovals were

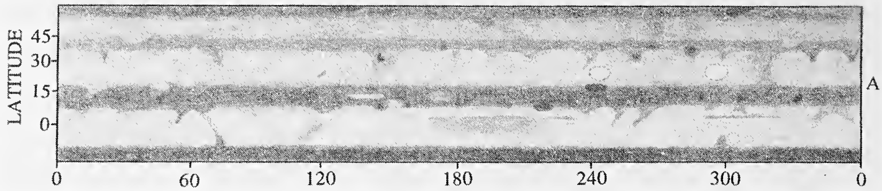

FIGURE 1. Map of Saturn constructed on the nights of 6-8 May 1989. The 35.5-centimeter Schmidt-Cassegrain telescope at TAMU observatory was employed at 325X in constructing this map; all observations were made in integrated light.

present in the equatorial and north tropical zones. These features, however, were not like the strong and brilliant features described elsewhere (Alexander, 1980; Sanchez-Lavega, 1989; Dollfus, 1963). The north equatorial belt had several faint irregularities in May 1989. Over a one- to two-week period, I was able to record central meridian transits of four features within this belt in the 20 to 70° latitude range on the May 1989 map; the results are consistent with a rotational period of 10^{h} 12^{m}, with an uncertainty of one minute. This is shorter than the rotational periods of 10^{h} 13^{m} 55^{s} (1980), 10^{h} 13^{m} 58^{s} (1981), 10^{h} 13^{m} 49^{s} (1982), 10^{h} 13^{m} 39^{s} (1983), and 10^{h} 13^{m} 37^{s} (1984) measured for the north equatorial belt (Heath, 1981, 1984, 1985*b*, 1985*c*, 1986, 1987, 1989). Heath (1985*c*), however, pointed out that there was slight acceleration in this belt between 1981 and 1983. Perhaps this acceleration has continued into 1989. Unfortunately, the spot activity in the north equatorial belt subsided in the period from 1985 to 1987, and no rotational periods were reported for this time interval (Health, 1989; Benton, 1989). The zonal wind speed derived from the 10^{h} 12^{m} rotational period is 290 meters per second, which is consistent with the Voyager 2 results (Smith et al., 1982). Traces of an equatorial band, similar to the equatorial band on Jupiter (Schmude, 1989), were visible on 6 May at system I longitude of 200° and 7 May at 310°. The north temperate belt was relatively distinct in 1989; this feature also contained some faint irregularities. One distinct irregularity also was seen near this belt and traces of it may be present in the green light photograph made on 30 March 1989. Interestingly, Espenak and co-workers (1989) observed an irregularity at a similar latitude in the infrared (λ=7.8 μm). In most instances, the north polar region was dark and seemed to blend in with the rest of the planet; essentially, it lacked a high contrast border. No trace of the polygon discussed elsewhere (Godfrey, 1988) was visible within the north polar region of Saturn.

Photographs of Saturn were made with a 35-millimeter camera and Kodak TP-2415 film. One of these is reproduced in Figure 2. The equatorial belt, Crape band, and disc shadow on the B ring all are

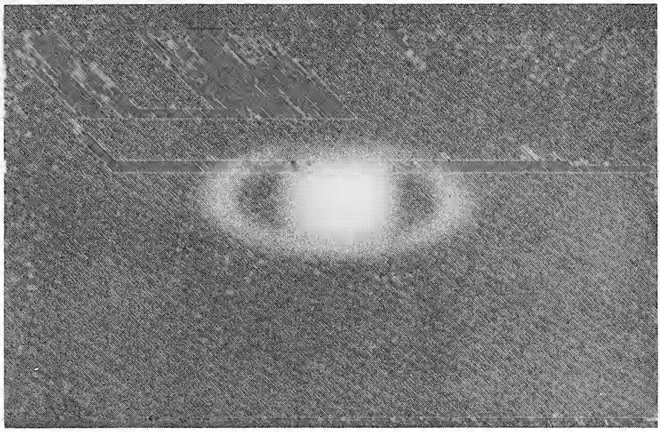

FIGURE 2. Photograph of Saturn made on 30 March 1989 using the 35.5-centimeter telescope at the Texas A&M University Observatory at 10:20 UT; three-second exposure through a Kodak filter #58.

evident in the photograph, but the north temperate belt is weak or absent.

INTENSITY OF DISC FEATURES

The intensity of features on Saturn's disc were estimated on a scale from 10 (darkest) to 0 (brightest) over a four-month period from 30 March to 21 July 1989. These estimates were made through three different effective wavelengths that included integrated, red, and green light. The average intensities measured by the British Astronomical Society (BAA) in the period 1980 to 1986 also are reported in Table 1; all BAA estimates were made in integrated light. The general trend in intensity reported here is in exact agreement with the BAA results; however, there are small discrepancies in absolute intensities. The results listed in Table 1 also are consistent with the seasonal darkening of the north equatorial belt and north polar region (McKim and Blaxall, 1984). Essentially, both of these features became darker during Saturn's northern spring between 1953 and 1961; a similar trend appears to have occurred during that same season in the 1980s. One notable difference between the three different wavelengths is the intensity difference between the north equatorial belt and the equatorial zone 2.5, 1.9, and 1.8 for integrated, green, and red light, respectively. This result is consistent with the north equatorial belt having a significant amount of red color, which is consistent with its observed brownish color.

Table 2 lists the colors of the visible features on Saturn. The colors reported here are similar to those reported for the 1986 (Heath, 1989) and 1987 (Benton, 1989) oppositions. The northern hemisphere of Saturn

TABLE 1. Intensity of various features on Saturn in integrated, green, and red light, along with the average intensities measured by the BAA during the 1980 to 1986 apparitions. Intensity is measured from 10 (darkest) to 0 (brightest), plus or minus one standard deviation.

Feature	Integrated	Green (#58)	Red (#25A)	BAA
North polar region	4.4±0.4	4.2±0.1	4.3±0.3	3.9
North temperate zone	3.3±0.3	3.4±0.3	3.3±0.2	3.0
North temperate belt	4.0±0.3	3.9±0.1	3.9±0.1	3.7
North tropical zone	2.9±0.3	3.0±0.3	2.9±0.3	2.8
North equatorial belt	5.0±0.4	4.6±0.4	4.6±0.3	4.7
Equatorial zone	2.5±0.3	2.7±0.2	2.8±0.3	1.8
Crape band	5.8±0.5	6.2±0.8	5.8±0.5	—

had a "warm" tone in 1989 meaning that gray and brown hues were common; green and blue colors correspond to a cold tone (McKim and Blaxall, 1984) and were not observed in 1989. A warm tone also was observed for Saturn's northern hemisphere in 1959 and 1960—the last time that planet was at its 1989 position.

LATITUDES OF DISC FEATURES

Three different methods were used in evaluating the latitudes of the belts and zones on Saturn. Micrometer data were taken on 11 May 1989. Ten measurements were made for each disc feature. An average value, along with the standard deviation of the measurements, was used in computing Saturnicentric latitudes (Alexander, 1980). Results are listed in the first column of Table 3. The best photographs of Saturn, made on 30 March 1989, also were used in evaluation of latitudes. Position of the northern and southern edges and the center of the equatorial belt were measured from three photographs made through green, red, and blue light. Computed Saturnicentric latitudes from the photographs also are listed in Table 3. The differences in latitude between the three colors lie within the estimated uncertainty of 3°. Finally, the positions of various features were estimated visually; this has been termed the "Haas" method

TABLE 2. Observed colors of various features on Saturn's disc.

Feature	Color
North polar region	Gray with no other hues
North temperate zone*	Yellow with a gray hue
North temperate belt	Gray with a brown hue
North tropical zone*	Yellow with an orange hue
North equatorial belt*	Brown with a gray hue
Equatorial zone*	Yellow-white with an orange hue

*These regions displayed some color variations.

TABLE 3. Saturnicentric latitudes of main features on Saturn in 1989.

Feature[a]	Micrometer	Photograph Green (#58)	Photograph Red (#25A)	Photograph Blue (#47)	Mean "Haas"	Overall suggested Value[b]
NTB	39.2±2.0°	—	—	—	40.5±1.1°	40°N
NEBn	23.6±3.4°	21.6°	19.5°	21.6°	20.6±1.4°	22°N
NEBc	16.1±2.9°	15.3°	14.3°	14.3°	15.1±0.9°	15°N
NEBs	10.2±3.6°	9.0°	9.0°	6.8°	9.7±1.0°	9°N

[a] NTB=north temperate belt, NEB=north equatorial belt with n, c, and s referring to the northern, central, and southern portions (edges) of the belt.
[b] Estimated uncertainty is 3°.

(Benton, 1988). Saturnicentric latitudes then were computed from these estimates and also are listed in Table 3. The suggested Saturnicentric latitudes listed in Table 3 are based on the average of all measurements, with the micrometer values receiving a triple weight because they are the average of 10 separate measurements. The mean Saturnicentric latitudes of the NTBc, NEBn, and NEBs (see Table 3 footnotes for a description of the nomenclature) determined by the BAA for the seven oppositions between 1980 and 1986 are 40°, 25°, and 12°N, respectively (Heath, 1981, 1984, 1985*b*, 1985*c*, 1986, 1987, 1989), whereas Voyager I and II images show latitudes of 36°, 20°, and 5°N, respectively (Hollis, 1985*a*); finally, the photographs of Saturn made on 3 July 1989 (Di Cicco and Robinson, 1989) carefully were measured by me and suggest Saturnicentric latitudes of 38°, 21°, and 9° for these three features. The results recorded in Table 3 are thus in good agreement with the 3 July 1989 photographs and are in reasonable agreement with the results reported by the BAA (1980 to 1986) and Voyager (1980 and 1981). The latitude of the north equatorial belt reported here lies almost between those of the BAA and Voyager. This discrepancy may be due to changes within the belt; however, this seems unlikely as the width from all three studies lies within two degrees. One possibility is that there is a tendency for the observer to underestimate the distance between the north equatorial belt and the northern limb. This also can explain the 4° discrepancy for the north temperate belt between the Voyager measurements and the visual estimates made both by the BAA and me.

SUMMARY

A study of Saturn was made in 1989, which included the gathering of visual, photographic, and micrometer data. These data have been used to produce a map of Saturn and define the approximate Saturnicentric latitudes of the two principal belts on that planet. The latitudes of the north equatorial and north temperate belts were determined from

micrometer, photographic, and visual estimates. Saturnicentric latitudes presented here are in good agreement with the belt latitudes on high resolution 1989 photographs of Saturn. The relative intensities of various disc features were estimated in integrated light and the results are consistent with previous observations; there is some evidence that the north polar region and north equatorial belt may have darkened slightly during the 1980s, which is consistent with a seasonal darkening of these features. Their relative intensities did not vary much through red and green light.

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A LATE PLEISTOCENE HERPETOFAUNA FROM THE LOWER TEXAS PANHANDLE

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ABSTRACT.—The amphibians and reptiles contained in the Carrol Creek local fauna were found in a late Pleistocene sinkhole deposit in Donley County of the lower Texas Panhandle. A radiocarbon date of 32,400 ± 560 years before present was obtained from a sample of mollusk shells. The herpetofauna, represented by 12 taxa (10 genera and six species), gives evidence of at least a semiaquatic environment near the fossil site during the late Pleistocene. All represented taxa are found near the Carrol Creek deposit today, indicating there was little effect on the Texas Panhandle herpetofaunal assemblage by environmental and climatic changes in the late Pleistocene. *Key words*: fossil herpetofauna; Pleistocene; Texas Panhandle.

A herpetofauna containing at least one salamander, one frog, one lizard, and nine snakes is reported herein from the late Pleistocene Carrol Creek local fauna, Donley County, Texas. The study area is located on the west side of Carrol Creek, approximately 13 kilometers north of Clarendon and 1.5 kilometers west of Highway 70. The fossil deposit, considered to be a stream-bed sinkhole filling, was formed when dissolving gypsum beds from the underlying Permian rocks caused an abrupt slumping (Kasper, 1989). Mollusks and small vertebrates were washed into the depression as it filled with clay and fine sand. Modern Carrol Creek is a permanent stream that flows almost due south into Greenbelt Reservoir, an impoundment of the Salt Fork of the Red River.

Approximately 3375 kilograms of matrix were sampled and screen-washed from the fossil deposit. A large sample of mollusk shells from the site was radiocarbon dated at 32,400 ± 560 years before present (Beta Analytic Inc., Beta-25354). Numerous fish bones, including abundant catfish spines, were found but not studied, and two fragmentary bird bones could not be identified. Kasper (1989) reported two plant fossils and 17 mammalian taxa in the Carrol Creek fauna.

ACCOUNTS OF SPECIES

In the following accounts of species, catalog numbers (in parentheses) refer to specimens housed in the Midwestern State University Collection of Fossil Vertebrates. The herpetological skeletal collection of Georgia College was used to make taxonomic determinations.

Ambystoma tigrinum (Green)

The one vertebra (12525) is badly damaged, but it is clearly like *Ambystoma tigrinum* based on its relatively large size and upswept neural arch (Holman, 1969). This species is the only salamander found in Donley County today (Dixon, 1987), where it probably spends most of its time burrowed beneath the ground.

Rana sp. indet.

The material includes one scapula and one ilium (12523). The scapula is like those of *Rana* and differs from *Bufo* and *Scaphiopus* in that the coracoid articular process is close to the clavicular articular process, which creates a narrow glenoid opening. In *Bufo* and *Scaphiopus*, the clavicular process projects laterally, resulting in a wider glenoid opening. Ranid scapulae do not appear to be specifically diagnostic.

The ilium is badly worn, but the remnant of a well-developed ilial blade and lack of a dorsal prominence-protuberance complex is distinctive of ranid species. The fossil ilium represents a rather small ranid about the size of living *Rana blairi*, the only leopard frog presently found at Carrol Creek (Dixon, 1987).

Cnemidophorus sp. indet.

The fragmentary dentary (12526) is characteristic of the genus *Cnemidophorus* based on its narrow, tapering shape, subpleurodont trilobed teeth, and Meckel's groove open to the symphysis (Estes and Tihen, 1964). Although three species of *Cnemidophorus* have present distributions that include (or are near) the fossil site (Dixon, 1987), specific determination cannot be made using dentary characteristics.

Coluber sp. indet. or *Masticophis* sp. indet.

The genera *Coluber* and *Masticophis* cannot be separated based upon vertebral characters (Holman, 1969, 1979; Parmley, 1986*a*). The two fossil vertebrae (12527; Fig. 1C-D) from Carrol Creek are easily identified to *Coluber (=Masticophis*) by their long, narrow shape, long accessory processes, relatively low and long neural spines, and uniformly narrow hemal keels (Parmley, 1988*a*). The species *Coluber constrictor* and *Masticophis flagellum* are common prairie snakes in the Texas Panhandle (Dixon, 1987).

Elaphe guttata (Linnaeus) or *Elaphe obsoleta* (James)

The two vertebrae (12528) have higher neural arches than those of similar-sized species of *Lampropeltis*, but lower than those of *Pituophis*. The specimens are similar in size and subcentral ridge development to *Elaphe guttata* and *E. obsoleta*, which are difficult to separate on the basis of vertebral characters (Parmley, 1986*b*). *Elaphe guttata* occurs in Donley County today (Dixon, 1987), and *E. obsoleta* is found near enough to have lived at Carrol Creek 32,000 years ago.

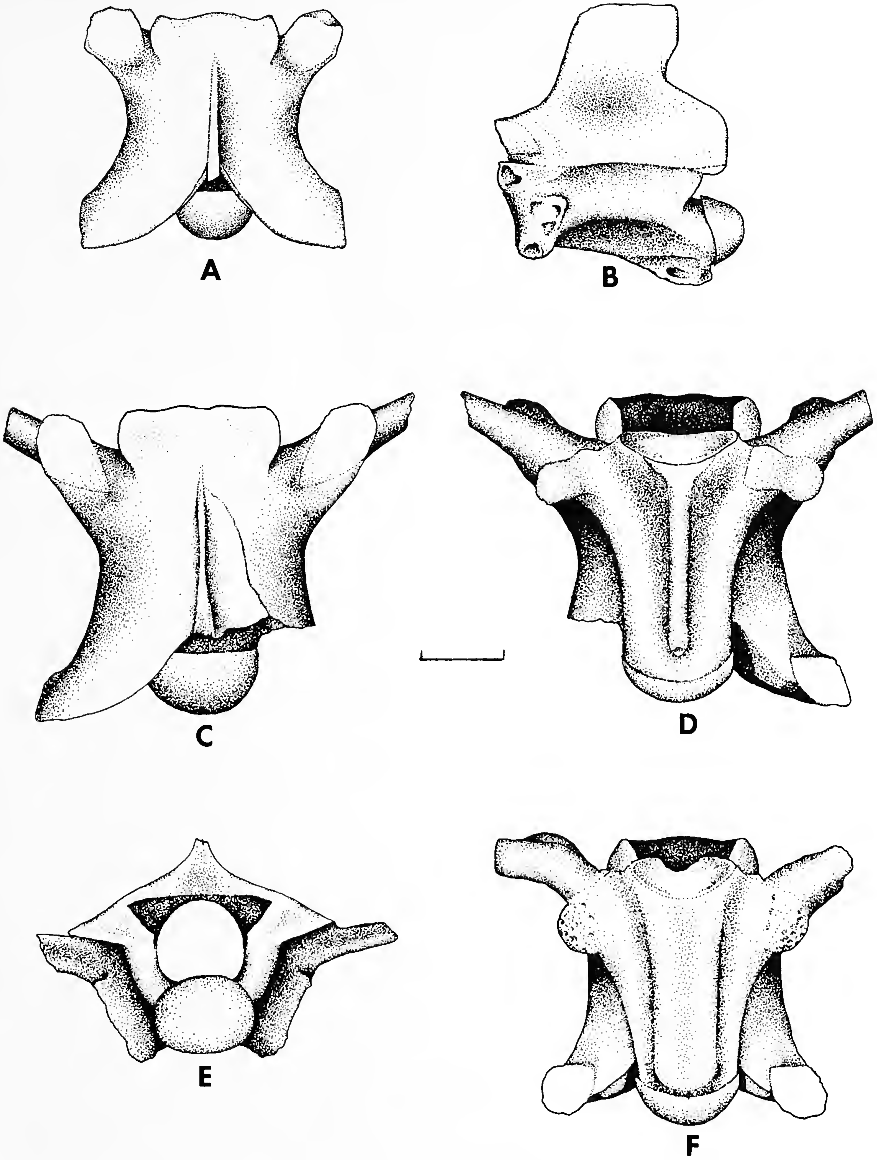

FIGURE 1. Carrol Creek snake vertebrae: *Nerodia erythrogaster* in dorsal (A) and lateral (B) views, *Coluber* (=*Masticophis*) in dorsal (C) and ventral (D) views, and *Heterodon* sp. in posterior (E) and ventral (F) views. Scale line equals 1 mm.

Heterodon sp. indet.

Although too fragmentary for specific identification, the two vertebrae (12558; Fig. 1E-F) clearly represent the genus *Heterodon* based upon the depressed neural arches, the wide and obsolete hemal keels, and weakly developed subcentral ridges (Holman, 1962; Parmley, 1988*b*). Both Texas species, *Heterodon nasicus* and *H. platyrhinos*, occur in Donley County today (Dixon, 1987).

Lampropeltis triangulum (Lacepede)

Trunk vertebrae of *Lampropeltis triangulum* (at least those from midcontinental North America) are distinctive based on their small size, low neural spines, depressed neural arches, and moderately to poorly developed hemal keels (Parmley, 1988*b*). The Carrol Creek fossil (one vertebra, 12529) is similar to those of smaller individuals of *L. triangulum*, which occurs throughout the Texas Panhandle today (Dixon, 1987).

Lampropeltis cf. *getulus* (Linnaeus)

Vertebrae of *Lampropeltis getulus* and *L. calligaster* are difficult to distinguish. One Carrol Creek vertebra (12530) is cautiously referred to *L. getulus* based on the presence of a flat zygosphene (usually arched in *L. calligaster*), better developed hemal keels, and relatively higher neural spines. Both species occur near the fossil site today (Dixon, 1987).

Nerodia erythrogaster (Forster)

The single fossil vertebra (12557; Fig. 1A-B) is placed in the genus *Nerodia* rather than *Thamnophis* or *Regina* based on the short and wide dorsal neural arch region (Brattstrom, 1967), vaulted neural arch, higher neural spine, and the wide, ventrally directed hypapophysis. The fossil has a higher neural spine than specimens of *N. sipedon*, but lower than that of *N. rhombifera*. Modern specimens of *N. erythrogaster* match the fossil vertebra in all respects, representing a small individual of the species. *Nerodia erythrogaster* is the only species of *Nerodia* presently occurring in the Texas Panhandle (Dixon, 1987).

Thamnophis cf. *proximus* (James) or *sirtalis* (Linnaeus)

The two vertebrae (12531) are similar to specimens of the genus *Thamnophis* and differ from those of *Nerodia* and *Regina* in being more gracile, narrower through the neural arch region, and in having narrower, more posteriorly directed hypapophyses (Parmley, 1988*b*). The fossil vertebrae are like those of *Thamnophis proximus* and *T. sirtalis* (which are difficult to separate) in being rather elongate and gracile in form, with high neural spines that are weakly concave along the anterior and posterior borders (Parmley, 1988*a*). *Thamnophis proximus* presently occurs at Carrol Creek, and *T. sirtalis* is recorded in the adjoining county (Dixon, 1987).

Thamnophis sp. indet.

Nine vertebrae (12532) are assigned to the genus *Thamnophis* based on the characters discussed above, but they are too fragmentary for specific identification.

Crotalus sp. indet.

The Carrol Creek fossil vertebra (12533) is wide through the middorsal neural arch region, has a thick, posteriorly directed hypapophysis, and has a moderately depressed neural arch (in posterior view), as in modern crotaline vertebrae. The presence of small cotylar foramina set in shallow pits suggests the genus *Crotalus*, rather than *Agkistrodon* or *Sistrurus* (Parmley, 1988*b*). *Crotalus atrox* and *C. viridis* presently have distributions that include Carrol Creek (Dixon, 1987).

Discussion

Included in the Carrol Creek herpetofauna are 12 taxa encompassing 10 genera and six species, of which several taxa indicate an aquatic environment. The presence of a tiger salmander (*Ambystoma tigrinum*) and a small leopard frog (*Rana* sp.) indicates permanent water, needed for reproduction, at Carrol Creek 32,000 years ago. Also indicating mesic habitat are a water snake (*Nerodia erythrogaster*), two garter or ribbon snakes (*Thamnophis* sp., and *T. proximus* or *T. sirtalis*), and a hog-nosed snake (*Heterodon* sp.). These taxa prefer wetland environments where they mainly prey on fish, frogs, and tadpoles. The remaining six reptilian taxa are not habitat specific, and could have lived either on nearby prairie or been associated with an aquatic environment, as they do today.

As far as can be determined, the entire Carrol Creek herpetofauna is represented by living taxa, and the fossil site is within or near their modern distributions (Dixon, 1987), indicating little change has occurred in the herpetofaunal assemblage of the Texas Panhandle over the past 32,000 years. In contrast, the Carrol Creek mammalian fauna, with four extinct and three extralimital taxa, provides evidence of major environmental change. Most of the mammals are indigenous prairie taxa, but several extralimital and extinct species support evidence of a marshy, riparian zone, and a more equable, moister climate than is present today at Carrol Creek (Kasper, 1989). Thus, while late Pleistocene environmental and climatic changes can be associated with the local and final extinction of select Carrol Creek mammalian species, these changes appear to have had nominal effect on the herpetofauna of the Texas Panhandle. However, it should be noted that other late Pleistocene faunas of Texas do include extralimital herpetological species, showing that at least minor herpetofaunal shifts from the late Pleistocene to the Recent did occur (see, for example, Parmley, 1986*a*, 1990).

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A POWER COMPARISON OF EIGHT TEST STATISTICS FOR DETECTING UNIVARIATE NON-NORMALITY

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Abstract.—This paper presents a comparison of the powers of eight proposed test statistics for testing the assumption of univariate normality. The comparison is accomplished via a Monte Carlo simulation. The Epps-Pulley statistic is found to be the best omnibus test statistic for detecting nonnormality within the framework of the skew-exponential-power family of distributions examined in this paper. *Key words*: Monte Carlo simulation; skew-exponential-power density function; kurtosis; skewness.

The problem of testing the hypothesis of univariate normality of a set of observations has been of interest to experimenters for many years due to the popularity of normal-based inference procedures. More specifically, the normality assumption generally made in regression analysis has been a driving force in motivating tests for univariate normality. As a result, many test statistics have been suggested as possible solutions to the normality-testing problem. Some of these test statistics include tests by Lilliefors (1967), D'Agostino (1971), D'Agostino and Pearson (1973), Bowman and Shenton (1975), and Shapiro and Wilk (1975).

This paper presents the results of a comparison of the powers of eight test statistics for testing univariate normality. The family of distributions utilized for the non-normal alternative distributions is the skew-exponential-power family. This family of distributions is discussed in the second section of the paper. The eight test statistics for testing the assumption of univariate normality are described in the third section. In the next section, we describe the Monte Carlo simulation utilized to find the empirical power of each of the competing test statistics and give the results of the power comparisons. Some concluding remarks are given in the final section.

THE SKEW-EXPONENTIAL-POWER FAMILY OF DISTRIBUTIONS

The set of alternative non-normal distributions used in the Monte Carlo study to compare the powers of the eight test statistics for univariate normality is the skew-exponential-power family of distributions as formulated by Azzalini (1986). This family of univariate densities is defined for all real x as

$$f(x) = 2H(\lambda x)\, g\,(x;r) \tag{1}$$

where $g\,(x;r) = (2\Gamma\,(1 + (1/r))\,\nu)^{-1} \exp\,[-\,|\,(y - \mu)\,/\nu|^{\,r}\,]$ and ν, μ, and r are fixed numbers such that $\nu = \sigma\ /\ [c(r)]^{1/2}$, $c(r) = \Gamma(3/r)$

$/\Gamma(1/r)$, $\sigma^2 = \mathrm{Var}(X)$, $r > 0$, and $\mu = E(X)$. The function $H(\cdot)$ may be taken to be any absolutely continuous distribution function having a density that is symmetric about zero.

The two parameters governing the degree of non-normality of the density function are r, which controls the tail-width of the distribution, and λ, which is a measure of skewness. Note that for $r = 2$ and $\lambda = 0$, expression (1) is the univariate normal density.

Eight Test Statistics for Detecting Univariate Non-normality

A primary concern of this paper is the comparison of the power of eight test statistics for detecting non-normality—four well-known statistics and four recently proposed statistics. For completeness, we shall give a brief description of these eight test statistics.

The Lilliefors Statistic

The Lillifors test for univariate normality, which is a Kolmogorov-Smirnov type test formulated by Lilliefors (1967), is described as follows. Let $X_1, X_2, \ldots, X_n$ be a random sample of size n from some univariate distribution function $F(\cdot)$, and let

$$Y_i = (X_i - \bar{X})/S, \; i = 1,2,\ldots,n,$$

be the studentized sample values where

$$\bar{X} = (1/n) \sum_{i=1}^{n} X_i \text{ and } S^2 = \frac{\sum_{i=1}^{n} (X_i - X)^2}{(n - 1)} .$$

Let $\Phi(\cdot)$ denote the standard normal distribution function. The Lilliefors test statistic is defined as

$$L = \sup_t \mid \Phi(t) - F^*(t) \mid$$

where $F^*(t)$ denotes the empirical distribution function of the n studentized sample values $y_1, y_2, \ldots, y_n$. Empirical critical values for the Lilliefors test statistic for varying sample sizes were given in Mason and Bell (1986).

The Sample Kurtosis Statistic

The sample kurtosis statistic for testing univariate normality has been shown to be useful for testing normality against heavy-tailed non-normal distributions. The test statistic is of the form

$$b_2 = \frac{\sum_{i=1}^{n} (X_i - \bar{X})^4 / n}{\{\sum_{i=1}^{n} (X_i - \bar{X})^2 / n\}^{3/2}}$$

where $\bar{X}$ is the mean of a random sample of size n. D'Agostino and Tietjen (1971) provided empirically based quantiles for this test statistic for sample sizes from seven to 50.

The Sample Skewness Statistic

The sample skewness statistic for testing univariate normality, which is based on the third standardized sample moment, has been shown to be useful for testing normality against alternatives of non-normality due to skewness. The test statistic is of the form

$$\sqrt{b_1} = \frac{\sum_{i=1}^{n} (X_i - \bar{X})^3 / n}{\{\sum_{i=1}^{n} (X_i - \bar{X})^2 / n\}^{3/2}}$$

where $\bar{X}$ is the mean of a random sample of size n. Empirical critical values for various sample sizes were given by Pearson (1965).

The Epps-Pulley Statistic

Epps and Pulley (1983) derived a test for univariate normality based on the empirical characteristic function of the studentized values

$$Y_i = (X_i - \bar{X}) / S, \; i = 1,2,\ldots,n.$$

The test statistic is of the form

$$EP = 1 + (2/n) \sum_{1 \leq j \leq k \leq n} \exp(-\tfrac{1}{2}(Y_j - Y_k)^2) - 2^{\frac{1}{2}} \sum_{j=1}^{n} \exp(-\tfrac{1}{4} Y_j) + n/3^{\frac{1}{2}} \; .$$

The asymptotic distribution under the null hypothesis of normality is an infinite weighted sum of independent χ_1^2 -variates. Empirical critical values for selected sample sizes were given by Baringhaus et al. (1989).

The Shapiro-Wilk Statistic

The Shapiro-Wilk statistic, derived by Shapiro and Wilk (1975), may be formulated as follows. Let $y_1 \leq y_2 \leq \ldots \leq y_n$ be the order statistics for a random sample of size n. Let

$$\bar{X} = (1/n)\sum_{i=1}^{n} X_i \text{ and } S^{2*} = \sum_{i=1}^{n} (X_i - X)^2;$$

and let

$$b = \sum_{i=1}^{[n/2]} a_{n-i+1} (y_{n-i+1} - y_i)$$

where [·] denotes the greatest integer function and the coefficients $\{a_i\}$ were given in Shapiro and Wilk (1975). The Shapiro-Wilk statistic is of the form $W = b^2 / S^{2*}$. Empirical critical values for selected sample sizes also were given in Shapiro and Wilk (1975).

A Lagrange-Multiplier Statistic Derived Within the Pearson Family

Jarque and Bera (1987) derived a Lagrange-multiplier test for univariate normality within the Pearson family. This statistic is of the form

$$LMP = n\,[\,(\sqrt{b_1}\,)^2/6 + (b^2 - 3)^2/24]$$

where $\sqrt{b_1}$ and b_2 are the sample skewness and sample kurtosis statistics, respectively. The asymptotic distribution of LMP is χ^2 with two degrees of freedom. Small sample empirical critical values were generated by Jarque and Bera (1987).

The Looney-Gulledge Statistic

Looney and Gulledge (1985) have proposed a statistic for testing univariate normality based on goodness-of-fit for a normal probability plot. This test is formulated as follows. Let $x_1, x_2, \ldots, x_n$ be a random sample from a distribution whose cdf is of the form $F\,[(x-\mu)/\sigma]$ where μ and σ are location and scale parameters. Let $y_1 \leq y_2 \leq \ldots \leq y_n$ be the order statistics of the sample and let $p_i = (i - .375) / (n + .25)$ be Blom's plotting position for the normal distribution. Finally, let $v_i = \Phi^{-1}(p_i)$ where Φ denotes the standard normal distribution. Then the Looney-Gulledge statistic is of the form

$$LG = \frac{\sum_{i=1}^{n} (y_i - \bar{y})(v_i - \bar{v})}{[\sum_{i=1}^{n} (y_i - \bar{y})^2]^{1/2}\,[\sum_{i=1}^{n} (v_i - \bar{v})^2]^{1/2}}.$$

The null hypothesis of normality is rejected for sufficiently small critical values. Small sample critical values have been generated by Looney and Gulledge (1985).

A Lagrange-Multiplier Statistic Derived Within the Skew-Exponential-Power Family

Let $\hat{\mu}$ and $\hat{\sigma}$ be the maximum likelihood estimates of μ and σ, respectively, and let m be the sample mode. A new Lagrange-multiplier test for normality within the skew-exponential-power family of distributions recently has been formulated by the authors of this paper. The new statistic for detecting univariate non-normality is of the form

$$\mathrm{LMS} = \frac{4.9726967}{n}\left[\hat{u}'\hat{w} - 0.3648186\right]^2 + n\left[(\bar{x} - m) / \hat{\sigma}\right]^2$$

where $\hat{u} = (\hat{u}_1, \hat{u}_2, \ldots, \hat{u}_n)'$, $\hat{w} = (\hat{u}_1 \ln|\hat{u}_1|\, \hat{u}_2 \ln|\hat{u}_2|, \ldots, \hat{u}_n \ln|\hat{u}_n|)'$, and $\hat{u}_i = (X_i - \hat{\mu})/\hat{\sigma}$. Empirically derived critical values have been calculated by the authors.

A COMPARISON OF THE POWERS OF THE EIGHT TESTS FOR UNIVARIATE NORMALITY

The Monte Carlo routine for comparing the power of the eight competing statistics for testing univariate normality statistics has been performed as follows. Ten thousand sets of random variates of sample size n, n = 10, 30, and 50, from each non-normal skew-exponential-power distribution considered, have been generated. Each test statistic has been evaluated for each set of sample sizes and for various skew-exponential-power distributions. The empirical powers have been calculated as the proportion of rejections at the $\alpha = .1$ level and are displayed in Table 1.

The alternative distributions considered are of varying kurtosis from light-tailed to heavy-tailed. Skewness ranged from nonskewed to moderately skewed. Table 1 reveals that no test statistic is uniformly most powerful among the non-normal distributions considered in this study. The Lilliefors test statistic performs well against symmetric heavy-tailed distributions but is poor against light-tailed distributions. As suspected, the skewness statistic $\sqrt{b_1}$ displays excellent power against skewed distributions but has low power against symmetric distributions. The LMP statistic performs well for all except symmetric light-tailed distributions. The LMS statistic has excellent power against symmetric light-tailed distributions and has good power for detecting symmetric heavy-tailed distributions, but performs poorly against moderately skewed distributions. The kurtosis statistic b_2 yields excellent power against symmetric light- and heavy-tailed distributions but is relatively poor power against skewed distributions. The Looney-Gulledge statistic performs well in situations other than the symmetric light-tailed one. The Shapiro-Wilk test has good power in most situations studied but is not

TABLE 1. Empirical power comparisons for eight test statistics for detecting univariate non-normality.

	$\alpha = .1$ $n = 10$	
Method	$r = 1, \lambda = 0$	$r = 6, \lambda = 0$
L	.3211	.1278
$\sqrt{b_1}$	.4220	.0550
LMP	.4042	.0394
LMS	.2634	.1624
b_2	.3364	.1392
EP	.4146	.0973
W	.4039	.1144
Method	$r = 1, \lambda = 1.5$	$r = 1, \lambda = 3$
L	.5629	.6006
$\sqrt{b_1}$	.4913	.5435
LMP	.4423	.4931
LMS	.2881	.3125
b_2	.3014	.3290
EP	.5106	.5704
LG	.5128	.5595
W	.5148	.5681
	$\alpha = .1$ $n = 30$	
Method	$r = 1, \lambda = 0$	$r = 6, \lambda = 0$
L	.3634	.1498
$\sqrt{b_1}$	.4058	.0217
LMP	.5309	.0646
LMS	.4532	.3543
b_2	.4448	.4031
EP	.4570	.2224
LG	.5327	.1209
W	.4650	.2681
Method	$r = 1, \lambda = 3$	$r = 6, \lambda = 3$
L	.7154	.0996
$\sqrt{b_1}$	.8217	.0447
LMP	.8120	.0476
LMS	.5584	.1582
b_2	.4768	.1608
EP	.8050	.1084
LG	.8022	.0600
W	.8058	.1160
	$\alpha = .1$ $n = 50$	
Method	$r = 1, \lambda = 0$	$r = 6, \lambda = 0$
L	.9547	.2560
$\sqrt{b_1}$	.6880	.0180
LMP	.9170	.1985
LMS	.9450	.5449
b_2	.8728	.6356
EP	.9456	.3712
LG	.9694	.2138
W	.9491	.3429

TABLE 1. Continued.

Method	$r = 1, \lambda = 1.5$	$r = 6, \lambda = 1.5$
L	.9839	.1264
$\sqrt{b_1}$	.9916	.2313
LMP	.9913	.2021
LMS	.9280	.1829
b_2	.9944	.1483
EP	.9949	.2562
LG	.9941	.1970
W	.9944	.1825

superior for any alternative distribution examined. Finally, the Epps-Pulley statistic appears to be the best omnibus test for detecting non-normality against the non-normal distributions considered here.

COMMENTS

In summary, the EP test statistic for univariate normality is quite easy to apply and yields good power against the alternative skew-exponential-power distributions examined in this paper. However, the set of alternative non-normal distributions we examined is limited. Also, we see that the traditional test statistics for detecting non-normality, such as the Lilliefors and Shapiro-Wilk tests, may not be as powerful against a large class of alternative non-normal distributions as some of the newer test statistics. Finally, we note from Table 1 that for sample sizes less than 30 and for certain light-tailed distributions ($r = 6, \lambda = 0$ and $r = 6, \lambda = 3$), the $\sqrt{b_1}$, LMP, and LG statistics possess powers that are less than, or equal to, the level of the test. Hence, users should be especially wary of these test statistics if the sample size is relatively small and they have no information that their data are sampled from distributions that are not light-tailed.

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GENERAL NOTES

GENETIC HOMOGENEITY IN GEOGRAPHICALLY REMOTE POPULATIONS OF PARTHENOGENETIC *CNEMIDOPHORUS NEOMEXICANUS* (SAURIA: TEIIDAE)

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Cuellar (1977) found an unusually high level of genetic homogeneity in four populations of the parthenogenetic lizard, *Cnemidophorus neomexicanus*, located over a 256-kilometer transect in northern New Mexico; more than 99% of the 132 allografts exchanged among 56 lizards were permanently retained. Low clonal diversity in *C. neomexicanus* also has been documented through allozyme electrophoretic analyses of several populations in New Mexico; Parker and Selander (1984) found only two clones based upon a malate dehydrogenase locus among 112 specimens from seven localities and Cole et al. (1988) found only two clones based upon a transferrin *a* locus in 23 specimens from four localities. Recently, we captured a live individual of *C. neomexicanus* from a disjunct population in eastern New Mexico (Leuck et al., 1981; Walker et al., 1990) and a second live individual from the newly discovered southernmost outpost of the parthenogen near the Rio Grande in southern Texas (Cordes et al., 1989). It became apparent that an exchange of allografts between individuals of *C. neomexicanus* from localities separated by a hiatus of about 640 kilometers would represent a highly significant test of genetic homogeneity. Because there is little likelihood of obtaining additional material from these populations, the implications of the results of allograft exchanges between the two available lizards are herewith presented.

A live adult *C. neomexicanus*, University of Arkansas Department of Zoology (UADZ 3740-New Mexico), was obtained on 3 August 1989 at the North Area Campground at Conchas Lake, San Miguel Co., New Mexico, and a live subadult (UADZ 3908-Texas) was captured on 26 September 1989 at 3.3 km. S Candelaria, Presidio Co., Texas. Husbandry methods pertaining to captive lizards and surgical techniques involved in graft exchanges were described by Abuhteba and Cordes (1990). Each pair of allografts consisted of 2.0-millimeter circular skin patches excised from one of the dorsolateral stripes of each donor; these were reciprocally exchanged to the donor site perpendicular to the recipients dorsolateral stripes. The break in stripe continuity facilitated subsequent evaluations as well as photographic records (Fig. 1).

Our analyses were made possible by the evidence presented in several previous studies. First, individuals within gonochoristic species such as *C. sexlineatus* and *C. tigris* not only reject xenografts from other species, they also reject intraspecific allografts (Maslin, 1967; Cuellar and Smart, 1977). Second, Maslin (1967) has established that parthenogenetic *C. neomexicanus* rejects xenografts from other species such as *C. tesselatus*. The latter results indicate that the acceptance of homografts within individuals of *C. neomexicanus* and the high frequency of acceptance of allografts between individuals of *C. neomexicanus* are related to high levels of genetic homogeneity, not to the absence of an immune response in this parthenogen (Cuellar, 1977).

Our experiment consisted of exchanges of pairs of allografts between UADZ 3740 from New Mexico and UADZ 3908 from Texas on 10 October 1989 (Fig. 1A), 10 November 1989 (Fig. 1B), and 10 December 1989 (Fig. 1C). Both lizards returned to their daily routines of basking, feeding, and inactivity within 24 hours of surgery. Periodic examination of each of the three allografts on both lizards revealed that each allograft healed into place without any sign of complications (Fig. 1). UADZ was sacrificed on 19 March 1990 and tissues from this animal were deposited in the frozen tissue collection at the Louisiana State

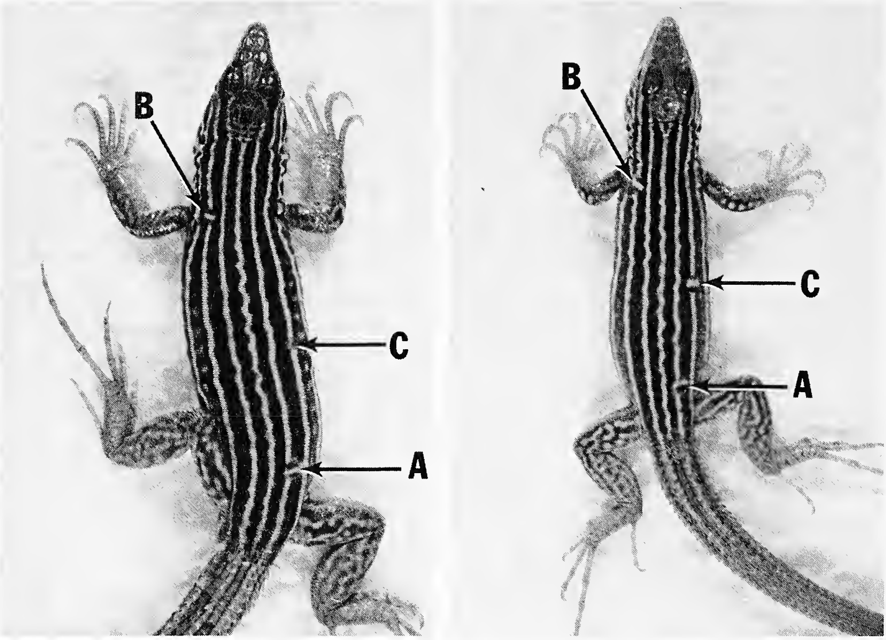

FIGURE 1. Accepted allografts exchanged between UADZ 3740-New Mexico (left, San Miguel County, New Mexico) and 3908-Texas (right, Presidio County, Texas) on (A) 10 October 1989, (B) 10 November 1989, and (C) 10 December 1989.

University Medical Center. Tissues from UADZ 3908 will be stored at that facility following conclusion of additional experiments.

The implications of our experimental trials are profound. Based upon the absence of an immune response to allografts exchanged between two lizards from populations latitudinally separated by a hiatus of about 640 kilometers, we infer that they are cloned descendants, many generations removed, of the same parthenogenetic female. These data, coupled with the more comprehensive experiments of Cuellar (1977), indicate that the level of genetic homogeneity in *C. neomexicanus* is indeed astonishingly high. In fact, all of the available data on histocompatibility in *C. neomexicanus* can be reconciled to an evolutionary model in which the entire taxon is comprised of the descendants of a single parthenogentically capable hybrid *C. marmoratus* (= *C. tigris*) × *C. inornatus* female as initially suggested by Cuellar (1977). Moreover, electrophoretic data indicate that surprisingly little postformational change in the basic hybrid genotype has occurred at other gene loci (Parker and Selander, 1984; Cole et al., 1988).

Collections of *Cnemidophorus* in New Mexico were made under authority of New Mexico Department of Game and Fish permit no. 1850; collections in Texas were made under authority of Texas Parks and Wildlife Department permit no. 61. Mr. Al Real, general manager of the Mesquite Ranch, Presidio County, provided lodging and field assistance. The Graduate Studies Committee, University of Arkansas, provided a Graduate Grant-in-Aid of Research Award in support of field work associated with this study.

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STATUS OF THE JAVELINA, *TAYASSU TAJACU*, IN NORTH-CENTRAL TEXAS AND SOUTHERN OKLAHOMA

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Hall (1981) mapped northern Texas as within the range of the javelina or collared peccary, *Tayassu tajacu*, on the basis of a supposed record from Montague County, which we have been unable to verify and that was not recognized by Sowls (1984). The species was introduced west of Montague County in north-central Texas during the mid-1900s (Dalquest, 1968; Dalquest and Horner, 1984), although no voucher specimens for Texas from north of the Hill Country have been reported previously. Two recent acquisitions in the Midwestern State University (MWSU) Collection of Recent Mammals are reported herein, as are observations that first document the occurrence of *T. tajacu* in Oklahoma.

On 16 February 1987, a farmer shot one of three adult javelinas from his porch, 12 mi. N Jacksboro, Jack Co., Texas, where they were foraging in a winter wheat field. An unsexed skull (MWSU 15262), that of a young adult, was retrieved by MWSU biology student Dennis Smith. The weathered skull of a subadult javelina was recovered 2 mi. N Holliday, Wichita Co., Texas, by MWSU biology student Toni L. Robertson on 25 January 1990. The locality is on an oil lease in mesquite scrubland, near where at least two live animals were observed a few years earlier by the collector's husband. This specimen (MWSU 16874) constitutes the northernmost vouchered record of *T. tajacu* from Texas.

We have no way of knowing how many times and places the javelina may have been introduced in the region during past years, or if the northern herd is isolated from central Texas populations. However, animals still survive today from those stocked on the

Waggoner Ranch during the 1940s and 1950s. No formal census ever has been taken of the ranch herd although estimates have ranged as high as several hundred individuals.

Signs and sightings of the animals routinely are noted in each of the six Texas counties included among Waggoner Ranch holdings (Archer, Baylor, Foard, Knox, Wichita, and Wilbarger counties). All are presumed to have descended from the mid-century introductions on the ranch. The Jack County population may be wanderers from the Waggoner herd or they may represent another stocking effort. Animals range north as far as the Red River in some areas, and sign has been observed on the Red River floodplain of Tillman County, Oklahoma, immediately adjacent to Wichita County. Javelina forays into Oklahoma evidently are limited to the periphery of that state; to date the species does not appear to be established there.

Although resident white-tailed deer (*Odocoileus virginianus*) are censused routinely on the Waggoner Ranch, only rough estimates are available for the javelina. The unusually severe winter of 1983-84 reduced the population by about half, and recovery is still incomplete; young animals apparently were particularly affected by the snow and freezing temperatures. Sowls (1984) suggested that respiratory diseases might be a major limiting factor, particularly during severe winters. Following extended periods of temperatures below 20° F, surviving animals have been reported to "walk funny," as if walking on an uncomfortable surface, and exhibit disoriented behavior. The coarse but sparse coat apparently does not offer sufficient insulation during cold periods; observations suggest debilitation and the effects of hypothermia.

Texas Parks and Wildlife game wardens Butch Shoop and Luett McMahan and Waggoner Ranch wardens Ronny Jones and Glen Collier kindly shared with us their knowledge of north Texas peccaries. Bob Grant, J. Knox Jones, Jr., and Richard W. Manning provided assistance in our search of relevant literature.

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INTEGRATION BY PARTS

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This note is intended to help organize the integration by parts methods. This method is especially helpful to the teacher who uses integration by parts as a tool. The usual formula,

$$\int u\,dv = uv - \int v\,du\,,$$

can be arranged in a matrix,

$$\begin{array}{ccc} + & D & I \\ \searrow & u & dv \\ -\int\rightarrow & du & v. \end{array}$$

The "uv" term is referred to as a diagonal product and the "vdu" term as a horizontal product. Always alternate the signs of the products as you go down the matrix, and if a horizontal product is used, it must be integrated.

1.—Integral problems that require repeated application of the integration by parts method:

$$\int x^3 e^x dx = x^3 e^x - 3x^2 e^x + 6xe^x - 6e^x + c$$

$$\begin{array}{lll} + & D & I \\ \searrow & x^3 & e^x \\ - \searrow & 3x^2 & e^x \\ + \searrow & 6x & e^x \\ - \searrow & 6 & e^x \\ & 6 & e^x \ . \end{array}$$

2.—Integral problems where "u" is not a polynomial:

$$\int x \ln x \, dx = \frac{x^2}{2} \ln x - \int \left(\frac{1}{x}\right)\left(\frac{x^2}{2}\right) dx$$

$$\begin{array}{lll} + \searrow & D & I \\ & \ln x & x \\ -\int \rightarrow & \frac{1}{x} & \frac{x^2}{2} \ . \end{array}$$

Note that in this problem the horizontal product was integrated the first place possible, but this is not necessary, because

$$\int x \ln x \, dx = \frac{x^2}{2} \ln x - \left(\frac{1}{x}\right)\left(\frac{x^3}{6}\right) + \int \left(-\frac{1}{x^2}\right)\left(\frac{x^3}{6}\right) dx$$

$$\begin{array}{lll} + \searrow & D & I \\ - \searrow & \ln x & x \\ \searrow & \frac{1}{x} & \frac{x^2}{2} \\ +\int \rightarrow - & \frac{1}{x^2} & \frac{x^3}{6} \end{array}$$

gives the same result.

3.—Integral problems where the horizontal product is an integration by parts problem:

$$\int (\ln x)^2 \, dx = x \, (\ln x)^2 - \int \left(\frac{2 \ln x}{x}\right) x \, dx = (\ln x)^2 - 2 \left[x \ln x - \int \left(\frac{1}{x}\right) x \, dx\right.$$

$$\begin{array}{lllllll} & D & I & & & D & I \\ \searrow & (\ln x)^2 & dx & & \searrow & \ln x^2 & dx \\ \rightarrow & \frac{2 \ln x}{x} & x & & \rightarrow & \frac{1}{x} & x \ . \end{array}$$

4.—Integral problems where a horizontal product is a constant multiple of the origonal problem:

$$\int e^x \sin x \, dx = e^x (-\cos x) - (e^x)(-\sin x) + \int e^x (-\sin x) \, dx$$

$$\begin{array}{ll} \quad D & I \\ \searrow e^x & \sin^x \\ \searrow e^x & -\cos x \\ \rightarrow e^x & \sin x \, . \end{array}$$

5. Integration by parts problems that are more difficult:

$$\int \frac{x^3 e^{x2}}{(x^2+1)^2} dx = \frac{-x^2 e^{x2}}{2(x^2+1)} + \int x e^{x2} \, dx$$

$$\begin{array}{ll} \quad D & I \\ \searrow x^2 \, 2^{x2} & \dfrac{x}{(x^2+1)^2} \\ \rightarrow e^{x2}(2x)(x^2+1) & \dfrac{-1}{2(x^2+1)} \end{array}$$

$$\int x^2 \sqrt{x-1} dx = \frac{2}{3} x^2 (x-1)^{3/2} - \frac{8}{15} x (x-1)^{5/2} + \frac{16}{105} (x-1)^{7/2} + c$$

$$\begin{array}{ll} \quad D & I \\ \searrow x^2 & (x+1)^{1/2} \\ \searrow 2x & \frac{2}{3}(x-1)^{3/2} \\ \searrow 2 & \frac{4}{15}(x-1)^{5/2} \\ 0 & \frac{8}{105}(x-1)^{7/2} \end{array}$$

In conclusion, always alternate signs of the product terms; when the horizontal product term is used, it must be integrated.

ADDITIONAL DISTRIBUTIONAL RECORDS OF MAMMALS ALONG THE BOUNDARY OF THE KANSAN-TEXAN BIOTIC PROVINCES IN NORTH-CENTRAL TEXAS

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Garner and Bluntzer (1975) reported several distributional records of mammals from the boundary region of the Kansan-Texan biotic provinces in Texas. Three additional records are noteworthy and are reported herein.

Sylvilagus aquaticus aquaticus (Bachman).—An adult female swamp rabbit (TSU 587) was taken 3 mi. (4.8 km.) E Zephyr, Brown County, by Dr. Eston O. Morrison, with bow and arrow, on 23 April 1975. Additionally, Garner sighted *S. a. aquaticus* on several occasions along Rush Creek, 8.5 mi. (13.7 km.) E Ranger, Eastland County, in November 1981. Moreover, Tarleton students have reported sightings along Palo Pinto Creek below the dam on Palo Pinto Reservoir, Palo Pinto County. In our opinion, swamp rabbits occur sparsely along the Palo Pinto and other nearby tributaries of the Brazos River. Davis (1974) indicated the western limits of distribution for this species in Limestone and Falls counties along the Brazos. Hall (1981) listed marginal locations from the Medina River, 18 mi. (29 km.) SW San Antonio, Bexar County, and from Travis and Limestone counties to the south and east, and from Montague County to the north. Schmidly (1983) reported examining specimens from McClennan, Falls, and Dallas counties to the east. Our specimen extends the known range 100 miles (160 kilometers) to the west from McClennan County and 175 miles (280 kilometers) north from the San Antonio record. Dalquest and Horner (1984) reported specimens from Cooke County and sightings in Montague and Wise counties.

Microtus pinetorum auricularis (Le Conte).—An adult female pine vole (TSU 1006) was trapped in a modified Sherman live trap 2 mi. (3.2 km.) NE Stephenville, Erath County, on 6 October 1989, in a post oak (*Quercus stellata*)-mesquite (*Prosopis glandulosa*) association. The understory supported poison ivy, *Rhus toxicodendron*, Johnson grass, *Sorghum halapense*, and several species of grammas (*Bouteloua* sp.). The trap site was adjacent to fields planted with peanuts. Extensive live-trapping was carried out on the area from 23 August through 11 November 1989. Trapping results yielded the following species and numbers of specimens in addition to the lone vole captured: *Chaetodipus hispidus*, 18; *Peromyscus leucopus*, 35; *Baiomys taylori*, 6; *Mus musculus*, 4.

Populations of *M. pinetorum* probably occur as relicts throughout the Western Cross Timbers Region of Texas. Dr. Phillip Murry, a paleontologist at Tarleton State University, assured the authors that pine voles are one of the most common rodents taken from archaeological sites throughout this area. Cleveland et al. (1984) recorded a specimen from 22.4 km. (14 mi.) W Hillsboro, Hill County. They noted that the preferred habitat of this species is in transitional areas; transitional habitats in the vicinity of Stephenville are considerably more xeric than those in Hill County. Our specimen extends the known distribution 50 miles (80 kilometers) to the west from the Hill County record.

Two subspecies of *M. pinetorum* occur in Texas—*M. p. nemoralis* in the extreme northeastern part of the state and *M. p. auricularis* in the remainder of the range in Texas (Hall, 1981; Schmidly, 1983). *M. p. nemoralis* differs from *M. p. auricularis* by its slightly larger size and duller coloration (Schmidly, 1983). Specimens of *M. p. nemoralis* from Missouri that we examined are much larger and darker than our specimen. The specimen reported by Cleveland et al. (1984) was obtained near the Brazos River. We also assigned our specimen to *M. p. auricularis* because the local drainage system is associated with the Brazos River and may have acted as a corridor for dispersal of the species.

Conepatus mesoleucus mearnsi (Lichtenstein).—A specimen of the western hog-nosed skunk was found dead along a highway (U.S. 281) 0.8 mi. (1.28 km.) S Interstate Highway I-20 near Santo, Palo Pinto County. Habitat consisted of dense post oak (*Q. stellata*) over a level terrain strewn with large boulders. Decomposition of the specimen prevented sex determination, preservation of the skin, and the recording of external measurements. The skull (TSU 1007) is intact and the teeth are noticeably worn. Terry Joy has sighted other individuals of the species near Brock in Parker County. Distributional records of the western hog-nosed skunk indicate a northward extension of its known range in Texas (Raun and Wilks, 1961; Packard and Garner, 1964; Schmidly, 1983, 1984; Manning et al., 1986). Schmidly (1983) reported a specimen from Collin County. Manning et al. (1986) reported a specimen from 5 mi. (8 km.) N Brownwood, Brown County. The specimen from Palo Pinto County extends the known range 80 miles (128 kilometers) northeast from Brown County, and 100 miles (160 kilometers) southwest from Collin County.

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DISTRIBUTIONAL RECORDS FOR SEVERAL SNAKES FROM HONDURAS

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While United States military personnel were conducting training in Honduras, a number of snakes were captured and preserved. An examination of the specimens revealed several noteworthy extensions of known range.

Loxocemus bicolor Cope.—The burrowing boa has been documented from only five localities in western Honduras (Wilson and Meyer, 1985). On 12 May 1989, a male *L. bicolor* was obtained 2.5 km. S Sabana Larga, Department of Yoro. This specimen represents a range extension of approximately 70 kilometers southeast of Tela, Department of Atlantida, and 90 kilometers northeast from 6.4 km. N Comayagua, Department of Comayagua (Wilson and Meyer, 1985).

Oxybelis fulgidus (Daudin).—On 7 May 1989, a vine snake was taken 14.2 km. SE Sabana Larga, Department of Yoro. This specimen represents a extension of known distribution of approximately 90 kilometers southeast of Progreso, Department of Yoro, and 130 kilometers southwest of Trujillo, Department of Colon (Wilson and Meyer, 1985).

Thamnophis proximus (Say).—On 24 September 1989, an adult female garter snake was captured under a board on the rifle range at Soto Cano Air Force Base, Department of Comayagua. This record extends the known range from 9 km. SE Ville de San Antonio, Department of Comayagua, northwestward by approximately 40 kilometers and is the northwesternmost record for this species in Honduras.

Boa constrictor Linnaeus.—This boa has been recorded as occurring throughout Honduras except for the north-central highlands (Wilson and Meyer, 1985). An adult female was captured 15.7 km. SE Sabana Larga, Department of Yoro. This locality fills in a gap between Guaymas District, Department of Atlantida, and El Zamorano, Department of Francisco Morazan, and is the first known from the north-central highland region.

Trimorphodon biscutatus (Dumeril, Bibron, and Dumeril).—A male lyre snake was taken 2.5 km. S Sabana Larga, Department of Yoro. This specimen represents a range extension of 40 kilometers southwest of 0.5 km. N Coyoles, Department of Yoro, and is only the second documented record of *T. biscutatus* from northern Honduras.

All specimens are deposited in the Texas Cooperative Wildlife Collection, Texas A&M University. We thank Sergeants Martin, Hankle, and Marthers for aid in collecting specimens, Dr. James Dixon for identifying the snakes, and Dr. J. Knox Jones, Jr., for his critical review and comments on the manuscript.

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REMAINS OF SMALL MAMMALS RECOVERED FROM BARN OWL PELLETS FROM CROSBY COUNTY, TEXAS

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On 7 May 1988, one of us (Manning) and David A. McCullough flushed a pair of barn owls (*Tyto alba*) from an abandoned farmhouse located 6 mi. S and 3 mi. E Cap Rock, Crosby County, Texas. The locality is both a few miles south and a few miles east of the Llano Estacado escarpment, just south of the Salt Fork of the Brazos River. Mesquite grassland, on relatively sandy soil, is the dominant vegetative association in the immediate area, but some cultivated fields (cotton) were noted nearby. A total of 57 cast pellets from the owls was collected. We returned to the same locality on 25 February 1990 and obtained an additional 91 pellets; a single owl occupied the house at that time. On a third visit (27 April 1990), we flushed a barn owl from a nest containing five eggs, and collected 49 pellets; a screech owl (*Otus* sp.) was found roosting in another room in the house.

Remains of 14 species of small mammals were recovered from the pellets. Species identified, number of individuals (based only on cranial parts in order to avoid the possibility of double counting), and percent of total are given in Table 1. Other than mammals, parts of insects (grasshoppers and beetles) were found in pellets from the first two samples, and remains of six passerine birds were found in those obtained in February 1990. Parts of two passerines and one charadriiform were recovered from pellets collected in April 1990.

We have no direct knowledge as to how long owl pellets remain intact after regurgitation. Scattered pellet matrix and skeletal parts of prey species at several places in the abandoned homestead indicated breakdown of pellets. Presumably, pellet integrity is related, in part at least, to a number of environmental variables—precipitation, relative humidity, wind, temperature, and so forth. It seems reasonable to assume that pellets deposited in a relatively protected setting, such as an abandoned house (even though open to the elements), might survive intact for as long as three to six months. If this is true, remains found in pellets recovered on 27 April and 7 May could represent animals taken in late winter and early spring, whereas those obtained in late February probably represent prey species captured in autumn and in early and mid-winter.

Based on data presented in Table 1, the small muroid rodents *Reithrodontomys* and *Baiomys*, and the hispid pocket mouse, *Chaetodipus hispidus*, are important staples in owl

TABLE 1. Number of individual mammals (percent of total in parentheses) recovered from barn owl pellets from Crosby County, Texas.

Species	May 1988 (57 pellets)*	February 1990 (91 pellets)*	April 1990 (49 pellets)
Cryptotis parva	9 (6.1)	7 (3.0)	1 (0.9)
Notiosorex crawfordi	1 (0.7)	—	—
Sylvilagus sp.	—	1 (0.4)	—
Geomys bursarius	—	3 (1.3)	2 (1.7)
Perognathus flavus	5 (3.4)	55 (23.9)	10 (8.7)
Chaetodipus hispidus	14 (9.5)	46 (20.0)	24 (20.8)
Dipodomys ordii	4 (2.7)	8 (3.5)	23 (20.0)
Reithrodontomys montanus	61 (41.2)	65 (28.3)	40 (34.8)
*Peromyscus***	6 (4.0)	10 (4.3)	3 (2.6)
Baiomys taylori	21 (14.2)	19 (8.3)	10 (8.7)
Onychomys leucogaster	5 (3.4)	3 (1.3)	1 (0.9)
Neotoma micropus	3 (2.0)	5 (2.2)	—
Sigmodon hispidus	17 (11.5)	8 (3.5)	—
Unidentified muroid	—	—	1 (0.9)
Mus musculus	2 (1.3)	—	—

*Includes also a few disassociated cranial parts from bottom of collecting sacks.

**Mostly *Peromyscus maniculatus* but at least one *Peromyscus leucopus* included.

diets throughout the year. Other species such as *Peromyscus* and *Dipodomys* also are taken year round, but in smaller numbers. There are, however, differences between the samples, most notably in the numbers of silky pocket mice (*Perognathus flavus*). *P. flavus* hibernates in the colder months, likely accounting for the relatively small numbers of this heteromyid in pellets obtained in April and May. Considering larger species, immature individuals evidently are more readily captured by barn owls than are adults, which also would result in seasonal variation. All *Sigmodon* save one, most *Neotoma*, all *Geomys*, and the one *Sylvilagus* were young animals. Nothing in our data suggests that barn owls are other than opportunistic predators.

Most pellets contained remains of more than one mammal, and some revealed a surprisingly high number, mostly species of small size. For example, one pellet contained evidence of at least seven different individuals (four *Cryptotis*, one *Notiosorex*, one *Perognathus*, and one *Peromyscus*), a second yielded nine (one *Cryptotis*, four *Perognathus*, one *Reithrodontomys*, and three *Baiomys*), yet another had nine (eight *Reithrodontomys* and one *Baiomys*), and a fourth contained seven (one *Chaetodipus*, three *Reithrodontomys*, and three *Baiomys*).

There are relatively few published records of mammals from Crosby County; those recorded here provide, therefore, several new records from that area. Perhaps most notable are the two shrews, *Cryptotis parva* and *Notiosorex crawfordi*. The pygmy mouse, *Baiomys taylori*, also is noteworthy because, although represented in relatively large numbers, it is a rather recent immigrant, probably reaching Crosby County from the southeast no more than about two decades ago.

THE EASTERN COTTONTAIL, *SYLVILAGUS FLORIDANUS*, IN EASTERN NEW MEXICO

Frederick B. Stangl, Jr., and Mark A. Earhart
Department of Biology, Midwestern State University, Wichita Falls, Texas 76308

A hiatus in the mapped range of *Sylvilagus floridanus* in New Mexico (Hall, 1981) separates *S. f. cognatus* of the southwestern two-thirds of the state (see also Findley et al., 1975) from *S. f. llanensis* of the Texas Panhandle (Jones et al., 1988), where the species is uncommon westwardly. A recent record of the eastern cottontail from Union County, New Mexico (Dalquest et al., 1990), provided the first documentation for *S. floridanus* from the eastern part of the state. We report herein a second specimen of this species from eastern New Mexico, which is deposited in the Collection of Recent Mammals, Midwestern State University (MWSU). These new records suggest the two subspecies of the eastern cottontail are not geographically separated from each other as Hall's (1981) map implied.

The skull of an adult female (MWSU 17021) was salvaged on 9 December 1989 from a hunter who had shot the animal in an alfalfa field, 6 mi. SW Clovis, Curry County. Several other cottontails, presumably of the same species, and jackrabbits (*Lepus californicus*) were observed in the same vicinity. As more specimens of *S. floridanus* from the previously presumed hiatus become available, the extent of any intergradation between the subspecies *cognatus* and *llanensis* can be determined, and distribution of the two races more specifically delineated.

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Floyd F. Davidson, 1906-1990
President of the Academy, 1965

The legacy of Floyd Davidson extends beyond the Baylor University campus. His legacy is people—hundreds of them touched by this single life.

Born in Ferris, Texas, in 1906, Floyd entered Baylor and received the B.A. in 1932 and M.A. the following year. After a six-year period as a high school principal, his love of learning forced him back into higher education and he entered the University of Texas where he completed the doctorate in 1941. After serving in the army during World War II, he joined the Baylor Biology faculty and became one of its leading scientists. As one of those who entered the university teaching profession in the era prior to todays narrow specialization, Floyd taught an eclectic array of subjects ranging from animal histology to phycology—the field of his research interest.

The question of the production and regulatory role of algal organic products fascinated him. His first publication following the war was on plant hormones and the growth of marine algae. His later publications continued in the same area as he sought to understand the ecological consequences of the release of antibiotics by algae. To support this work, Floyd obtained the first research grant awarded by the Federal Water Pollution Control Administration section of the National Institutes of Health.

Floyd left a legacy of service to university, the city, and the Texas academic community. He served faithfully as Chairman of Biology at Baylor until his mandatory retirement. Love of the alma mater drew him back to campus, and he effectively served as Director of the Retired Professors Center.

The local community was not without Floyd's service, he was deacon of the First Baptist Church, Past Master of the Masonic Lodge, an active Rotarian, and a worker, although without sons, in the Heart of Texas Boy Scout Council. A active supporter of the Texas Academy of Science, he also served the Texas Ornithological Society and the North Texas Biological Society.

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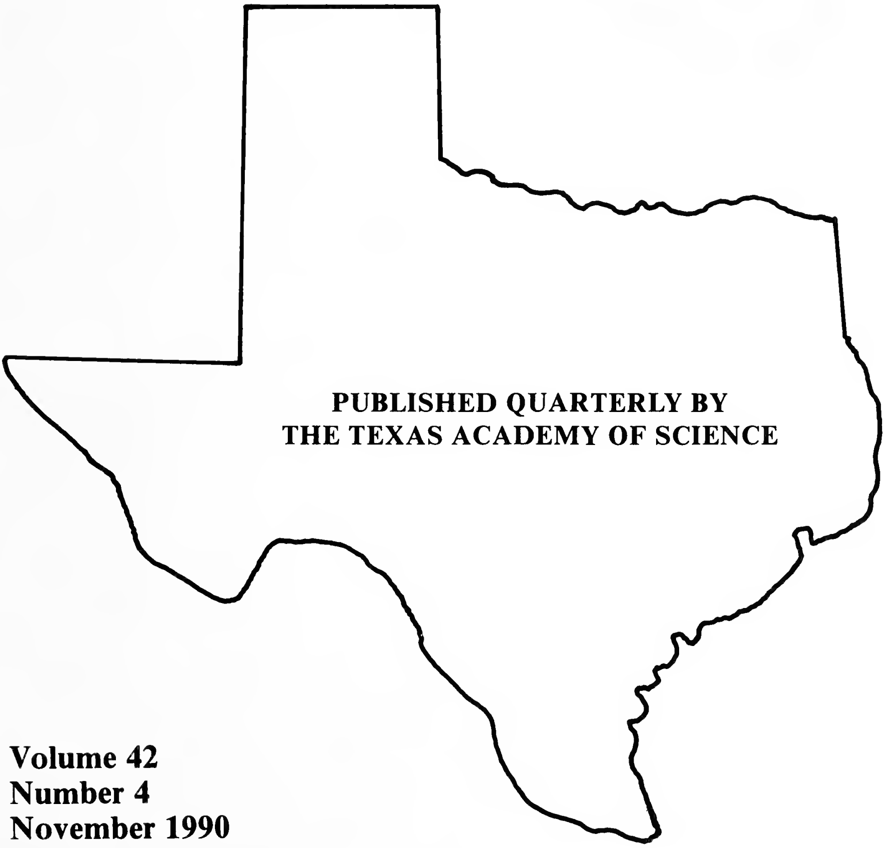

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ANALYSIS OF ASYMMETRY AND MORPHOMETRIC VARIATION IN NATURAL POPULATIONS OF CHROMOSOME-DAMAGED MICE

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Abstract.—Increased fluctuating asymmetry (FA) has been postulated to result from increased heterozygosity, inbreeding, hybridization, increased selection, and environmental stress, among other things. The general suggestion is that the genome, if critically disrupted, is unable to buffer adequately against ontogenetic accidents. Environmental stress, in contrast to the other factors listed above, might act either directly (physiologic disruption during ontogeny) or indirectly (through disruption of the genome) to increase FA. We examined FA and overall morphometric variation in two species of sigmodontine rodents from a hazardous waste dump site and from nearby waste-free control areas. The mice from the waste site previously had been shown to have significantly higher levels of chromosome damage than those in the control areas. Differences in FA were found to be nonsignificant between waste and waste-free sites. In contrast, analysis of overall morphometric variation showed both species to differ significantly between sites, although the nature of this response contrasted sharply between the species. The finding of no differences in fluctuating asymmetry associated with the site differences is judged to be real, and we conclude that if genomic characteristics do function to buffer the organism against asymmetry, this capability may not be affected by disruption at the gross chromosomal level. *Key words*: fluctuating asymmetry; developmental stability; morphometrics; mutagens; environmental stress; *Peromyscus*; *Sigmodon*.

Asymmetry is the difference in right-side and left-side expression of a characteristic in a bilateral organism. Mathematically, there are three expressions of asymmetry. Directional asymmetry pertains when the populational mean of the right-minus-left values is not zero. Antisymmetry, which includes skewness and kurtosis, occurs when the distribution of right-minus-left values is non-normal. Fluctuating asymmetry (FA) is the remaining right-left difference, and is expressed within a population as a normal distribution with a mean of zero. An evaluation of populational FA will measure, therefore, the amplitude (variance) of this normal distribution, generally with respect to that of another (reference) population.

The study of fluctuating asymmetry *per se* began with the work of a small group of researchers including Thoday (1953, 1956, 1958), Van Valen (1962), and Soulé (1966, 1967). Interest in the phenomenon then waned, but has revived within the last decade, perhaps due to a better general understanding of the genetics and evolutionary processes that might be involved. Early perceptions of the importance of FA were summarized by Jackson (1973), who pointed out that "the level of fluctuating asymmetry has been considered a measure of buffering capacity in development, since any differences between paired structures that are nonconsistent are thought to result from developmental accidents (Thoday, 1958)," and further (following Soulé, 1967) that "in particular, any factors that destroy coadapted gene complexes were hypothesized to increase asymmetry." Gene complexes presumably will become coadapted in stable populations in stable environments. Instability of either the population or the environment could presumably disrupt the genomic buffering capacity or render it ineffective in a novel or variable environment (Graham and Felley, 1985). Conditions under which this might occur, and which have been suggested as potentially resulting in increased FA, are hybrid zones, increased inbreeding, directional selection, and systemic or environmental stress (Palmer and Strobeck, 1986).

The relationship of systemic stress to fluctuating asymmetry is of particular interest, because there are two potential pathways for induction of FA by stress. It could be accomplished indirectly, by disruption of the genome (the mechanism presumably common to the conditions listed above); or it could occur by a more direct means in which the stress does not disrupt the genome, but exceeds some threshold beyond which it cannot buffer against ontogenetic accidents.

Previous evaluations of FA and environmental stress have not shown a clear pattern of results. Several studies have shown increased FA with increased stress, including various stress factors on several kinds of mammals and a fish species (Palmer and Strobeck, 1986). For instance, Bailit et al. (1970) found positive correlations between FA and general environmental stress in human populations; Siegel and Smookler (1973) and Siegel and Doyle (1975*a*) found an association with noise stress in *Rattus*; and Scuilli et al. (1979) found positive associations between FA and heat, cold, noise, and nutritional stresses in *Rattus*.

A number of studies concerning systemic stress effects on FA have had ambiguous results. Thoday (1956) and Bradley (1980) found results to differ among lab populations of *Drosophila* in studies of temperature effects on FA. Siegel and Doyle (1975*b*) similarly found no clear trend in studies of noise, cold, and behavioral stress on *Mus* and *Peromyscus* populations. Ames et al. (1979) found in studies of centrarchid fishes that heat did not affect FA levels, although mercury levels did. Jagoe and Haines (1985) were unable to determine with certainty whether FA levels in natural fish populations were affected by water pH levels. Few studies have shown no change in FA with increased stress—Palmer and Strobeck (1986) listed only one, in which Angus and Schultz (1983) evaluated FA levels in fishes subject to elevated temperatures.

It is extremely important also to ascertain more definitively the relationship between fluctuating asymmetry (and other complex forms of morphometric variation), and any conditions involving genetic reorganization within and among populations. Several workers have examined the relationship between FA and enzyme heterozygosity levels. Most generally, these studies have found an inverse relationship between asymmetry and heterozygosity levels both among and within populations (for example, Soulé, 1979; Kat, 1982; Vrijenhoek and Lerman, 1982; Biémont, 1983; Leary et al., 1983, 1984, 1985*a*, 1985*b*; and Wayne et al., 1986). However, see Leary et al. (1984) for conflicting results, and Willig and Owen (1987*a*) for an opposing point of view on the Wayne et al. paper. Also, Patterson and Patton (1990) reported nonsignificant correlations between FA and heterozygosity among populations of pocket gophers. To our knowledge, no investigator has evaluated the relationship between fluctuating asymmetry and genetic variation at the gross chromosomal level, or with respect to variation in DNA content.

In the context of this background, we undertook to evaluate asymmetry and other morphometric variation in natural populations of two species of cricetid rodents occurring on a heavily polluted site in Brazos County, Texas, in comparison with appropriate control populations. Our sample specimens of both species of mice from the polluted site had been shown to have approximately four-fold increases in chromosomal lesions per cell, and similar increases in number of cells (per individual) in which chromosomal lesions were found (McBee et al., 1987). Also, one species (*Peromyscus*) was examined using flow cytometry and was shown to have a significantly higher coefficient of variation of intraindividual cellular DNA content on the polluted site (McBee and Bickham, 1988). Thus, with the animals clearly registering genetic responses to the environmental contaminants, these populations should be exemplary models with which to evaluate fluctuating asymmetry and other morphometric phenomena potentially associated with systemic stress and genetic disruption.

MATERIALS AND METHODS

Rodents were collected from natural populations occurring on a petrochemical waste disposal site and on two nearby control sites. Site conditions, trapping localities, and protocol were described in detail by McBee et al. (1987). Of the several species occurring on the sites, the white-footed mouse, *Peromyscus leucopus*, and the hispid cotton rat, *Sigmodon hispidus*, were trapped in sufficient numbers for the statistical analyses described here (Table 1). All animals used in this study were adults (see McBee et al., 1987, for age criteria). Preliminary tests indicated that individuals from the two control sites could be combined into a single sample. This was done to increase within-cell sample sizes in all statistical tests. In tests for directional asymmetry and antisymmetry, comparisons could be made between sexes and between experimental and control-site groups, with two groups in each of the two classification variables. In tests for fluctuating asymmetry, sexes also were combined to achieve adequate samples for each species.

Ten bilaterally symmetric osseous characters were measured on each side from the dental, cranial, and postcranial regions of each specimen. These characters and their acronyms are:

TOOTH—length of maxillary molariform toothrow; ORB—greatest anterior-posterior diameter of orbit as circumscribed by zygomatic arch; INCF—length of incisive foramen; MAXZY—minimum anterior-posterior breadth of maxillary portion of zygomatic arch; MTOOT—length of mandibular molariform toothrow; LATPR—height from base of mandible to tip of posterio-lateral process (approximately opposite mandibular foramen); POSTM—length from tip of angular process to anterior face of molar shelf; ATLAS—distance on atlas from tip of spinous process to inferior tip of occipital fossa rim; METAC—length of third metacarpal; and METAT—length of third metatarsal.

Each asymmetry value was made scale-free by dividing the character's right-minus-left difference by the mean of the right and left value for that individual. Scale-freeness of each character was confirmed for each species separately by evaluating the product-moment correlations across all specimens between each individual's asymmetry value, and a size variable defined as the right-left mean for that individual.

Directional asymmetry (DA) was evaluated for each character within each group (defined as a particular species-sex-site combination). In each case, a *t*-test was used to evaluate the null hypothesis that the mean was not different from zero. DA was corrected for within each of these groups separately by subtracting the group mean asymmetry value from each specimen's value for that character. For each species, antisymmetry (skewness and kurtosis) was tested for in each sex-site group, and again in each site combination. These tests were done on the values that had been corrected for directional asymmetry. For tests of fluctuating asymmetry, directional asymmetry was corrected for within each species-site combination only, so that the mean of each of these four groups would be zero for each character. The Shapiro-Wilk statistic (SAS Institute, Inc., 1985) was used to evaluate antisymmetry of each character for each species-sex-site group, and for each species-site group.

Given normal (or normalized) distributions with zero means, tests for differences in fluctuating asymmetry are simply tests for heterogeneity of variances. We did this using two methods. We first used a multivariate generalization of the Scheffé-Box test (Sokal and Rohlf, 1981) for heterogeneity of variances among groups. Because this test greatly reduces the cell sample sizes (to approximately the square root of the number of individuals for each cell), error degrees of freedom were sufficient only to test for differences between species and sites (but not sexes—a two-way test). Secondly, each variable also was tested individually for between-site differences in FA by means of Levene's test (Brown and Forsythe, 1974) for heterogeneity of variances, which is very robust to non-normal sample distributions. Also, for the experimental-site populations alone, a multiple regression analysis was performed to assess the effects of three measures of genetic disruption in *Peromyscus* (two in *Sigmodon*) on each asymmetry variable across all individuals.

General morphometric difference between control and experimental sites, between species, and due to interactive effects also were assessed with a two-way MANOVA, and with a two-way ANOVA of each character separately, of the same characters used in the asymmetry analyses, but not transformed to asymmetry values. Regression analysis of the 10 morphometric characters on the three measures of genetic disruption was used to evaluate which genetic measure(s) might best predict the observed site-related differences in each species.

RESULTS

All but one asymmetry variable was found to be scale-free; metatarsal length in *Sigmodon* had a correlation value with its size variable of -0.37, $P < 0.044$. Of the remaining variables, maxillary zygomatic breadth in *Sigmodon* was most significantly correlated with its size variable ($r = -0.166$, $P > 0.26$); in *Peromyscus*, maxillary toothrow length was most strongly size-related ($r = 0.122$, $P > 0.27$). Directional asymmetry was found in 11 of the 40 possible cases for *Peromyscus* (Table 1). Neither direction is prevalent, however; the right-side mean is larger in 18 of 40 cases, and in six of the 11 significant cases. Directional asymmetry in *Peromyscus* appears not to be especially associated with either site or either sex, and it is consistently present only in one character (POSTM). In *Sigmodon*, also, neither direction is prevalent, and significant DA was found only in the number of cases (two of 40) that would be expected by chance, even if independence among characters is assumed. For each group, regardless of t-statistic significance level, the mean for each variable was subtracted from the individual values of that variable for the following tests of antisymmetry. The remainders thus represented zero-mean asymmetry distributions.

Results of the Shapiro-Wilk test indicated that none of the species-sex-site groups exhibited antisymmetry; the highest level was in metatarsal length for male *Peromyscus* from the experimental site, with $P > 0.77$. Because of the possibility that antisymmetry was not being detected due to small samples, the sexes were combined to evaluate antisymmetry of each species at each site (raw group means were recalculated and values corrected for directional asymmetry in these combined groups). In no case was antisymmetry significant (highest level for Shapiro-Wilk tests, metatarsal length in *Peromyscus* at the experimental site, $P > 0.80$). Asymmetry values, therefore, were considered to be normally distributed around a zero mean in the ensuing tests for fluctuating asymmetry.

The two-way multivariate Scheffé-Box test failed to detect overall differences in fluctuating asymmetry levels between species (Wilks' $F_{(10,6)}=0.55$, $P > 0.80$) or sites ($F_{(10,6)}=0.55$, $P > 0.80$), or to find an interactive effect ($F_{(10,6)}=0.35$, $P > 0.93$). An examination within each species of each character separately, by means of Levene's test, supported the multivariate results (Table 2). No variable shows significant heterogeneity of variances between sites for either species. For *Peromyscus*, the highest value was for metacarpal length ($F_{(1,48)}=1.68$, $P > 0.20$); for *Sigmodon*, the highest level was for orbital breadth ($F_{(1,22)}=2.55$, $P > 0.12$).

When fluctuating asymmetry levels were examined in the specimens from the experimental site for a relationship to measures of genetic disruption, none was found for any character in *Sigmodon* (Table 3). For *Peromyscus*, two of the 10 characters (TOOTH and MAXYZ) showed significant model effects in the multiple regression against the measures of genetic disruption. Of these, FA levels for TOOTH varied negatively with chromosomal lesions per cell and with DNA coefficient of variation, but positively with number of cells showing lesions; in contrast, MAXZY showed a positive relationship with lesions per cell and with DNA coefficient of variation.

Table 1. Sample sizes, and degree, direction, and significance[1] of directional asymmetry (DA), for each of eight species-sex-site groups. DA values are expressed as percentages of means. Positive values are right-sided. Occasional missing characters were encountered; therefore, sample sizes represent maximum cell size in each case.

	Peromyscus				*Sigmodon*			
Site	Control		Experimental		Control		Experimental	
Sex	F	M	F	M	F	M	F	M
N	14	23	20	26	13	21	6	7
Characters								
TOOTH	−0.16	−0.28	−1.04*	−0.52*	−0.17	−0.13	0.68	0.07
ORB	0.30	0.16	0.34	0.23	−0.03	−0.03	0.67	−0.25
INCF	0.45	−0.23	−0.65	−0.00	0.57	0.68	−1.33	0.11
MAXZY	−0.11	−1.14	−1.99	0.18	0.10	0.08	−2.14	−1.43
MTOOT	0.17	−0.81*	0.22	0.36	0.24	−0.31	0.01	−1.79*
LATPR	1.11*	0.61	0.64	0.84*	0.02	−0.73*	−0.59	−0.43
POSTM	0.51*	0.37*	0.69**	0.46**	−0.16	−0.28	−0.03	−0.78
ATLAS	−0.72	−0.46	−1.09*	−0.09	0.26	1.13	−0.47	0.41
METAC	−0.90*	0.80	−0.18	−0.06	0.01	−0.20	−0.19	−1.20
METAT	−0.56	−0.02	−0.37	−0.61	0.03	0.09	0.20	0.31

[1] t-test of $H_0{:}\bar{X}=0$; *$0.05 \geq P > 0.01$, **$0.01 \geq P$.

Results of the two-way MANOVA and ANOVAs of morphometric values (not transformed to asymmetry values) are shown in Table 4. The two species are different in each of the 10 characters, of course, as well as in the MANOVA evaluation of all 10 characters together. The multivariate tests also are highly significant for site and for species-site interaction, indicating that inter-site differences for the two species are dissimilar. Table 4 shows that differences between the species in site response include: 1) strength of overall response (for *Peromyscus* in the single-species test, Wilks' $F_{(10,100)}=4.59$, $P = 0.0001$; for *Sigmodon*, $F_{(10,44)} = 2.83$, $P = 0.0083$; 2) number of characters affected (eight for *Peromyscus*, two for *Sigmodon*); and 3) direction of response (*Peromyscus* is smaller on the experimental site in all individually significant characters, whereas *Sigmodon* is larger on that site in its two significant characters).

Results of the regression analysis of untransformed morphometric characters on measures of genetic disruption do not show a clear trend (Table 5). Four characters in *Peromyscus* vary negatively with number of cells per individual with lesions, and one with DNA variation. However, four vary positively with lesions per cell, and one with cells per individual. In *Sigmodon*, six vary negatively with cells per individual.

Discussion

Analysis of Fluctuating Asymmetry

Several points are worth emphasis concerning the analytic protocol

Table 2. Levene's test for heterogeneity of variances of asymmetry values between sites, for *Peromyscus* and *Sigmodon*. A significant *F*-value would indicate a significant between-site difference in FA for that character.

	Peromyscus				*Sigmodon*			
	s^2				s^2			
Characters	Waste	Control	*F*[1]	*P*	Waste	Control	*F*[2]	*P*
TOOTH	.000009	.000016	1.33	0.255	.000025	.000004	1.45	0.241
ORB	.000004	.000004	0.00	0.962	.000004	.000009	2.55	0.124
INCF	.000009	.000025	0.43	0.513	.000025	.000025	0.68	0.417
MAXZY	.000100	.000144	0.15	0.701	.000625	.000324	0.34	0.567
MTOOT	.000004	.000016	0.25	0.623	.000036	.000009	0.09	0.768
LATPR	.000009	.000016	0.07	0.798	.000016	.000009	0.23	0.633
POSTM	.000001	.000004	0.30	0.586	.000009	.000004	0.83	0.373
ATLAS	.000016	.000036	0.31	0.583	.000036	.000025	1.11	0.304
METAC	.000009	.000009	1.68	0.201	.000025	.000009	0.30	0.588
METAT	.000004	.000004	1.15	0.290	.000004	.000004	0.53	0.474

[1] df = 1,48 for *Peromyscus*.
[2] df = 1,22 for *Sigmodon*.

described herein. First, the right-minus-left asymmetry values must be made scale-free, in order that they will be comparable both among characters and among populations. The straightforward method of scaling described herein does in fact ensure that asymmetry values are comparable not only among populations with different mean values for given characters, but also among characters. It should be noted that z-scores, often used to compensate for scaling discrepancies, cannot be used for this analysis, because they also equalize variances among populations, thereby removing the differences in FA one is attempting to evaluate.

Second, any measurement of fluctuating asymmetry requires that each compared sample be normally distributed for all characters. Correction for antisymmetry (to a normal distribution) is not trivial. This problem was mentioned by Van Valen (1962), and has been alluded to intermittently since that time, but no author has offered a direct method of approaching the problem (see Palmer and Strobeck, 1986, for a discussion of several indirect approaches). We suggest one of two techniques. Either should enhance normality, although neither is necessarily precise, and exact circumstances will dictate which method works better in a given case. For data suffering primarily from skewness (high absolute value of the g_1 statistic), the procedure of Box and Cox (1964) should work well (Miththapala et al., 1990). This is an iterative procedure for estimating the best transformation to normality, within a family of power transformations (Sokal and Rohlf, 1981). For data that exhibit kurtosis (high value of g_2), a probit transformation may prove more useful. When data from a normal distribution are probit transformed, the result is a linear function. When non-normal data are so

Table 3. Regression of FA levels (variances of asymmetry values) onto measures of genetic disruption, in *Peromyscus* and *Sigmodon* from the waste site. *F*-value[1] is listed for the regression model, followed by regression coefficients[2] for the disruption measures.

	Peromyscus				*Sigmodon*		
Characters	Model	Lesions	Cells	CV−DNA	Model	Lesions	Cells
TOOTH	5.32*	−0.109*	0.006*	−0.009*	0.16	0.030	0.001
ORB	0.28	−0.009	0.001	−0.000	2.57	−0.052	0.006
INCF	0.57	0.075	−0.002	−0.000	0.43	0.117	−0.003
MAXZY	6.82*	0.382*	−0.002	0.042**	0.11	−0.213	0.007
MTOOT	0.85	0.036	−0.003	−0.004	1.46	−0.198	0.006
LATPR	0.32	0.067	−0.001	−0.000	6.58*	0.048	0.006
POSTM	1.42	−0.017	−0.001	−0.002	3.17	0.033	0.003
ATLAS	0.59	0.040	0.001	−0.006	0.00	0.002	−0.000
METAC	0.18	0.035	−0.003	−0.003	0.43	0.034	0.004
METAT	0.62	0.031	−0.005	−0.001	0.51	0.051	−0.002

[1] Probability of a greater *F*-value: $*0.05 \geq P > 0.01$.

[2] For H_0: parameter = 0, probability of greater absolute value of T: $*0.05 \geq P > 0.01$; $**0.01 \geq P > 0.001$.

transformed, the result is an approximation of a line. The best linear fit then may be calculated, and the asymmetry values adjusted to the cumulative frequency values predicted by this linear function. These adjusted values are then "detransformed" back to the resulting "best-fit" normal curve. This method would have the advantage of producing an exactly normal curve, but would suffer the hazard of all best-fit linear models, namely susceptibility to undue influence by outlying individuals. Both methods must be used with caution and an understanding of their behavior.

As pointed out above, comparison of fluctuating asymmetry levels is simply comparison of sample variances, once given normal distributions with means of zero. As with any question concerning a multi-character comparison of populations, we axiomatically prefer a multivariate approach (Willig et al., 1986; Willig and Owen, 1987*b*). In cases where a multivariate difference is found to exist between populations, this can be quantified for comparison with other studies by use of Kendall's *W* statistic (Jackson, 1973; Soulé, 1979). The multivariate generalization of the Scheffé-Box test allows use of the multivariate test, but it suffers a substantial reduction of power associated with fewer degrees of freedom. Therefore, we chose to use this test in concert with the (univariate) application of Levene's test. Levene's test was particularly appropriate because we had chosen not to transform the data to normal distribution, and Levene's test would be especially robust to any undetected non-normality in the data. We recommend this procedure in cases (such as the present one) in which antisymmetry is negligible, because either of the transformations described above (particularly the probit approach) will introduce some additional error into the analysis.

Table 4. Two-way MANOVA and ANOVA results (based on morphometric variables not transformed to asymmetry values), showing differences between species and between sites, and interactive effects; and showing site differences for each species separately[1].

	Two-way tests[2]			One-way tests					
				Peromyscus			*Sigmodon*		
Characters	Species	Site	Species × site	Control	Experimental	*F*	Control	Experimental	*F*
TOOTH	7979.45***	11.23***	15.50***	3.68	3.70	0.68	6.16	6.43	15.35***
ORB	1038.90***	1.37	5.23*	8.97	8.73	19.42***	11.64	11.85	0.65
INCF	938.64***	0.62	0.93	4.65	4.53	6.24*	7.25	7.31	0.06
MAXZY	211.71***	6.78*	0.75	0.95	0.88	8.72**	1.46	1.32	1.94
MTOOT	7616.56***	3.90*	1.23	3.55	3.59	2.03	6.47	6.59	2.08
LATPR	1146.38***	0.03	4.49*	4.85	4.70	6.40*	8.04	8.35	1.13
POSTM	2861.26***	0.00	5.04*	9.03	8.87	6.78*	14.87	15.26	1.38
ATLAS	1011.71***	0.78	4.57*	4.20	4.10	8.29**	5.42	5.52	0.80
METAC	1703.76***	3.80	18.66***	3.73	3.58	24.99***	4.86	5.01	3.75
METAT	1007.51***	2.64	19.93***	8.32	7.98	23.49***	10.36	10.75	4.55*
MANOVA[3]	1053.49***	4.32***	4.76***			4.59***			2.83**

[1] *$.05 \geq P > 0.01$; **$0.01 \geq P > 0.001$; ***$0.001 \geq P$.

[2] *F*-values listed for two—way tests (significance levels as above).

[3] Wilk's exact *F*, df = 10,153 (2-way); 10,100 (*Peromyscus*); 10,44 (*Sigmodon*).

Table 5. Results of regression of morphometric variables (not transformed to asymmetry values) on genetic disruption variables. Regresion coefficient is listed, with significance[1] value for H_0: $T = 0$.

	Peromyscus			*Sigmodon*	
Characters	Lesions	Cells	CV-DNA	Lesions	Cells
TOOTH	0.055	0.017	−0.004	0.139	−0.019
ORB	1.320*	−0.075*	−0.017	−2.689	−0.229
INCF	1.951***	−0.064*	−0.012	−1.227	−0.239*
MAXZY	−0.232	−0.013	−0.014	1.145	−0.132*
MTOOT	0.501	0.036*	0.005	0.454	−0.064
LATPR	2.016**	−0.110***	0.026	−0.606	−0.297*
POSTM	3.622***	−0.071**	−0.012	−0.757	−0.263*
ATLAS	0.284	−0.029	−0.071*	1.278	−0.152***
METAC	−0.285	0.025	−0.001	0.413	−0.076*
METAT	−0.687	0.066	−0.012	1.059	−0.130

[1] *$0.05 \geq P > 0.01$; **$0.01 \geq P > 0.001$; ***$0.001 \geq P$.

A final point is that populations can be evaluated for FA variability among individuals. Directional asymmetry and antisymmetry are inherently populational characteristics; that is, they are measures of the deviation of the sample from a hypothetical sample with the same variance, but with a zero mean and normal distribution. Once these hypothetical samples are described (by appropriate corrections for DA and antisymmetry), they can be tested for interpopulation differences (heterogeneity of variances). In addition, the individuals of a particular population can each be examined to determine where in the distribution they lie, and these values compared with other (for example, genetic) variables on an individual-by-individual basis. Thus, it should be possible to determine whether FA levels track genetic phenomena at one or more different organizational levels (for example, hybridization as evidenced by chromosomal, electrophoretic, or DNA data).

Only one other study of which we are aware has evaluated FA levels on an individual-by-individual basis. Wooten and Smith (1986) found no relationship between asymmetry and degree of individual heterozygosity in house mice. Our comparison of individual FA levels with measures of genetic disruption, in the experimental-site population, was inconclusive. No such relationship was found in *Sigmodon*. In *Peromyscus*, we found three positive associations between FA level and a measure of genetic disruption, but we also found two negative associations. Further tests on other populations with known genetic data are certainly indicated.

Fluctuating Asymmetry and Stress

One problem pertaining to interpretation of previous studies of fluctuating asymmetry is that they are difficult to compare, for lack of established or comparable protocols for assessing variation in FA levels.

It is quite probable, in fact, that some of these papers have not accurately evaluated FA at all (see Willig et al., 1987*a*, and Modi et al., 1987, for a discussion of this issue). A second problem in interpreting a series of published papers, such as those listed earlier in which increased heterozygosity was generally associated with decreased FA levels, is that the failure to demonstrate a populational difference does not demonstrate that the null hypothesis is true (that the samples have in fact been taken from one statistical population), and thus there often is no clear conclusion from such tests; investigators generally are reluctant to report, or are editorially discouraged from reporting, statistically nonsignificant results. It is, indeed, hard to obtain convincing negative results, and for all of these reasons it will be less likely over the long run to see a large list of papers in which the null hypothesis (in this case, no relation between FA and heterozygosity) is not rejected.

In the present study, no differences, either multivariate or univariate, were found in fluctuating asymmetry levels between sites or between species. However, it is important to note that this data set is sufficient to demonstrate overall morphometric differences between sites in each species, and to detail the complex differences in site response between species. We suggest, therefore, that our finding of no differences in FA is real, and believe that these are unambiguous results showing that a demonstrably mutagenic environment had no detectable effect on FA in two species of cricetid rodents. If genomic characteristics do function to buffer these organisms against asymmetry, such capabilities may not be affected by disruption at the gross chromosomal level.

General Morphometrics and Stress

The results of the morphometric analysis are especially interesting in the context of the asymmetry results. In the two-way tests using both species (Table 4), significant differences between sites are found in three characters, and the multivariate result shows the two sites to be quite different. Also, the majority of characters show a significant interactive effect, and the multivariate interactive effect is highly significant. This means that the two species differ considerably in the nature of their response to site differences.

Patterns of differentiation were shown to be fairly complex when site differences were examined separately in each species. There is an apparent difference in overall strength of response, though that may be due to the smaller sample of cotton rats from the waste site. There are differences in: 1) number of characters involved, 2) which characters are involved, and 3) direction of response. In all significant characters, *Peromyscus* is smaller on the waste site, but in both significant characters and most of the others, *Sigmodon* is larger on that site.

It is unclear why these differences in response might occur between species. Certainly several possibilities exist, which we are unable to evaluate. Ages may be distributed unequally between sites and species. Even among adults, some cricetids (especially *Sigmodon*) are known to vary in size among age classes. If such a discrepancy occurs in our specimens, it could be a result of sampling error, or differing life history responses to the contaminants.

It is conceivable also that the observed differences are "real"; that is, all other relevant variables are in fact equal between groups, and we are observing species-differential phenotypic responses to genetic disruption. If this is the case, however, the response differences must again be fairly complex in nature. From the regression analysis of untransformed variables on measures of genetic disruption (Table 5), it appears in general that an increase in the number of affected cells per individual is associated with smaller size in both species (not just *Peromyscus*). Also, in *Peromyscus* an increase in chromosomal lesions per cell is associated with an increase in size in at least some characters. Thus, no measure of genetic disruption appears to explain observed inter-site differences in either species, much less to explain the inter-species differences in site response.

We conclude with two caveats. First, in any study of correspondence between morphologic and genetic or chromosomal characteristics, one cannot simply evaluate a single common species as a model system. In the present case, two relatively closely-related species responded quite differently in morphology although their chromosomal responses were quite comparable. Second, although the hypothesis of environmental stress leading to disruption of genomic buffering is intuitively pleasing, the mechanisms have not been demonstrated. The literature is quite unclear on the nature of this pathway, and in fact on whether such a mechanism exists. Our results suggest that if this mechanism does exist, genomic buffering capabilities do not suffer from genetic disruptions at the gross chromosomal level.

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DISCRIMINATION OF TWO SPECIES OF COTTON RATS (*SIGMODON*) USING CHARACTERS OF THE UPPER FIRST MOLAR

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Abstract.—The yellow-nosed cotton rat, *Sigmodon ochrognathus*, is almost unknown from the fossil record, but this may reflect our past inability to discriminate between this species and the hispid cotton rat, *Sigmodon hispidus*, in Pleistocene faunas. Characters of the upper first molar help to separate the two species. The occlusal surface of that tooth in *S. ochrognathus* is consistently smaller than in specimens of *S. hispidus*, except in instances of extremely worn teeth. The anterocone is recessed posteriorly in *S. ochrognathus*, often leaving a pronounced bulging camber on the anterior face of the tooth, which contrasts with the usually relatively flat face of the molar in *S. hispidus*. Reevaluation of *Sigmodon* material from Pleistocene faunas is merited where either species is suspected to have occurred. *Key words*: maxillary first molar; *Sigmodon*; Rodentia; discriminating characters.

Two species of cotton rats occur in Trans-Pecos Texas (Hall, 1981; Schmidly, 1977). *Sigmodon hispidus* is widely but sporadically distributed, restricted to areas of relatively dense plant cover. *S. ochrognathus* is found in sparsely vegetated, rocky meadows of some mountain ranges in the region (Hollander et al., 1990; Schmidly, 1977). Although the two species may occur in close proximity, they always seem to be segregated ecologically (Baker, 1969).

Cotton rat remains are sometimes abundant in Trans-Pecos Pleistocene cave faunas where either or both of the two species of *Sigmodon* might be represented. No satisfactory means of separating the dentitions of the two taxa yet has been proposed, and material typically has either been identified to the generic level only (for example, Harris, 1970), or tentatively assigned to *S. hispidus* (Lundelius, 1979; Dalquest and Stangl, 1984). A single Pleistocene record exists for *S. ochrognathus* (U-Bar Cave, southwestern New Mexico—Harris, 1989), on the basis of discriminant analysis (A. H. Harris, personal communication).

This study presents a reliable means of separating *S. hispidus* from *S. ochrognathus* by characters of the upper first molar. The significance of this finding is twofold. First, reassessment of western Texas *Sigmodon* fossils may produce additional Pleistocene records for *S. ochrognathus*. Second, the known presence or absence of the yellow-nosed cotton rat from Pleistocene faunas will permit addressing some interesting biogeographic questions posed by the recent extralimital record for *S. ochrognathus* in the Guadalupe Mountains (Hollander et al., 1990).

Materials and Methods

Fifty specimens each of *Sigmodon hispidus berlandieri* from New Mexico, Texas, and

Mėxico, and *S. ochrognathus* from Trans-Pecos Texas were selected from the Collection of Recent Mammals, Midwestern State University, for examination under a dissecting microscope with camera lucida attachment. Upper and lower occlusal surfaces were drawn under 40× magnification for detailed examination. After determination that the upper M1 afforded the desired resolution, the greatest lengths and widths of drawings of the right upper M1 were recorded to the nearest millimeter. Descriptive statistics were calculated using these units, and results then were converted to actual size.

RESLUTS AND DISCUSSION

Barn owls (*Tyto alba*) often reside in caves, and regurgitated pellets containing the remains of their prey are important contributions to mammalian faunas recovered from Holocene and Pleistocene cave sediments. Cotton rats (*Sigmodon*) are favored prey items of owls, and often have been well represented in faunas thus far studied. However, in Trans-Pecos Texas and in southern New Mexico, either *S. hispidus* or *S. ochrognathus* or both, might have occurred in the past. To distinguish between the remains of these two taxa, each species with different ecological requirements, may be important in reconstructing paleoenvironments, as well as determining post-Pleistocene environmental shifts. However, to date, specific determination with any degree of certainty has been an elusive task, and assignments beyond the generic level often have been tentative. Larger teeth usually were attributed to *S. hispidus*, whereas smaller teeth were identified to genus only (Harris, 1970, 1987; Lundelius, 1979; Dalquest and Stangl, 1984).

Paleomammalogists have found that lower dentitions often are more useful in specific identification of small mammals than are upper dentitions, and Martin's (1979) study of the dental anatomy and evolution of *Sigmodon* dealt largely with mandibular characters. He remarked on the generally smaller size of *S. ochrognathus* when compared to *S. hispidus*, but noted a considerable overlap in overall tooth size and alveolar lengths. Hence, Dalquest and Stangl's (1984:447) treatment of Pleistocene cotton rat material from a site where presence of the two species was suspected is typical: "The largest *Sigmodon* specimens in the Fowlkes Cave [Texas] collection can only be *S. hispidus* but some of the smaller fossils could be *S. ochrognathus*."

Occlusal Surface Area as a Character

The upper dental battery of *S. ochrognathus* appears distinctly smaller than comparably worn dentitions of *S. hispidus*, and this seems especially pronounced with the first molar (Fig. 1). This impression was affirmed by comparing measurements of greatest lengths and, to a lesser extent, widths of the occlusal surfaces of the right upper first molars (Table 1). An indirect and relative measure of occlusal surface area of the M1 was obtained by plotting lengths against widths (Fig. 2), and only the confounding effect of including excessively worn teeth prevents a nearly

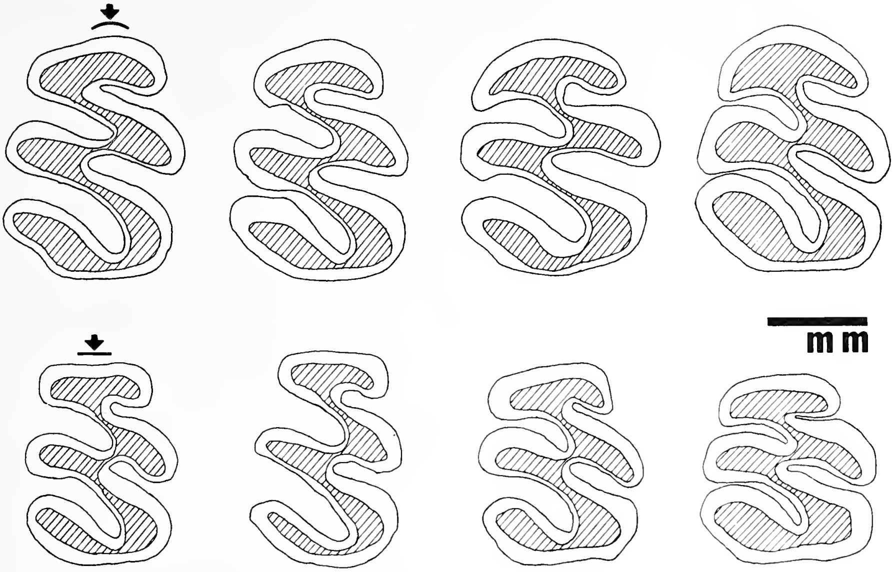

FIGURE 1. Occlusal surfaces of representative right upper first molars of *Sigmodon hispidus* (above) and *S. ochrognathus* (below). All teeth are lightly to moderately worn. Note anteriorly rounded anterocones of former as compared with flattened condition of latter (arrows).

complete separation of the two species of *Sigmodon* by this character, as supported by 99 percent confidence intervals of both length (1.92-2.06 and 2.26-2.33) and width (1.42-1.61 and 1.63-1.83) for *S. ochrognathus* and *S. hispidus*, respectively.

Four of the 100 specimens examined for both species were considered to be problematic. Of the 50 *S. hispidus*, only two possessed both the flattened anterocone and linear dimensions of the occlusal surface within the expected range of *S. ochrognathus*. Of the 50 *S. ochrognathus*, only two specimens exhibited both the rounded anterocone and linear

TABLE 1. Descriptive statistics comparing occlusal surface measurements of upper right first molars of two species of *Sigmodon* from Texas. Sample size was 50 for each species. Mean, standard deviation (SD), and extremes (in parentheses) are in millimeters; coefficient of variation (CV) also is given.

	Length	Width
Taxon	Mean ± SD (extremes) CV	Mean ± SD (extremes) CV
Sigmodon hispidus (50)	2.29±0.10 (2.05-2.52) 4.37	1.73±0.10 (1.14-2.29) 16.18
Sigmodon ochrognathus (50)	2.02±0.10 (1.86-2.29) 4.95	1.51±0.10 (1.10-2.05) 17.88

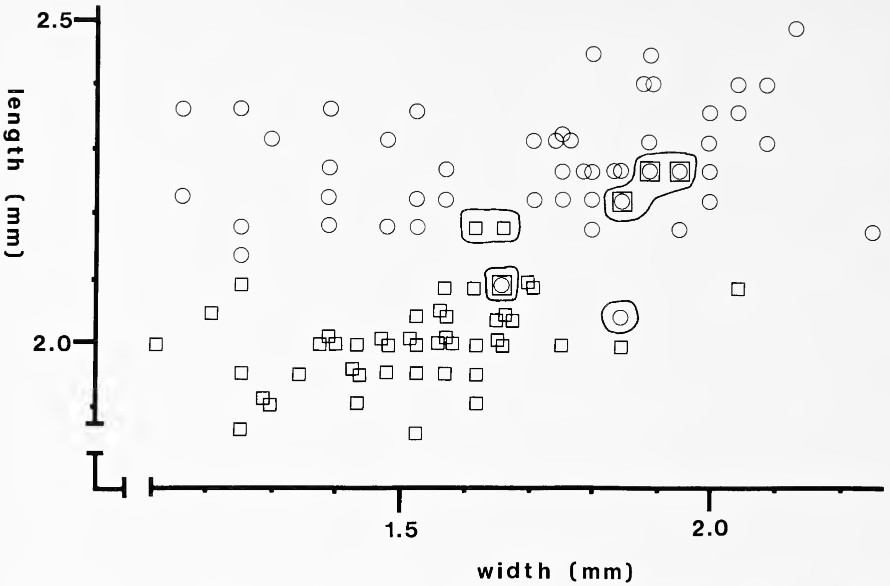

FIGURE 2. Scatter plot of occlusal surface measurements of right upper first molars of randomly selected specimens of *Sigmodon hispidus* (circles) and *S. ochrognathus* (squares). Problematic points (encircled) are explained in text.

dimensions within the expected range of the larger *S. hispidus*. Of the remaining three potentially problematic *S. ochrognathus* in which linear dimensions were identical to those of three *S. hispidus* (Fig. 2), the former are represented by excessively worn teeth, as compared to the moderately worn dentitions of their counterparts.

Anterocone as a Character

The shape and position of the anterocone is a useful discriminating character for the first upper molar until the tooth is heavily worn. The anterocone of *S. ochrognathus* is distinctly compressed or flattened anteriorly (Fig. 1) in 47 of 50 specimens exhibiting light to moderate wear. In most hispid cotton rats, the anterocone is convex, although the structure was compressed in 12 of 50 specimens.

Of more limited value is the anterior lateral profile of the M1. In the more hypsodont *S. hispidus*, the face of the anterocone usually slants posteriorly from the alveolus (Fig. 3). The anterocone in *S. ochrognathus* usually is recessed posteriorly, often leaving a decidedly convex bulge, or camber, that is obvious until the tooth is worn almost to the roots. However, this character varies considerably, especially among hispid cotton rats.

An important implication of the described comparative tooth morphology is that specimens of the two species in comparable stages of tooth wear and of similar alveolar lengths may differ considerably in

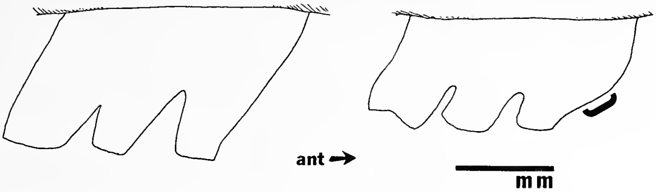

FIGURE 3. Lateral view of extreme profiles of upper first premolars of *Sigmodon hispidus* (left, lightly worn), and *S. ochrognathus* (moderately worn). Bracket indicates camber or convexity of anterior face of anterocone, more often characteristic of *S. ochrognathus*.

linear dimensions of the occlusal surface. With wear, occlusal tooth length changes little in either species (average coefficient of variation 4.61) as compared with the width of the occlusal surface (average coefficient of variation 17.03).

We add a cautionary note. Utility of these characters in discriminating *S. hispidus* from *S. ochrognathus* may be limited in areas where other species of *Sigmodon* occur or are suspected once to have occurred.

SUMMARY AND CONCLUSIONS

Characters of the upper first molar in cotton rats can be useful in discrimination of *S. hispidus* and *S. ochrognathus* from fossil collections that potentially contain both species. Pleistocene faunas containing cotton rats merit reexamination for the possible inclusion of *S. ochrognathus*, presently recorded in the fossil record only from a single locality in southwestern New Mexico. Documentation of the yellow-nosed cotton rat could permit both a more precise portrayal of paleoenvironments, and an addressment of the biogeographic history of the species.

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PETROLOGY AND GEOCHEMISTRY OF THE SIERRA HECHICEROS VOLCANIC SEQUENCE, CHIHUAHUA AND COAHUILA, MEXICO

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ABSTRACT.—Major element and trace element contents of volcanic rocks from eastern Chihuahua are transitional from a typical calc-alkalic trend present in the Sierra Madre Occidental of western México to the alkalic suite of the eastern Trans-Pecos Magmatic Province. The composite volcanic section of the Sierra Hechiceros, which is 1600 meters thick, includes one basaltic unit, two dacitic units, and three rhyolitic units. Phenocryst phases in these rocks include plagioclase, opaques, clinopyroxene, sanidine, and minor apatite, orthopyroxene, and zircon. Sr and Ba both decrease with increasing silica content, suggesting feldspar fractionation. The large negative Eu anomaly of the rhyolites suggests that crystallization of plagioclase was an important component in the evolution of these rocks. The slight depletion in the middle REE indicates that crystallization of clinopyroxene, zircon or apatite, also may have occurred in the fractionation process. Finally, the smaller negative Eu anomaly for the initial caldera-forming lower Palomas tuff may indicate a higher oxygen fugacity during the evolution of this magma. *Key words*: volcanic rocks; Mexico; geochemistry; petrology.

The Sierra Hechiceros is a northwest-southeast trending mountain range or series of ranges that straddle the Chihuahua-Coahuila border approximately 50 kilometers south of Big Bend National Park (Fig. 1). It is near the eastern margin of the broad transition zone between the Sierra Madre Occidental to the west and the Trans-Pecos Magmatic Province to the east. The area of study lies within the Bolson (Basin and Range) subdivision of the Mesa Central (Clark and De La Fuente, 1978).

The oldest rocks exposed in the range are fossiliferous Cretaceous marls (Sue Peaks Formation?) of restricted areal extent that are faulted against Tertiary basalt in the north end of the range. Elevations within the sierra range from less than 1000 meters on the north and east flanks, to 1960 meters at the crest of the range southwest of Los Hechiceros Quemados (Fig. 2). Ranges to the north and west of the study area are composed primarily of Tertiary volcanic rocks. These areas include the hills around Manuel Benevides (Chuchla, 1981; Gregory, 1981; Immitt, 1981), the southern Sierra Rica and eastern Sierra Azul, and the Sierra El Virulento (Moll, 1979), a small range southeast of the Sierra Rica (Fig. 2). Investigators in these areas have provided the basis for our understanding of the origin of the Tertiary igneous rocks in the region, and our work extends the geologic mapping and petrologic studies into the previously unstudied Sierra Hechiceros. Outcrops of volcanic rocks are sparse east of the Sierra Hechiceros except for the small group of hills, the Cerros Colorados, east of La Selva (Fig. 2).

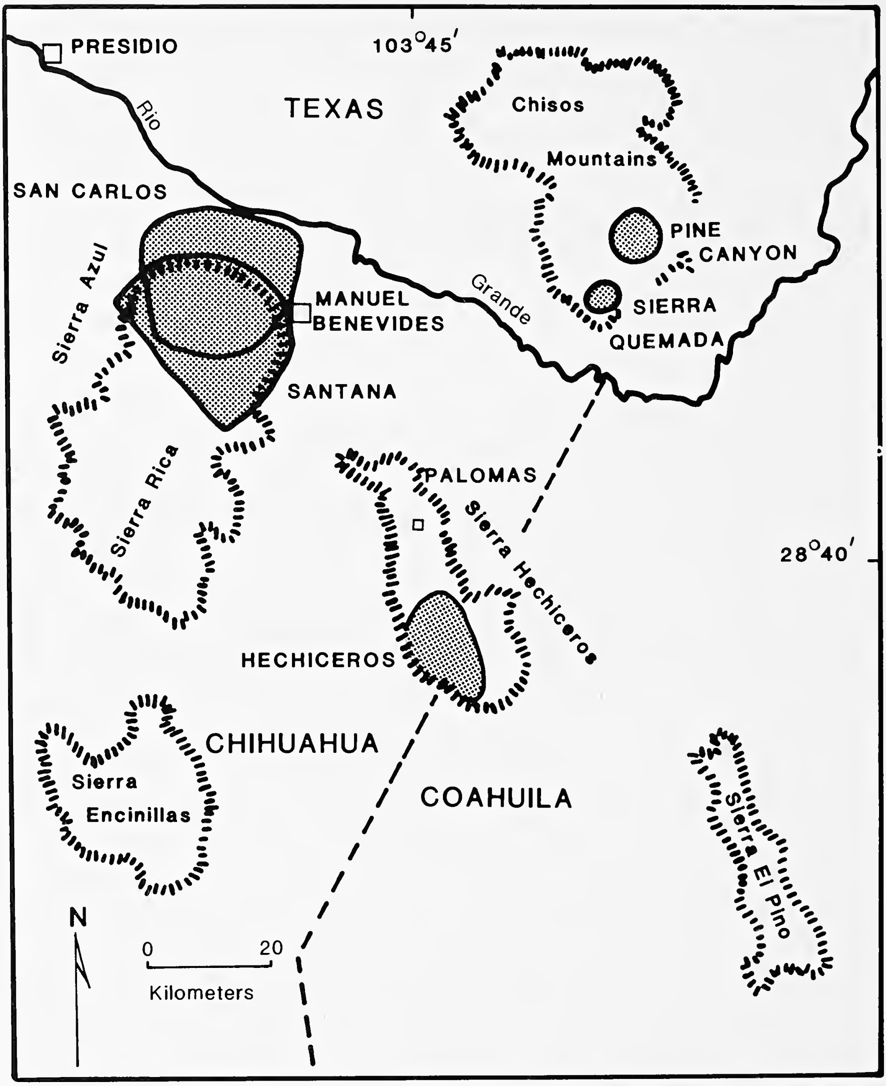

FIGURE 1. Map of volcanic mountain ranges and Teritary calderas (Shaded) in Big Bend area and adjacent Chihuahua and Coahuila, México. Outline and location of calderas, except for the Hechiceros caldera, from Henry and Price (1984).

VOLCANIC STRATIGRAPHY AND PETROGRAPHY

The composite stratigraphic section of the Sierra Hechiceros includes more than 1600 meters of Teritary volcanic and volcaniclastic rocks (Fig. 3). Formation names are used informally and, where applicable, we have extended contacts into the area from adjacent areas and used the same formation name. Intrusive rocks are rare within the range and consist of discontinuous outcrops of thin, heavily weathered or altered dikes.

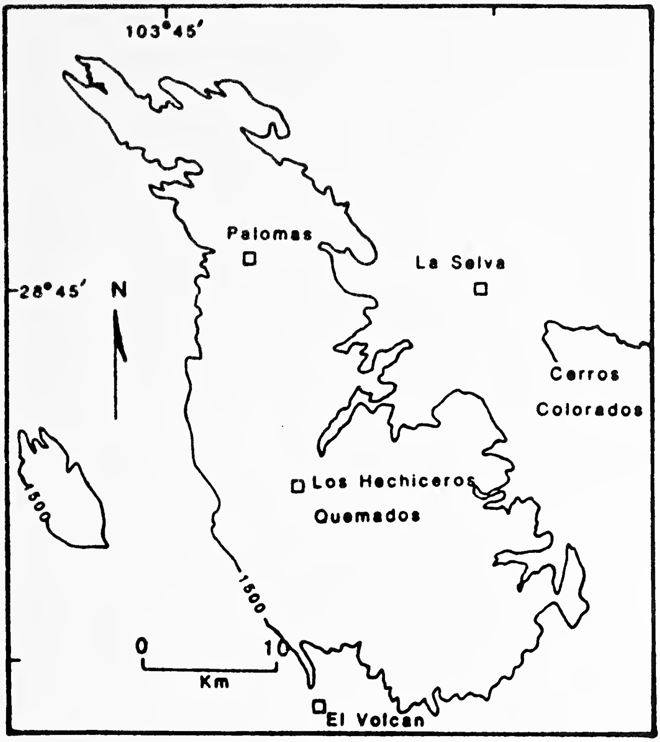

FIGURE 2. Map of the Sierra Hechiceros and vicinity, showing principal villages. Outline of range is the contour line at 1500 meters elevation. Small range to west is the Sierra El Pando.

The volcanic sequence includes basaltic, dacitic, and rhyolitic lava flows, and rhyolitic air-fall and ash-flow tuffs. The sequence can be subdivided into a precaldera suite, which erupted between 34 and 29 Ma, and a post-caldera sequence that erupted from the Hechiceros caldera in the south-central part of the range (Ritter, 1987) at about 29 Ma.

The El Matadero formation is the oldest unit in the range that contains volcanic material. It consists of interbedded basalt flows and volcaniclastic rocks, air-fall tuffs, conglomerates, and a thin, persistent ash-flow tuff near the top of the unit. The 34 Ma date on this ash-flow tuff (Gregory, 1981) constrains the timing of volcanism in the study area. The El Matadero formation can be traced from the Sierra El Matadero, 15 kilometers north of Manuel Benevides to La Selva (Fig. 2), midway on the northeast flank of the Sierra Hechiceros. Within the range it is exposed only on the northeastern slope, and its content changes from a mixture of basalt flows and conglomerates in the northern exposures, to a sequence that consists almost entirely of basalt flows (more than 10 individual flows) in the vicinity of La Selva. The high proportion of

K-Ar Ages(Ma)	Units
	Tertiary conglomerate
	Tinaja Blanca formation
29	El Jobero formation
29	Palomas tuff
	Agua Dulce formation
	La Mota dacite
29.8	La Cuesta tuff
	San Antonio dacite
34	El Matadero formation
	Sue Peaks Formation

FIGURE 3. Composite stratigraphic section of the Sierra Hechiceros showing available K-Ar ages.

basalt to sedimentary units in this area suggest a nearby, but as yet unidentified, source.

Phenocryst mineralogy in the El Matadero basalts includes plagioclase, opaques, and titanaugite. The basalts of the El Matadero formation occupy the same stratigraphic position as the Bee Mountain and Alamo Creek basalts of the Chisos Formation of Big Bend National Park (Gregory, 1981; Henry and McDowell, 1986). The El Matadero tuff has been correlated (Gregory, 1981) to the Mule Ear Springs tuff member of the Chisos Formation. In the study area, this tuff is 10 meters thick and moderately welded (Hardy, 1987).

The San Antonio decite (Fig. 3) is a series of lava flows as much as 300 meters thick, but thinning southwardly (Hardy, 1987) to approximately 20 meters thick in the vicinity of La Selva. Vitrophyre occurs as lenticular zones, but is commonly altered to clay. Phenocryst mineralogy is dominated by zoned and embayed twinned plagioclase, which is rimmed by fritted feldspar. The embayed and fritted texture is

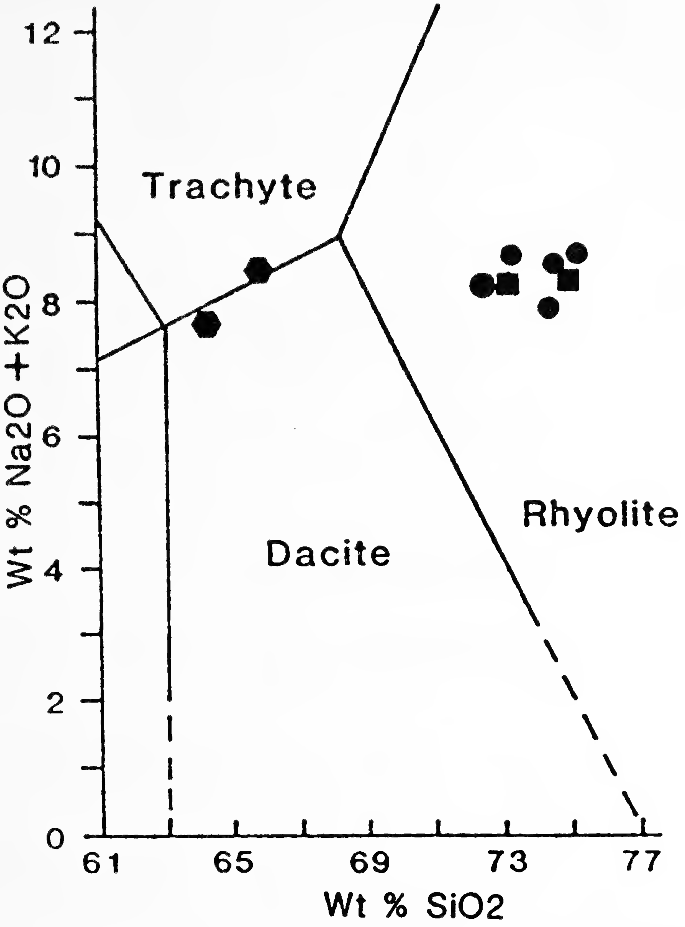

FIGURE 4. Total Alkali-Silica Diagram (LeMaitre, 1984) showing Hechiceros dacites (hexagons) and rhyolites. Circles represent Palomas tuff, squares are El Jobero formation.

suggestive of disequilibrium in the system (Chuchla, 1981; Nelson et al., 1987; Hardy, 1987). Smaller and less abundant phenocryst phases include clinopyroxene, orthopyroxene, opaques, and minor apatite and zircon.

The La Cuesta tuff is a crystal-vitric ash-flow tuff that has been dated at 29.8 Ma (Gregory, 1981). Because it thickens to the south, toward the Sierra Hechiceros, it was believed (Gunderson, 1983) to have originated in this range. However, our fieldwork indicates no evidence for this.

The La Mota dacite (Fig. 3) crops out only in the vicinity of the village of Palomas (Fig. 2). Vents for this unit are most likely within the range but have been subsequently covered by younger volcanic units. The major phenocryst phase is plagioclase, with subordinate clinopyroxene and opaques, as well as minor orthopyroxene, in a partially devitrified brown

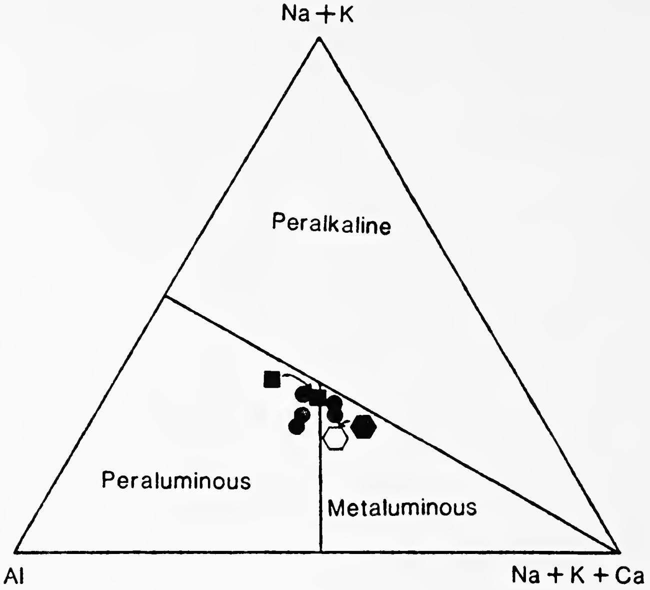

FIGURE 5. Ternary classification diagram (Shand, 1951) in molar percent. Symbols same as in Figure 4.

glass matrix. Like the San Antonio dacite, the La Mota dacite also exhibits fritted feldspar in glomerocrysts.

The Agua Dulce formation is a heterogeneous unit consisting of tuffaceous beds, conglomerates, probably emplaced as debris flows, and air-fall tuffs. The best exposures of this unit are in the west-central part of the range, northwest of Los Hechiceros Quemados.

The Palomas tuff (Fig. 3) is a vitric-crystal, rhyolitic ash-flow tuff erupted from the Hechiceros caldera (Ritter, 1987) in the southern part of the sierra. Its three members consist of a basal unwelded ash-flow or air-fall tuff, overlain by two welded ash-flow tuff members that form prominent cliffs along both sides of the range. The mineralogy of all three members is similar, but the basal member does not exhibit the prominent eutaxitic texture that charaterizes the upper two members. Phenocryst mineralogy includes quartz and sanidine and minor plagioclase in a devitrified groundmass. Eruption of the Palomas tuff produced the collapse of the Hechiceros caldera, which subsequently was filled by rhyolite lava flows of the El Jobero formation. Both units have been dated at 29 Ma.

Rhyolite flows of the El Jobero formation (Fig. 3) exceed a thickness of 500 meters within the caldera. The intracaldera facies exhibit an intrusive texture characterized by a fine-grained, interlocking crystalline groundmass. Phenocryst phases constitute up to 30 percent of the rock

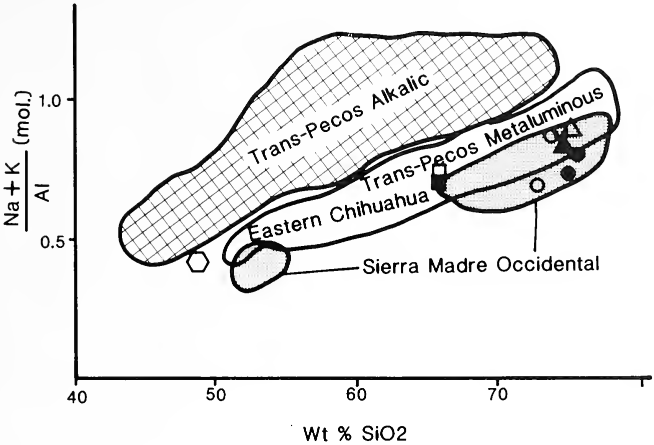

FIGURE 6. Peralkalinity versus weight percent silica for Hechiceros samples compared to those of adjacent provinces (from McDowell and Clabaugh, 1979). Squares are Hechiceros dacites, rhyolites are circles and triangles. Open hexagon is El Matadero Basalt (Gunderson, 1983).

and consist of quartz and sanidine, with minor plagioclase and clinopyroxene.

The Tinaja Blanca formation is a volcaniclastic unit preserved in a down-dropped block between the Sierra Los Angeles to the west and the

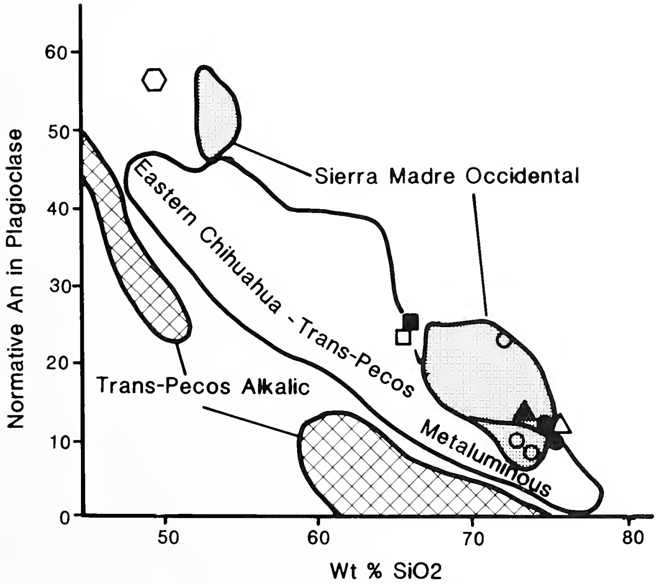

FIGURE 7. Normative plagioclase composition versus weight percent silica for Hechiceros samples compared to those of adjacent provinces (modified from McDowell and Clabaugh, 1979). Open hexagon is analysis of El Matadero basalt from Gunderson (1983).

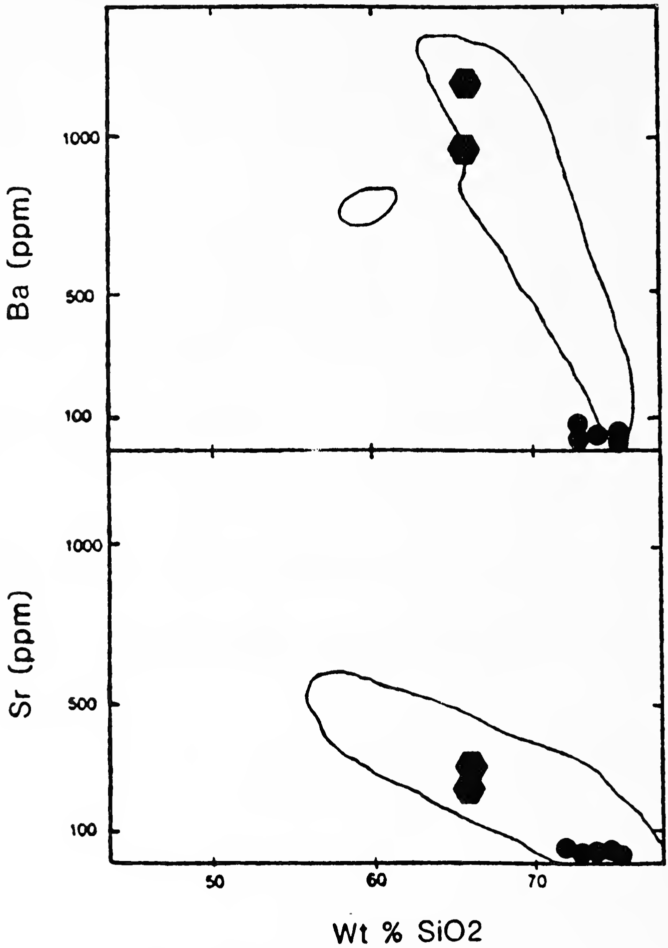

FIGURE 8. Sr and Ba contents of rocks from the Sierra Hechiceros plotted versus silica. Outlines denote range of variation for intermediate silicic rocks in eastern Chihuahua (from Gunderson, 1983).

Sierra Hechiceros to the east. Like the Agua Dulce formation, it represents an interval of time when ash-fall deposits, and probably unwelded ash-flows as well, were reworked and interbedded with other sedimentary units.

GEOCHEMISTRY

Analytical Techniques and Samples

All major elements and Sr, Ba, and Zn were analyzed by Christopher Henry at the Texas Bureau of Economic Geology. Rare earth elements and Sc, U, and Th were analyzed by INAA by a commercial laboratory, using 50 grams of a minus-100-mesh sample. Precision, based on

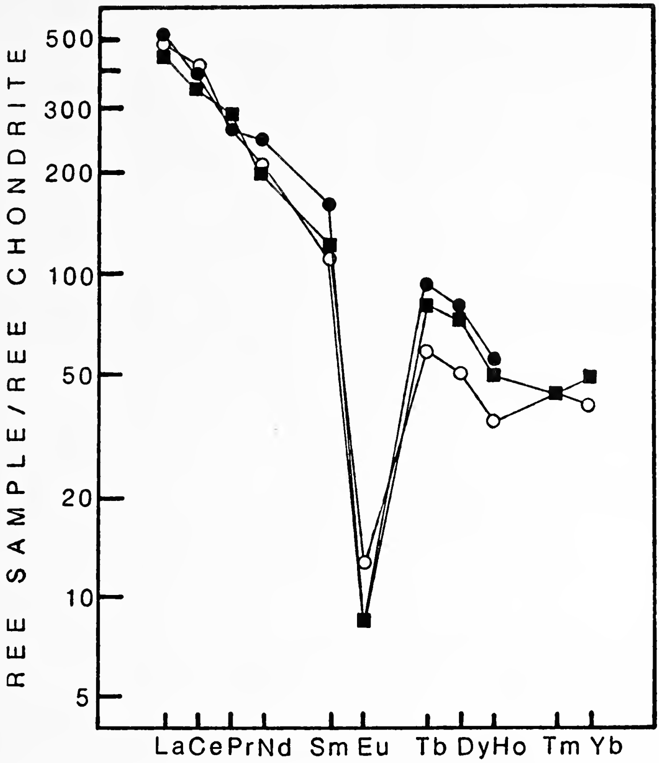

FIGURE 9. Rare earth elements plot of rhyolites from the sierra Hechiceros. Solid squares represent intracaldera El Jobero formation, open circles are lower Palomas tuff, solid circles are upper Palomas tuff. Chondrite values from Anders and Ebihara (1982).

comparison with an internal standard, is better than 10 percent for all elements except U, which is better than 17 percent.

Because of the scarcity of vitrophyre in these Tertiary-aged rocks, all chemical samples are devitrified whole rocks. To insure a representative sample, at least three kilograms of rock was collected for each sample, and weathered and altered portions were discarded prior to crushing and splitting.

Major Element Chemistry

Whole-rock chemical analyses are presented in Table 1, and CIPW normative compositions are presented in Table 2. Analyses are plotted on a total alkali-silica diagram (LeMaitre, 1984) in Figure 4. Except for the El Matadero basalts, for which no analyses are available for samples from the Sierra Hechiceros, the volcanic rocks are dacite and rhyolite span a silica range from 64 to 75 weight percent. All of the rhyolites plot clearly within the rhyolite field because of their high (72 to 75 weight percent) silica contents. The dacite analyses straddle the trachyte-dacite boundary. All of the units are subalkaline (Fig. 5) and most are metaluminous. The only available analyses of El Matadero basalts are from areas northwest of the Sierra Hechiceros (Gunderson, 1983), where they exhibit a silica range of 47 to 54 weight percent.

The transitional nature of the Sierra Hechiceros rocks is probably most evident on plots on which the major-element chemistry of these rocks is compared to that of adjacent igneous provinces (Figs. 6 and 7). These figures suggest that these rocks are more similar to the rocks of the Sierra Madre Occidental than they are to the rocks of the Trans-Pecos province.

Trace Element Chemistry

In the rhyolites, Sr varies from less than 10 parts per million in the El Jobero formation to 50 ppm in the Palomas tuff (Fig. 8). Sr contents in the two dacites range from 250 to 290 ppm. Ba ranges from 30 to 60 ppm in the rhyolites, compared with 940 to 1140 ppm in the dacites (Fig. 8).

The low Ba and Sr contents in the rhyolites are suggestive of fractional crystallization. In the Infiernito caldera system, Trans-Pecos Texas, Ba concentration is nearly constant at about 1100 ppm over the silica range 61 to 67 weight percent, then drops sharply to about 140 ppm (Henry et al., 1988). Ba is strongly partitioned into both alkali feldspar and biotite (Leeman and Phelps, 1981; Nash and Crecraft, 1985). Precipitation of sanidine, and possibly biotite, at high silica levels caused Ba to be rapidly depleted (Henry et al., 1988). A similar scenario is probable for the Hechiceros system except that biotite is found only in the precaldera ash-fall tuffs. The decreased Sr content in the rhyolites suggests the influence of plagioclase crystallization.

Zn contents range from 70 to 158 ppm in the dacites, and 119 to 179 ppm in the rhyolites. Although Zn concentration increases slightly with increased silica, the trend is not well defined because of the large Zn variation in the dacites. High concentrations of Zn may indicate complexing of this element by F, allowing it to be retained in the melt, as has been suggested by Nelson et al. (1987) for rocks of the eastern Trans-Pecos Magmatic Province.

U contents of the rhyolites (three analyses) range from 6.9 to 10 ppm and Th contents range from 20.6 to 26.1 ppm. By comparison, metaluminous rhyolitic rocks in the Eagle Mountains of Trans-Pecos Texas average five parts per million U and peralkaline rhyolites in the Chinati Mountains range from 4.2 to 13.4 ppm U and 15.3 to 39.8 ppm Th (Cepeda et al., 1981).

Sc contents of the rhyolites range from 0.74 to 1.4 ppm, within the range of Sc contents for rhyolites of the eastern Trans-Pecos Magmatic Province (Nelson et al., 1987). REE analyses of three samples (one each of the lower and upper Palomas ash-flows, and the intracaldera El

TABLE 1. Major and trace element analyses of Sierra Hechiceros samples.

	Palomas tuff upper ash-flow tuff		Palomas tuff lower ash-flow tuff			El Jobero formation		La Mota dacite	San Antonio dacite
	UB-101	Em-100	LT-101	P1-25	P3-81	STR	E1J-101	Pa-101	G1
SiO_2	74.49	75.27	72.17	73.11	74.19	73.05	74.78	64.33	65.59
Al_2O_3	12.99	12.93	14.89	12.61	12.37	13.30	12.49	15.87	15.56
Fe_2O_3	2.01	1.93	2.24	1.90	1.93	1.86	2.12	2.63	2.90
FeO	0.12	0.12	<0.05	0.12	0.09	0.89	0.29	1.49	2.17
MnO	0.05	0.03	0.04	0.04	0.04	0.05	0.04	0.10	0.11
MgO	0.37	0.07	0.21	0.05	0.06	<0.04	0.11	1.03	0.84
CaO	1.08	0.64	1.69	2.11	1.77	1.00	0.76	3.24	2.76
Na_2O	2.57	3.21	2.88	3.27	3.31	3.32	3.27	4.67	4.08
K_2O	5.21	5.68	5.29	5.54	5.36	5.06	5.25	3.18	4.44
TiO_2	0.15	0.14	0.21	0.15	0.16	0.22	0.17	0.90	0.91
P_2O_5	<0.25	<0.25	<0.25	<0.25	<0.25	<0.25	<0.25	<0.25	<0.25
H_2O (TGA)	0.85	0.73	0.99	0.19	0.22	0.33	0.50	2.18	1.37
CO_2	0.31	<0.01	0.06	0.98	0.64	<0.01	<0.01	<0.01	<0.01
Total	100.18	100.75	100.67	100.08	100.13	99.08	99.78	99.62	100.74
Ba	47.8	24	63	40	43.5	40	28	940	1140
Sr	18	23	53	25	20	10	9	293	252
Zn	145	170	161	179	138	119	132	69	158

Jobero formation) are plotted on Figure 9. REE contents are normalized using the chondritic values of Anders and Ebihara (1982).

The overall REE trend with a large LREE enrichment and a steep negative slope is typical of a calcalkaline trend. The most obvious characteristic of the plot is the large negative Eu anomaly, suggesting the removal of substantial amounts of plagioclase during fractionation. The slightly concave upward pattern caused by minor depletion of MREE suggests that in addition to plagioclase, crystallization of apatite, clinopyroxene, and zircon occurred during fractionation. All four of these phases are present in the dacites.

The size of the Eu anomaly is slightly smaller for the lower Palomas tuff than the other two units. Feldspar accumulation would decrease the size of the negative Eu anomaly, but the El Jobero lavas have the highest feldspar contents. However, the magnitude of negative Eu anomalies decrease with increasing oxygen fugacity (Drake, 1975). It is possible that the lower Palomas magna chamber had a higher oxygen fugacity than the upper Palomas or El Jobero magma chambers. A similar circumstance was reported (Cameron and Cameron, 1986) in the Chinati Mountains, where the initial caldera-forming Mitchell Mesa Rhyolite exhibits a lesser magnitude Eu anomaly than the subsequent caldera-filling lavas.

The rocks of the Sierra Hechiceros are all peraluminous or metaluminous and silica-saturated in contrast to the strongly alkalic rocks of the eastern Trans-Pecos Magmatic Province, which includes both silica undersaturated and peralkalic rocks. This calc-alkalic suite of dacites and rhyolites has Thornton-Tuttle differentiation indices that range form 76.76 to 94.11. The trace element data and phenocryst mineralogy strongly suggest that crystallization of plagioclase, combined with one or more of the following minerals—clinopyroxene, apatite, or zircon, are responsible for fractionation in this system.

The rocks of the Sierra Hechiceros are some of the youngest in the Trans-Pecos volcanic field. However, their overall petrographic and chemical characteristics places them in the high K facies of the cals-alkalic suite of Cameron et al. (1979). This suite in most respects more closely resembles the rocks of the Sierra Madre Occidental then the adjacent Trans-Pecos alkalic province. The similarity to rocks of the Sierra Madre Occidental is particularly surprising because of the proximity of the Sierra Hechiceros to the Trans-Pecos alkalic province. The apparent similarity may be more a function of the categorizing of rock types into metaluminous versus peralkalic. As shown on Figure 5, Sierre Hichiceros rocks are all metaluminous or peraluminous, but clustered close to the peralkalic boundary. Only a slight increase in depth of generation might produce more alkalic rock types. Alternatively, an increase in the dip of the subduction zone may be responsible for the change in rock types to the east. However, we see no evidence for this

TABLE 2. CIPW normative compositions of Sierra Hechiceros samples.

	Palomas tuff upper ash-flow tuff		Palomas tuff lower ash-flow tuff			El Jobero formation		La Mota dacite	San Antonio dacite
	UB-101	Em-100	LT-101	P1-25	P3-81	STR	E1J-101	Pa-101	G1
q	37.80	33.37	31.24	31.20	32.71	32.65	34.11	19.96	17.62
c	1.88	0.34	1.38	—	—	0.56	0.04	—	—
or	31.01	33.57	31.29	32.79	31.68	30.28	31.29	19.26	26.44
ar	21.92	27.17	24.39	27.69	28.01	28.43	27.85	40.54	34.77
an	3.54	3.17	8.43	3.37	3.09	5.01	3.81	13.33	11.16
wo	—	—	—	0.23	0.51	—	—	—	—
di-di	—	—	—	0.26	0.32	—	—	2.49	1.86
di-hd	—	—	—	—	—	—	—	—	0.22
hy-en	0.92	0.17	0.52	—	—	—	0.27	2.64	2.12
hy-fs	—	—	—	—	—	—	—	—	0.28
mt	0.12	0.07	—	0.09	—	2.41	0.59	2.59	4.24
il	0.29	0.27	0.09	0.29	0.29	0.42	0.32	1.75	1.75
hm	1.93	1.88	2.24	1.84	1.93	0.22	1.74	0.91	—
tn	—	—	—	—	0.02	—	—	—	—
ru	—	—	0.16	—	—	—	—	—	—
cc	0.70	0.00	0.14	2.23	1.45	0.00	0.00	0.00	0.00
Total	100.02	100.01	100.06	99.99	100.01	99.98	100.01	100.47	100.46
Norm. plag. (% An)	13.6	10.4	25.68	10.8	9.9	15.0	12.0	24.7	24.0
TTDI	90.73	94.11	86.92	91.68	92.40	91.36	93.25	76.76	78.83
$\frac{Na + K}{Al}$ mol	0.774	0.88	0.699	0.90	0.91	0.82	0.89	0.70	0.74

based on any increase of K_2O content. A more likely explanation would be that the Sierra Hechiceros area lies at a point where the depth to the subduction zone increases gradually eastward from one producing calc-alkaline magmas below the Sierra Hechiceros to depths where alkalic magmas are produced in the Trans-Pecos volcanic field.

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REPRODUCTIVE DATA ON SNAKES FROM NORTHEASTERN TEXAS

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ABSTRACT.—Reproductive data from 17 species of snakes from northeastern Texas suggest that egg-laying occurs in late May and June with hatching in late July. Viviparous snakes produced clutches in July, August, and September. Clutch sizes were within known ranges for each species (Fitch, 1970), but so few data on offspring size of snakes are available from the literature that few comparisons can be made. Coefficients of variation of length of offsprings ranged from 0.52 to 10.29 percent. Offspring mass CV's ranged from 0.99 to 25.07 percent. Clutch size and offspring size for *Agkistrodon contortrix* and *Storeria dekayi* were correlated to snout-vent length of females. *Key words*: snakes; reproduction; northeastern Texas; offspring size variation.

Baseline data on reproductive traits of snakes are available for many species throughout North America (Fitch, 1970, 1985). Some reproductive traits (that is, clutch size, offspring size) have been shown to be correlated to female length in some species and more recent works typically include female snout-vent length (SVL). Two parameters, however, female mass and offspring size, rarely are reported (Seigel and Ford, 1988). Female mass can be an indicator of nutritional status and health, and has been shown to be important as a determinate of some aspects of reproduction independent of maternal length (that is, clutch size—Ford and Seigel, 1989*a*; and Seigel and Ford, unpublished data). In addition, female mass is needed to calculate relative clutch mass (RCM), a reproductive characteristic shown to have implications for escape locomotion, and, therefore, a critical life history trait (Vitt and Congdon, 1978; Madsen, 1987; Seigel et al., 1987). Researchers attempting to use the literature to examine the ecological and evolutionary role of RCM in snakes have found the required data are often unavailable (Shine, 1980; Seigel and Fitch, 1984; Seigel et al., 1986). Length and mass of offspring have been reported even less frequently than female mass (Seigel and Ford, 1987), yet this information is needed to evaluate theories such as optimal offspring size (Smith and Fretwell, 1974; Brockelman, 1975). Indeed, mean values for offspring size are not available for most species of snakes, let alone data on variability within or among females that might occur for this trait.

Therefore, even short reports including information on these aspects of reproduction in snakes—from a variety of species and from different geographic areas—are of value. (Seigel and Ford, 1988; Ford and Seigel, 1989*b*). This study documents reproductive data for 17 species of snakes from mixed pine-hardwood habitats of northeastern Texas.

MATERIALS AND METHODS

Pregnant snakes collected in northeastern Texas (Anderson, Henderson, Smith, and Red River counties) by a variety of methods in the years 1980 to 1989 were maintained in an animal room at the University of Texas at Tyler. Females were caged separately, given water *ad libitum*, and fed appropriate prey items (contrary to many previous reports, most females ate in captivity when pregnant). Room temperature was maintained at 28° C on a light:dark cycle of 14:10 hours. Females were weighed every two weeks up to egg-laying or parturition; then measured from snout to vent (SVL) and weighed again. Each egg was measured with calipers (length and width) and weighed (weighed in mass if adhered together). Eggs were incubated at the same temperature as above in a moistened vermiculite substrate (72 grams per 100 milliliters of water). Each offspring born or hatched was measured, SVL and total length (TL), weighed, and sexed by manual eversion of hemipences of males. Venomous species were measured after killing by freezing in an ultracold freezer or by inducing the snake to crawl into a clear tube only slightly wider than the snake. By holding the animal's tail and allowing it to stretch out in the tube its length could be measured within one centimeter. Sex of offspring was not used for the two *Akgistrodon* species because inaccurate records were obtained owing to the strong hemipene retractor muscles. Dates of laying, parturition, and hatching were recorded.

Means, standard deviations, and coefficients of variation for offspring SVL, TL, and mass for each female's clutch were calculated using Statview 512 + (BrainPower, Inc., 1986). Linear regressions of clutch size and offspring size against female SVL were conducted for the two species that had eight or more reproduction records (*Agkistrodon contortrix* and *Storeria dekayi*). Because in snakes both clutch and offspring size often are correlated with female size, residuals from the previous regressions were used to compare the correlation between offspring size and clutch size (Ford and Seigel, 1989*b*).

RESULTS

Reproductive data for 11 viviparous and six oviparous species of snakes from northeastern Texas are shown in Table 1 and 2. Regressions of clutch size, offspring SVL, and mass against female SVL for *A. contortrix* and *S. dekayi* are given in Table 3. Correlations of the residuals of offspring size and clutch size for both species also are given in Table 3.

DISCUSSION

General reproductive pattern.—Oviparous snakes in northeastern Texas lay eggs in May and June; hatching usually takes place in late July. Viviparous snakes are born in July, August, and September. These are fairly typical parturition dates for south-temperate snakes (Kofron, 1979*a*, 1979*b*; Tennant, 1984). Clutch sizes were within the recorded range for each of the various species (Fitch, 1970, 1985; Seigel et al., 1987), but because clutch size was influenced by female SVL and nutritional status, little could be concluded from these data. Egg and offspring sizes can be discussed, because some evidence shows that these traits are less influenced by yearly variation in prey availability (Brodie and Ducey, 1989; Ford and Seigel, 1989*a*; Seigel and Ford, unpublished data).

TABLE 1. Reproductive data from viviparous snakes collected in northeastern Texas (Smith County unless noted) (A, Anderson County; H, Henderson County; R, Red River County). Specimens with numbers have collection data listed in Appendix 1. Measurements are in centimeters, mass is in grams. Mean, standard deviation, and coefficient of variation are given.

Female	Pre-	Post-	Clutch		Neonates			Parturition
SVL	mass	mass	size	Sex	SVL	Total length	Mass	date
					Agkistrodon contortrix			
47.0	89	59	4	U	16.2 ± 0.33 (2.04)	19.0 ± 0.64 (3.36)	4.5 ± 0.12 (2.64)	2 September 1987
50.0	·	120	6	U	·	·	·	26 September 1984
50.0	·	·	7	U	16.5 ± 0.41 (2.47)	19.5 ± 0.45 (2.29)	5.3 ± 0.38 (7.16)	21 September 1985
51.0	·	116	7	U	16.2 ± 0.39 (2.42)	19.2 ± 0.43 (2.26)	5.3 ± 0.25 (4.69)	15 July 1982
53.0	170	115	7	U	17.9 ± 0.56 (3.13)	21.2 ± 0.28 (3.25)	6.3 ± 0.45 (7.06)	16 August 1986
52.0	217	126	7	U	17.7 ± 0.36 (2.05)	20.8 ± 0.56 (2.69)	6.4 ± 0.25 (3.92)	10 August 1989
57.5^{H}	198	144	10	U	18.2 ± 0.21 (1.17)	21.5 ± 0.30 (1.4)	5.2 ± 0.22 (4.14)	6 August 1988
60.0	263	190	7	U	20.0 ± 0.48 (2.39)	23.6 ± 0.51 (2.18)	7.1 ± 0.49 (6.86)	30 July 1989
					Agkistrodon piscivorous			
56.01[1]	271	210	4	U	19.1 ± 0.84 (4.40)	22.8 ± 0.95 (4.18)	12.3 ± 1.66 (13.57)	7 September 1987
58.0	313	204	5	U	20.6 ± 0.55 (2.66)	24.7 ± 0.73 (2.97)	13.3 ± 0.57 (9.62)	25 August 1989
58.0	307	·	4	U	20.6 ± 0.48 (2.32)	24.6 ± 0.48 (1.94)	14.9 ± 0.24 (1.60)	28 August 1985

Table 1. Continued.

					Nerodia erythrogaster			
$·^{H}$	·	515	10	M (5)	19.2 ± 0.82 (4.25)	24.6 ± 0.91 (3.55)	4.6 ± 0.39 (8.50)	27 August 1988
				F (5)	19.5 ± 0.60 (3.08)	25.2 ± 0.48 (1.87)	6.3 ± 1.58 (25.07)	
					Nerodia fasciata			
64.0	·	283	15	M (4)	17.5 ± 0.84 (4.83)	23.8 ± 0.94 (3.94)	6.1 ± 0.64 (10.47)	20 August 1982
				F (11)	17.1 ± 0.71 (4.16)	22.8 ± 1.03 (4.49)	5.6 ± 0.60 (10.66)	
					Nerodia rhombifer			
106^{H}	·	1055	26	M (9)	22.1 ± 1.21 (5.48)	29.2 ± 1.46 (4.99)	9.1 ± 0.91 (10.01)	17 August 1988
				F (16)	22.1 ± 0.32 (1.46)	28.5 ± 0.46 (1.62)	9.6 ± 5.2 (5.41)	
110	·	1110	37	·	·	·	·	20 August 1984
110	·	1400	30	M (13)	21.2 ± 1.64 (7.74)	28.4 ± 2.20 (7.76)	9.3 ± 1.49 (16.04)	23 August 1982
				F (17)	20.8 ± 1.95 (9.38)	27.0 ± 2.64 (9.80)	9.5 ± 2.37 (25.00)	
					Sistrurus miliarius			
·	44.6^{R2}	25.4	6	M (3)	11.8 ± 0.50 (4.24)	13.6 ± 0.55 (4.04)	1.83 ± 0.058 (3.15)	12 August 1987
				F (3)	12.5 ± 0.15 (1.23)	14.2 ± 0.15 (1.07)	2.00 ± 0.100 (5.00)	
·	53.8^{A3}	22.0	8	·	·	·	2.48 ± 0.528	2 August 1986

Table 1. Continued.

·	54.9^{R4}	26.0	6	M (3)	13.8 ± 0.28 (2.05)	15.6 ± 0.21 (1.36)	2.9 ± 0.00 (0)	13 August 1987
				F (3)	13.9 ± 0.22 (1.58)	15.9 ± 0.44 (2.75)	2.9 ± 0.25 (8.44)	
36.9^{R5}	67.8	40.6	8	M (4)	13.1 ± 0.59 (4.54)	15.1 ± 0.59 (3.93)	2.95 ± 0.191 (6.49)	8 August 1987
				F (4)	13.3 ± 0.30 (2.25)	15.0 ± 0.29 (1.92)	2.73 ± 0.171 (6.27)	
·	67.8^{R6}	·	9	U	14.4 ± 0.22 (1.55)	16.4 ± 0.33 (1.99)	3.13 ± 0.218 (6.96)	10 August 1987
					Storeria dekayi			
18.5	6.76	3.39	7	M (5)	7.4 ± 0.21 (2.79)	9.9 ± 0.20 (2.02)	0.28 ± 0.014 (5.05)	23 July 1988
				F (2)	7.6 ± 0.14 (1.86)	9.7 ± 0.14 (1.46)	0.30 ± 0.007 (2.40)	
19.2	6.48	2.36	7	M (1)	7.0 (0.0)	9.6 (0.0)	0.29 (0.0)	14 August 1987
				F (5)	7.0 ± 0.13 (1.86)	9.3 ± 0.13 (1.45)	0.28 ± 0.013 (4.62)	
20.1	7.78	3.10	10	M (4)	7.0 ± 0.06 (0.83)	9.4 ± 0.08 (0.87)	0.28 ± 0.008 (2.92)	17 August 1987
				F (6)	7.0 ± 0.27 (3.83)	9.3 ± 0.34 (3.72)	0.27 ± 0.034 (12.78)	
20.2	7.79	3.70	7	M (4)	7.4 ± 0.06 (0.79)	9.9 ± 0.08 (0.83)	0.27 ± 0.032 (11.71)	8 August 1988
				F (3)	7.9 ± 0.06 (0.73)	10.2 ± 0.12 (1.13)	0.28 ± 0.017 (6.19)	

Table 1. Continued.

20.3	6.02	2.81	6	M (3)	7.1 ± 0.40 (5.67)	9.6 ± 0.67 (6.91)	0.21 ± 0.032 (15.07)	28 August 1987
				F (3)	7.6 ± 0.12 (1.53)	10.0 ± 0.21 (2.09)	0.26 ± 0.036 (13.87)	
20.6	9.67	3.87	11	M (6)	7.1 ± 0.19 (2.65)	9.6 ± 0.32 (3.29)	0.29 ± 0.021 (7.23)	3 August 1987
				F (5)	7.5 ± 0.24 (3.13)	9.8 ± 0.34 (3.48)	0.29 ± 0.025 (8.78)	
22.0	·	4.65	4	M (1)	7.6 (0.0)	9.4 (0.0)	0.34 (0.0)	8 September 1982
				F (3)	8.3 ± 0.06 (0.69)	11.1 ± 0.06 (0.52)	0.37 ± 0.021 (5.58)	
22.3	·	4.73	10	M (2)	7.5 ± 0.07 (0.95)	10.2 ± 0.35 (3.48)	0.36 ± 0.007 (1.99)	2 August 1983
				F (8)	7.6 ± 0.26 (3.35)	10.2 ± 0.26 (2.53)	0.35 ± 0.014 (3.98)	
23.2	9.72	4.4	6	M (1)	8.7 (0.0)	11.9 (0.0)	4.5 (0.0)	20 August 1988
				F (5)	8.5 ± 0.16 (1.93)	11.2 ± 0.26 (2.32)	0.44 ± 0.029 (6.49)	
24.0	·	4.42	11	M (6)	8.3 ± 0.12 (1.41)	11.1 ± 0.34 (3.09)	0.39 ± 0.021 (5.46)	25 July 1989
				F (5)	8.4 ± 0.21 (2.48)	11.2 ± 0.29 (2.56)	0.40 ± 0.031 (7.71)	
25.0	11.9	5.51	12	M (8)	7.9 ± 0.17 (2.15)	10.4 ± 0.23 (2.21)	0.29 ± 0.009 (3.08)	26 July 1988
				F (4)	8.0 ± 0.16 (2.04)	10.4 ± 0.13 (1.25)	0.29 ± 0.018 (6.30)	

Table 1. Continued.

26.1	13.6	7.7	7	M (4)	8.8 ± 0.17 (1.95)	11.8 ± 0.37 (3.12)	0.49 ± 0.057 (11.77)	6 July 1988
				F (3)	9.0 ± 0.45 (4.99)	11.5 ± 0.76 (6.57)	0.48 ± 0.093 (19.22)	
26.7	11.1	5.4	15	M (7)	7.3 ± 0.71 (9.65)	9.7 ± 0.83 (8.60)	0.28 ± 0.053 (18.68)	13 July 1987
				F (7)	7.6 ± 0.37 (4.94)	9.7 ± 0.50 (5.16)	0.35 ± 0.028 (7.98)	
28.0	14.1	7.35	13	M (6)	7.6 ± 0.29 (3.86)	10.4 ± 0.20 (1.92)	0.34 ± 0.024 (7.20)	17 July 1988
				F (7)	7.6 ± 0.43 (5.60)	10.0 ± 0.52 (5.17)	0.32 ± 0.036 (11.27)	
28.5	12.7	7.42	14	·	·	·	0.34	1 August 1987
					Storeria occipitomaculata			
22.1	9.5	4.58	10	M (5)	7.4 ± 0.28 (3.75)	9.8 ± 0.39 (3.99)	0.35 ± 0.030 (8.57)	6 July 1988
				F (5)	7.4 ± 0.09 (1.20)	9.6 ± 0.15 (1.59)	0.33 ± 0.015 (4.47)	
24.0	10.0	5.5	15	M (7)	6.8 ± 0.23 (3.40)	8.9 ± 0.33 (3.70)	0.22 ± 0.008 (3.51)	19 July 1988
				F (8)	7.1 ± 0.34 (4.86)	9.0 ± 0.43 (4.80)	0.22 ± 0.011 (4.74)	
					Thamnophis proximus			
63.2	·	53.6	17	M (6)	14.5 ± 0.24 (1.63)	20.1 ± 0.41 (2.02)	1.21 ± 0.043 (3.56)	
				F (10)	14.3 ± 0.57 (3.97)	20.0 ± 0.57 (2.84)	1.20 ± 0.068 (5.64)	12 August 1981

Table 1. Continued.

68.0	·	86.5	23	M (12)	13.8 ± 0.34 (2.45)	19.8 ± 0.48 (2.44)	1.06 ± 0.06 (5.65)	20 August 1982
				F (9)	13.0 ± 0.64 (4.90)	18.8 ± 0.99 (5.27)	0.97 ± 0.111 (11.42)	
70.0	124	75.4	18	M (10)	17.4 ± 0.36 (2.06)	24.4 ± 0.42 (1.73)	1.81*	10 July 1980
				F (8)	17.4 ± 0.36 (2.07)	24.3 ± 0.48 (1.98)		
75.5	177	124	18	M (11)	17.4 ± 0.40 (2.27)	24.8 ± 0.58 (2.35)	1.47*	18 July 1980
				F (5)	17.4 ± 0.38 (2.18)	24.3 ± 0.50 (2.05)		
					Virginia striatula			
18.3	5.5	3.3	4	M (3)	8.1 ± 0.06 (0.72)	10.1 ± 0.06 (0.57)	0.45 ± 0.0 (0.0)	16 August 1987
				F (1)	7.7 (0.0)	9.5 (0.0)	0.38 (0.0)	
		3.7[7]	5	U	· ·	· ·	0.58 ± 0.084 (14.4)	26 July 1986
					Virginia valeriae			
22.0	14.8	6.3	6	M (3)	8.8 ± 0.12 (1.32)	10.7 ± 0.15 (1.42)	0.85 ± 0.06 (7.22)	5 August 1989
				F (3)	8.9 ± 0.32 (3.60)	10.5 ± 0.36 (3.43)	0.81 ± 0.09 (11.16)	
23.0	12.4	7.4	3*	M (1)	9.4 (0.0)	11.5 (0.0)	0.85 (0.0)	10 August 1988
				F (1)	8.8 (0.0)	10.3 (0.0)	0.77 (0.0)	

Table 1. Continued.

24.8	14.7	7.8	7	M (2)	8.6 ± 0.50 (5.79)	11.0 ± 1.13 (10.29)	0.68 ± 0.057 (8.32)	11 August 1988
				F (4)	9.4 ± 0.13 (1.34)	11.0 ± 0.17 (1.55)	0.77 ± 0.057 (7.51)	

* Mean for the clutch.

TABLE 2. Reproductive data from oviparous snakes from northeastern Texas (Smith County). Superscript number refers to preserved collection data in Appendix 1. Measurements are in centimeters, mass is in grams. Mean, standard deviation, and coefficient of variation are given.

Female SVL	Pre-mass	Post-mass	Clutch size	Sex	Egg length Neonate SVL	Egg width Neonate Tot. length	Egg mass Neonate mass	Laying/hatching date
					Cemophora coccinea			
·	·	·	6	Eggs (4)	1.57 ± 0.126 (8.05)	0.84 ± 0.027 (3.17)	0.83 ± 0.108 (13.01)	27 June 1988
					Coluber constrictor			
70.0	·	107	9	Eggs	2.30 ± 2.42 (10.55)	1.28 ± 0.70 (5.47)	2.38 ± 0.16 (6.63)	
83.0	·	135	2*	Eggs	3.02 ± 0.028 (0.94)	1.09 ± 0.001 (0.13)	6.66 ± 0.042 (0.64)	20 May 1987
				F (2)	19.3 ± 0.35 (1.84)	25.2 ± 0.50 (1.97)	4.3 ± 0.04 (0.99)	11 July 1987
					Heterodon platirhinos			
66.0	·	280	30	Eggs	·	·	·	18 June 1988
					Masticophis flagellum			
116.0	·	322	11	Eggs	4.47 ± 0.29 (6.56)	2.33 ± 0.05 (1.98)	15.3 ± 0.61 (3.96)	29 June 1988
				M (4)	30.4 ± 0.55 (1.80)	40.1 ± 0.69 (1.72)	11.7 ± 0.28 (2.36)	
				F (6)	31.2 ± 0.28 (2.97)	40.6 ± 1.28 (3.15)	11.9 ± 0.74 (6.19)	
					Micrurus fulvius			
50.0	34.0	·	3	Eggs	·	·	·	29 May 1987

Table 2. Continued.

					Opheodrys aestivus			
		16.2[8]	6	Eggs	· ·	· ·	1.62 ± 0.117 (7.23)	6 June 1985
				U	·	·	·	10 July 1985
47.0	24.0	17.0	5	Eggs	27.9 ± 2.56 (9.15)	9.9 ± 0.50 (5.0)	1.77 (0.0)	19 June 1988
				M (1)	13.9 (0.0)	21.3 (0.0)	1.55 (0.0)	28 July 1988
				F (3)	13.8 ± 0.15 (1.11)	20.4 ± 0.46 (2.27)	1.35 ± 0.051 (3.81)	
50.0	25.0	17.0	4	Eggs	36.0 ± 0.70 (1.96)	9.03 ± 0.17 (1.89)	2.11 ± 0.082 (3.87)	19 June 1988
				M (2)	14.9 ± 0.42 (2.85)	22.4 ± 0.85 (2.22)	1.90 ± 0.085 (4.47)	30 July 1988
				F (2)	15.3 ± 0.28 (1.85)	22.5 ± 0.71 (0.32)	1.81 ± 0.007 (0.39)	

* Eggs laid the day after capture so possibly partial clutch.

TABLE 3. Regression analysis of reproductive data from two species of snakes from northeastern Texas.

Species	N	Y-intercept	Slope	r	P
Agkistrodon contortrix					
Clutch size × female SVL	8	−7.25	0.27	0.49	0.06
Young SVL × female SVL	7	2.49	0.28	0.85	0.003
Young mass × female SVL	7	−1.40	0.14	0.45	0.10
Residuals					
Young SVL × clutch size	7	0.008	−0.31	0.53	0.06
Young mass × clutch size	7	0.006	−0.22	0.18	0.34
Storeria dekayi					
Clutch size × female SVL	14	−5.76	0.66	0.42	0.01
Young SVL × female SVL	13	5.62	0.09	0.25	0.07
Young mass × female SVL	14	0.11	0.01	0.22	0.08
Residuals					
Young SVL × clutch size	13	−0.01	−0.14	0.54	0.003
Young mass × clutch size	14	$5.7\ e^{-20}$	−0.02	0.40	0.01

Coefficients of variation for mean offspring sizes indicate relatively low variability in these traits (viviparous neonate CVs for SVL ranged from 0.69 to 9.65 percent, TL from 0.52 to 10.29 percent, and mass from 1.60 to 25.07; egg length CVs ranged from 0.94 to 10.55 percent, widths from 0.13 to 5.47 percent, and mass from 0.64 to 13.01 percent; oviparous neonate CVs of SVL ranged from 1.80 to 2.97 percent, TL from 1.72 to 3.15, and mass from 0.99 to 7.23 percent). Litters of mosquitofish, for example, have an egg mass variation of 9.8 to 35.5 percent (Meffe, 1987). It is interesting to note that CVs for SVL and TL of offsprings are much lower than those for mass. This may relate to the fact that mass is a cubic factor (Meffe, 1990), but it also could reflect variability in the storage of lipids that remain in neonates at hatching or birth. It also is of interest that egg length is more variable than egg width in oviparous species. Possibly this relates to the packaging of eggs in the linear oviduct. Because a snake can become fatter but not significantly longer during pregnancy, changing the number of eggs placed in the fixed length of the oviduct could affect egg length more than width (Seigel and Ford, 1987).

Reproduction in Agkistrodon contortrix and Storeria dekayi.—For both of these species, clutch size and offspring size were correlated with female length (Table 3). However, offspring size in *A. contortrix* was more strongly related to female size, whereas for *S. dekayi*, clutch size had the stronger correlation. Larger females can accommodate a larger clutch mass, and apparently in these species the females accomplish this by having more and larger young. After adjusting for female length, offspring size in *S. dekayi* was strongly related to clutch size; but for *A.*

contortrix, neonate SVL was only marginally correlated to clutch size. *Agkistrodon* is heavy-bodied, and the size of its offspring may be less constrained by clutch size, although Stewart (1979) suggested that species with smaller clutch sizes should show a strong negative interrelationship of these two factors.

Continued documentation of primary reproductive data for snakes will elucidate some of these points and we encourage such reports. In particular, for geographic comparisons such as that for clutch sizes in New World reptiles by Fitch (1985), many more data are necessary.

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APPENDIX

Collection numbers for snakes deposited in collections: UTT, University of Texas at Tyler Vertebrate Collection; UTA, University of Texas at Arlington Collection of Vertebrates.

1. Off spring UTT 412-415.
2. UTA R19633, offspring UTA R19634-39.
3. UTA R18029, offspring UTA R18030-32.
4. UTA R19626, offspring UTA R19627-32.
5. UTA R19617, offspring UTA R19618-25.
6. UTA R22379, offspring UTA R22380-R22388.
7. UTA R18006, offspring UTA R18007-11.
8. UTA R16383, offspring UTA R15895-97.

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BIOLOGICAL MONITORING OF THE TEXAS SHELLFISH INDUSTRY: A CRITICAL REVIEW

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ABSTRACT.—Despite regulatory activities by federal and state shellfish agencies, bivalve mollusks continue to be implicated in serious outbreaks of human enteric disease. A review of the marine-biological and biomedical literature indicates that current monitoring procedures are inadequate to completely protect the consumers of clams and oysters from naturally occurring pathogenic marine *Vibrio* species or viruses if the shellfish are consumed in a raw or under-cooked state. It is concluded that the shellfish industry and the regulatory agencies must bear the responsibility of establishing adequate procedures to warn the public of risks associated with consumption of inadequately cooked bivalve mollusks. *Key words*: shellfish; indicator organisms; pathogens.

Molluskan shellfish have been a major constituent of the animal protein consumed by mankind for at least 50,000 years. Shell piles at some prehistoric sites, estimated to have taken centuries to accumulate, suggest that bivalve mollusks represented as much as 40 percent of the animal protein consumed by some human communities (Clark, 1964; Brothwell and Brothwell, 1969). References exist in Egyptian hieroglyphic regarding shellfish consumption (Darby et al., 1977), the Chinese developed cultivation methods several thousand years ago (Clark, 1964), and the Ancient Romans imported shellfish from such diverse areas as France, Britain, Africa, and the Black Sea, and cultivated them with the same hanging rope method still in use by fishermen in Lucrine Lake (Clark, 1964; Brothwell and Brothwell, 1969). Early European settlers of this continent also recognized the importance of a continuing supply of shellfish and several colonies, beginning with New Amsterdam in 1658 or 1659, enacted legislation on oyster harvesting (Houser, 1965; Larkin and Hunt, 1982). These measures probably were related more to conservation than to protection of public health.

Clams, oysters, mussels, and scallops comprise the molluskan class Bivalvia and, as sessile filter feeders, they concentrate organisms and toxins, thus acting as vectors in the transmission of human disease. Shellfish consume diatoms, algal spores, other planktonic life, and organic detritus, and under natural conditions feed about 90 percent of the time (Jorgensen, 1955). Feeding, which may occur whenever salinity, temperature, and turbidity are favorable, is affected through the creation of water currents by gill cilia. Under optimum conditions the maximum flow of water through the animal may be as high as 37 liters per hour or more than 200 gallons per day (Jorgensen, 1955). Apart from the apparent inability of the organism to discriminate between an edible species of diatom (for example, *Nitzschia*) and a nonedible bacterium (for example, *Vibrio*) with the resultant threat to human health, shellfish also accumulate heavy metals, pesticides, and hydrocarbons directly from the water (bioaccumulation) and concentrate them further through consumption of other organisms that have accumulated these substances in the course of their own metabolism (biomagnification) (Gutherie et al., 1979).

Because metals, bacteria, and viruses have an affinity for the surfaces of certain clay particles or organic compounds, there is a high probability that these disease-producing agents will be found in the intestines of shellfish bound for market. These particles constitute the "fluffy sediments" of the water-mud interface; concentrations of the disease-causing agents are higher in these interstitial waters than in overlying waters (de Groot et al., 1976), interstitial waters upon which shellfish depend for nutrition. Municipal and industrial wastes that find their way into the estuarine environment contain sufficient quantities of heavy metals to constitute a continuous source of contamination (Guthrie et al., 1979).

The first suggestion in modern European literature of any connection between human malady and the consumption of mollusks appeared in 1599. In *Dyett's Dry Dinner*, William Butler admonished his readers that, "It is unseemly and unwholesome in all months that have not an 'r' in their names to eat an oyster" (Bartlett, 1968). In 1737, Swammerdam published an account relating human illness to consumption of mullusks (cited in Malek and Cheng, 1974), and Pasquier concluded in 1818 that cases of gastrointestinal illness resulted from the eating of raw oysters collected in sewage-polluted waters (Wise et al., 1948). After the pioneering research of Pasteur, Lister, and Snow, the relationship between microorganisms and infectious diseases was established and an overwhelming body of scientific work accumulated that linked typhoid fever and enteric fever to the consumption of raw or partially cooked shellfish (see Wise et al., 1948, for a comprehensive list of publications). Recent research has enlarged the list of potential pathogens and parasites to include fungi, yeast, amoebae, trematodes, nematodes, and at least nine genera of bacteria, which, theoretically, may be transmitted to humans through consumption of bivalves (Bryan, 1973; Cheng, 1973; Janssen, 1974; Buck et al., 1977; Larkin and Hunt, 1982; and Siegal and Rogers, 1982).

In 1955, investigators in Sweden were the first to trace infectious hepatitis to oyster consumption (Clem, 1973). Since then, many researchers have published other accounts (Dougherty and Altman, 1962; Mason and McLean, 1962; Dismukes et al., 1969; Portnoy et al., 1975; Ohara et al., 1983), at least one of which indicated that "sentinel gastroenteritis" does not always precede a hepatitis outbreak (Mackowiak et al., 1976). In addition, other picornaviruses (including *Poliovirus,* *Coxsackievirus* A and B, *Echovirus*, and *Enterovirus*) as well as adenoviruses, papovaviruses, parvoviruses, and reoviruses (including *Rotavirus*) are potential contaminants of shellfish (Larkin and Hunt, 1982). Other disease factors of concern to potential consumers of bivalve shellfish are radionuclides (Hess and Smith, 1977), pesticides (Eisler, 1970; Rowe et al., 1970; Lowe et al., 1971; Mason and Rowe, 1976; Hofstetter, 1977; Brown, 1978; Butler et al., 1978; Emanuelsen et al., 1978), hydrocarbons (Blumer et al., 1970; Ehrhardt, 1972), heavy metals (Kopfler, 1974; Frazier, 1975*a*, 1975*b*, de Groot et al., 1976; Mason et al., 1976; Sims and Presley, 1976; Zaroogian and Cheer, 1976; Boyden, 1977; Hofstetter, 1977; Greig and Wenzloff, 1978; Latouche and Mix, 1981; Guthrie et al., 1979; Lytle and Lytle, 1982; Popham and D'Auria, 1983), and marine biotoxins (Schantz, 1973; Lo Cicero, 1974; Halstead and Schantz, 1984).

THE NSSP AND TEXAS SHELLFISH LAW

Between 1890 and 1925, several major outbreaks of enteric fever and typhoid occurred that clearly were traceable to the consumption of raw or partially cooked shellfish. In 1924 and 1925, there were 129 cases of typhoid in Chicago linked to two infected fishermen on Long Island (Wise et al., 1948). Grave concern over the future of the industry prompted a conference in 1925 that was sponsored by the U. S. Public Health Service. This conference, attended by state and local health authorities and representatives of the shellfish industry, resulted in the establishment of the National Shellfish Sanitation Program (NSSP). The NSSP outlined the concepts of a "cooperative control procedure," which specified the responsibilities of the Public Health Service, the industry, and the states in providing safe and wholesome shellfish for interstate shipment. The first operational manual of the NSSP was published in 1925 (Houser, 1965).

The responsibilities of the U. S. Public Health Service included: annual review of each state's control program, inspection of a representative number of processing plants, endorsing (or withholding endorsement of) the control program, and publishing a semimonthly list of all valid interstate certificates issued by control agencies of the several states. In addition, the Food and Drug Administration is responsible for training state and federal personnel, conducting research in shellfish-related fields, and developing standards for shellfish and the quality of growing water (Houser, 1965).

The responsibilities of the industry included: obtaining shellfish from safe sources, maintaining processing plants under agreed upon minimum sanitary standards, properly labeling all shellfish containers (including a valid certification number), and maintaining adequate records to account for the origin and disposition of all shellfish (Houser, 1965).

The responsibilities of the states included: adopting adequate laws and regulations to ensure sanitary control of the industry, conducting and monitoring sanitary and bacteriological surveys of growing waters (including the processing of a significant number of growing water and shellfish samples), designating and patrolling restricted areas, inspecting processing plants, and issuing numbered certificates to complying dealers (Houser, 1965).

Initially, the Texas shellfish program was administered by the Texas Department of Health, Division of Sanitary Engineering. Certification was voluntary and those dealers not wishing to sell in interstate markets were not compelled to comply with division regulations. Sanitary surveys were conducted in cooperation with the Division of Water Pollution Control. Under pressure from the industry and the Public Health Service, the 59th Legislature, in 1965, passed House Bill 194, "The Texas Shellfish Law." Codified in Vernon's Revised Civil Statutes of Texas as Article 4050f and later recodified by the 64th Legislature as Title 5, Subtitle D, Chapter 76, Subchapter D, Parks and Wildlife Code, the law provides for: the promulgation of appropriate rules and regulations; the inspection of processing plants and issuance of certificates; enforcement of closure lines; penalties for violation; the surveying of growing waters; and mapping and closing of "polluted" areas. The Division of Marine Resources (later renamed the Division of Shellfish Sanitation Control) was established to administer the law and the rules and regulations subsequently developed.

Dilemma of the Suitability of Indicator Organisms

The quality of estuarine waters and the consequent fitness of shellfish harvested therefrom for human consumption have been measured against the polluting influence of human activity (Olivieri, 1982; Pipes, 1982*a*). Fecal coliform bacteria currently are used as index organisms or markers of human fecal contamination of shellfish or shellfish waters. These are appropriate if recent pollution from fecal sources is suspected (Pipes, 1982*a*), and if this pollution is the only potential contamination of concern. Quantification of this class of organisms continues to be the major standard by which the safety of the product is measured (American Public Health Association, 1970). Progress continues to be made in improving procedures for identifying and quantifying these and other indicators of human fecal contamination in both organisms and their natural environment as well as in discovering new indicators (Robertson and Tobin, 1983; Cook and Pabst, 1984; Robertson, 1984; Matusik et al., 1988; DePaola et al., 1988). Indirect evidence for the general efficacy of these shellfish sanitation procedures is provided in the scientific literature concerned with the outbreak of certain enteric diseases. Prior to 1940, oysters and clams were a common vehicle in the transmission of typhoid and paratyphoid (Wise et al., 1948; Pipes, 1982*b*); however, since 1940, shellfish rarely have been implicated in the transmission of these diseases.

A recent independent sanitary survey of West Galveston Bay led to the conclusion that the Texas survey program has met its statutory and regulatory responsibilities insofar as this particular estuary is concerned (Gray, 1987). It may be assumed that control measures, as applied to this bay, are typical of those practiced all along the Texas coast, throughout the shellfish producing areas of other coastal states, and by the other shellfish exporting nations of the industralized world. Consequently, the industry is harvesting shellfish that generally meet current sanitary standards. Nevertheless, shellfish continue to be recognized as vectors in the etiology of human disease. Specifically, illness from small round-structured virus (Gill et al., 1983; Sekine et al., 1989), Norwalk virus (Gunn et al., 1982; Morse et al., 1986), and various *Vibrio* species (Wilson et al., 1981; Nolan et al., 1984; Howard and Lieb, 1988; West, 1989) continues to be associated with consumption of raw or inadequately cooked clams and oysters. Modern sanitary engineering and microbiology have not eliminated shellfish as a potential vector in human disease, and the absence of fecal coliform indicators evidently does not guarantee that growing waters or harvested shellfish have not been exposed to pathogens or other disease-causing agents.

Olivieri (1982) defined a valuable indicator by four criteria:

1. The indicator should always be present when the source of the pathogenic microorganisms of concern is present and absent in clean uncontaminated water.
2. The indicator should be present in numbers much greater than the pathogen or pathogens it is intended to indicate.
3. The indicator should respond to natural environmental conditions and water and wastewater treatment processes in a manner similar to the pathogens of interest.
4. The indicator should be easy to isolate, identify, and enumerate.

Natural limits to the use of indicators are the result of the inability of individual (or groups of) indicators to fulfill one or more of Olivieri's criteria. The presence of the various haloplilic *Vibrio* species that are part of the natural flora of an estuarine environment (Kelly, 1982; Oliver et al., 1982) would not be expected, necessarily, to be revealed by recovery of fecal coliform organisms. Alternatively, under some conditions, *Vibrio* organisms may exist in such numbers that preventing exposure to disease may be impossible if the contaminated seafood is eaten raw or only partially cooked (Blake et al., 1980). It has been suggested that *Vibrio* species be added to the list of organisms used as monitors of the sanitary quality of shellfish and waters in which they are grown (DePaola et al., 1988). While this is a clear departure from the traditional practice of using nonpathogenic organisms as indicators, it represents a possible means of reducing anxiety on the part of the shellfish-consuming public.

Additionally, not all pathogens seem to respond to natural or engineered conditions in a manner similar to that known for fecal-indicator organisms. It has been shown that tertiary treatment of wastewater effluents does not ensure that such effluents are free of pathogenic amoebae, bacteria, or viruses simply because fecal coliforms are not present (Seyfried et al., 1984). Pathogenic viruses may remain viable in water and sediments for several months after the indicator organisms have died (Gerba et al., 1979; Goyal et al., 1984; Rao et al., 1986). Depuration, the process of purifying shellfish by exposing them to treated seawater, does not seem to be an adequate protection against viral exposure (Canzonier, 1971; Mele et al., 1989). Furthermore, once in the benthic environment, these pathogens will continue to contaminate adjacent or even distant waters through natural or artificial disturbance of bottom sediments (Goyal et al., 1984; Rao et al., 1986). The use of inactivated polio virus (Wallis et al., 1985) and at least one bacteriophage (Havelaar, 1987) offer some hope as possible models for the action and movement of pathogenic viruses in estuarine environments.

Another factor that may be responsible for the transmission of bacterial disease is improper handling of shellfish by harvesters, processors, wholesalers, or retailers (Dupont, 1986). Bilge water or icemelt can represent a potential source of contamination; fishes, crabs, and other seafoods and produce may contain pathogenic or opportunistic organisms; and shellfish held at temperatures above 40 degrees Fahrenheit constitute a potential culture medium conducive to the propagation of pathogenic bacteria. Clearly, the proliferation, or even the presence, of fecal coliform organisms is not necessary for such conditions to prevail.

Nor can indicator organisms be expected to adequately model the presence of nonbiological pathogens. Heavy metals, organics, and other toxic chemical agents often are associated with municipal waste water, and recovery of fecal coliform indicators from shellfish or the waters in which they are grown may suggest the potential for exposure to these agents. However, because the indicators may die in the estuarine environment, and because these contaminants may originate in sources other than municipal waste water, the absence of indicators does not imply the absence of contaminants.

Conclusions

Although there is little solid epidemiological evidence, it is likely that the shellfish monitoring program is effective in some measure in prevention of disease. State and federal inspections serve to reduce mishandling of the resource and the marketing of illegally harvested shellfish. Current survey practices and sampling schedules probably reduce exposure to fecal contamination and nonbiological pollution of human origin. Based on the assumption that any reduction of shellfish harvesting from pathogen-polluted waters should reduce transmission of enteric disease, the monitoring program should not be discontinued. However, these measures are insufficient to completely protect the consuming public.

Sampling limitations and the natural limitations of indicator organisms contribute to the potential for shellfish to act as a vector in human disease. In particular, current standard procedures are inadequate to reveal the presence of certain pathogenic viruses or *Vibrio* species. Clearly, despite advances in the area, continued work is necessary in the search for organisms that mimic the activity of these pathogens. Furthermore, the cost effectiveness of new procedures has yet to be established, in the aggregate, against the economic viability of the industry. The addition of new indicators may necessitate more sampling and the performance of more expensive procedures. It could be anticipated that increased sampling or more expensive methodologies would represent a considerable burden upon the resources of the producer or the monitoring agencies.

In view of all of the possibilities for shellfish contamination, it is not surprising that many authors have recommended against the consumption of raw or partially cooked shellfish (Blake et al., 1980; Gill et al., 1983; DuPont, 1986; Morse et al., 1986; Mele et al., 1989). Until the problems associated with inappropriate indicators or inadequate sampling procedures can be overcome, the most prudent course of action on the part of the public is to avoid raw or undercooked oysters and clams. The persistent recurrence of raw shellfish-associated outbreaks of enteric illness over the past decade is evidence of the failure of public health professionals to properly communicate to the consuming public an adequate respect for the risks associated with eating raw or poorly cooked clams and oysters. If future outbreaks are to be prevented, or at least limited, state regulatory agencies and the shellfish industry must face the uncertainty of whether undercooked shellfish can be consumed safely, and establish adequate warning procedures as needed for the unsuspecting public.

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HELMINTH PARASITES OF UNISEXUAL AND BISEXUAL WHIPTAIL LIZARDS (TEIIDAE) IN NORTH AMERICA. IV. THE TEXAS SPOTTED WHIPTAIL (*CNEMIDOPHORUS GULARIS*)

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Abstract.—Two hundred eighty-nine Texas spotted whiptail lizards, *Cnemidophorus gularis*, from New Mexico, Oklahoma, Texas, and México were examined for helminth parasites. One hundred-fifteen (40 percent) were infected with one or more parasites, including 10 (three percent) with an unidentified species of *Oochoristica* Lühe, 1898 and *O. bivitellobata* Loewen, 1940, 69 (24 percent) with *Pharyngodon warneri* Harwood, 1932, 29 (10 percent) with an unidentified species of *Physaloptera* Rudolphi, 1819, two (0.7 percent) with *Pharyngodon kirbii* Specian and Ubelaker, 1974, one (0.3 percent) with *Parathelandros texanus* Specian and Ubelaker, 1974, 11 (four percent) with acanthocephalan cystacanths, and 15 (six percent) with unidentified larval nematodes. Prevalence of infection varied according to the region in which the lizards were collected as 55 percent from Texas, 50 percent from New Mexico, 23 percent from México, and 21 percent from Oklahoma harbored parasites. Prevalence also varied among different age, sex and size classes of *C. gularis* as 49 percent of the adult males, 39 percent of the adult females, 20 percent of the juveniles, and none of the hatchlings was infected. This paper, the fourth in a series of reports on helminths of species of *Cnemidophorus*, represents the first record of endoparasites from *C. gularis*. *Key words*: acanthocephalans; cestodes; helminths; nematodes; parasites; whiptail lizards; *Cnemidophorus gularis*.

The Texas spotted whiptail, *Cnemidophorus gularis* Baird and Girard, 1852, is a moderately large bisexual teiid lizard that ranges from southern Oklahoma south through Texas to southeastern New Mexico and northern Veracruz, México (Conant, 1975). The species inhabits semiarid grasslands, river floodplains, open brushy areas, and limestone hillsides. A plethora of information is available on various aspects of its ecology and natural history (Milstead, 1957*a*, 1957*b*; Ballinger and Shrank, 1972, 1973; Schall, 1978; Walker, 1981*a*, 1981*b*; Price, 1983); however, little is known concerning the parasites of this taxon. Loomis and Crossley (1963) reported the chigger mite, *Eutrombicula alfreddugesi*, from a single *C. sacki* (= *gularis*) and Whitworth and Wangberg (1985) reported flesh fly larvae, *Blaesoxipha plintopyga*, infesting *C. gularis* from Bexar and Kimble counties, Texas, respectively. Ayala and Schall (1977) and Telford (1978) failed to find hemoparasites in a small sample of *C. gularis* from Texas. To my knowledge, nothing has been published on the helminth parasites of this whiptail lizard.

The purposes of this paper, the fourth in a series of reports on the helminths of *Cnemidophorus*, is to provide prevalence data, intensities, and identities of parasites from a survey on a large sample of *C. gularis* from throughout its range and to compare those data with parasite information from previous reports on whiptail lizards (see McAllister et al., 1986; McAllister, 1990*a*, 1990*b*, 1990*c*).

MATERIALS AND METHODS

Two hundred eighty-nine hatchling, juvenile and adult *C. gularis*—183 males, 106 females; mean ± snout-vent length (SVL) = 70.0 ± 13.2, range 33-108 mm—were collected between 1950 and 1987 during seasons of lizard activity (late March to early October). Most had been fixed in formalin, stored in 70 percent ethanol, and were borrowed either from the Sul Ross State University Museum (SRSU), Dallas Museum of Natural History (DMNH), University of Texas at El Paso Collection (UTEP), Texas Cooperative Wildlife Collection (TCWC), University of Arkansas Department of Zoology (UADZ), University of Kansas Museum of Natural History (KU), Oklahoma State University Museum (OKSU), or University of New Mexico Museum of Southwestern Biology (UNM). These specimens (number examined in parentheses) were collected from Carter (6), Greer (15), Harmon (5), Jackson (2), Johnston (1), and Murray (10) counties of Oklahoma, Eddy (12) and Lea (2) counties of New Mexico, Andrews (1), Bandera (2), Brewster (13), Burnet (3), Denton (1), Garza (1), Gillespie (2), Hays (2), Hidalgo (14), Irion (1), Jeff Davis (7), Kendall (1), Kimble (1), Kleberg (1), Matagorda (1), McLennon (2), Pecos (19), Reeves (3), Starr (25), Stephens (1), Sutton (2), Tarrant (4), Taylor (1), Tom Green (1), Val Verde (5), Webb (3), and Wichita (1) counties of Texas, and the states of Coahuila (33), Tamaulipas (41), and Nuevo León (20) in México. Methods for processing hosts and staining and preparation of helminths have been previously described (McAllister, 1990*a*). For purposes of examination of hemoparasites, coccidians, and fresh helminth material, 24 *C. gularis* were collected alive in Johnson ($N = 9$) and Somervell ($N = 15$) counties of north-central Texas between May 1985 and August 1987. They were killed with an overdose of sodium pentobarbital (Nembutal ®) and blood was drawn from exposed ventricles, allowed to dry on glass slides, fixed in absolute methanol, stained with Giemsa, and examined for hematozoa. Feces from the rectum were placed in individual vials of 2.5 percent potassium dichromate and examined for coccidia following methods of Upton et al. (1988).

Representative helminths have been deposited in the United States National Museum Helminthological Collection (USDA, Beltsville, Maryland 20705) as follows: *Oochoristica* sp. (USNM 81121-81124), *Oochoristica bivitellobata* (USNM 81118-81120), *Pharyngodon warneri* (USNM 81125-81126), *Physaloptera* sp. (USNM 81127-81128), *Pharyngodon kirbii* (USNM 81129), *Parathelandros texanus* (USNM 81130), acanthocephalan cystacanth (USNM 81117). Voucher host specimens from Johnson and Somervell counties, Texas, are deposited in the Arkansas State University Museum of Zoology (ASUMZ 4579, 4645-4647, 4666-4669, 4685-4686, 5943-5944, 5963-5965, 5986-5989, 6012, 8413, 8468-8469, 8500-8503, 8534, 8542-8543, 8582-8583).

RESULTS AND DISCUSSION

One hundred fifteen (40 percent) *C. gularis* were infected with at least one kind of helminth (Table 1). These included 95 (83 percent) with a single species, 17 (15 percent) with two species, and three (three percent) with three species. In the subset of 24 lizards collected alive, blood was negative for plasmodial and trypanosomal parasites, and feces did not contain coccidian oocysts.

Prevalence among the sexes was not significantly different as 77 or 42 percent of all males and 38 or 35 percent of all females harbored

TABLE 1. Helminths found in *Cnemidophorus gularis*.

Helminth	Prevalence: Number infected/ number examined	Prevalence: Percent	Intensity: x̄ ± SE (range)
Cestoidea			
Cyclophyllidea			
Oochoristica sp.*	7/289	2	3.0 ± 0.8 (1-7)
O. bivitellobata	3/289	1	1.7 ± 0.7 (1-3)
Nematoda			
Spirurida			
Physaloptera sp.	29/289	10	3.8 ± 0.8 (1-22)
Unidentified larvae	9/289	3	3.8 ± 1.1 (1-12)
Oxyurida			
Pharyngodon kirbii	2/289	0.7	17.5 ± 7.5 (10-25)
P. warneri	69/289	24	33.9 ± 7.9 (1-500)
Parathelandros texanus	1/289	0.3	1.0 ± (1)
Unidentified larvae	6/289	2	11.0 ± 6.6 (1-45)
Acanthocephala			
Unidentified cystacanths	11/289	4	1.6 ± 0.2 (1-3)

* Prestrobilar, immature adults with genital primordia and unidentifiable mature adults.

parasites ($X^2 = 0.84$, 1 df, $P > 0.4$). Prevalence of infection varied among different age, sex, and size classes of *C. gularis*; 49 percent of the adult males and 39 percent of the adult females harbored parasites, whereas only 17 percent of the immature lizards were infected ($X^2 = 12.3$, 1 df, $P < 0.0005$) (Table 2). Prevalence also varied according to different parts of the range of *C. gularis* as 55 percent of the individuals examined from Texas, 50 percent from New Mexico, 23 percent from México, and 21 percent from Oklahoma harbored helminths (Table 3).

The most common parasite was the oxyurid nematode, *Pharyngodon warneri* Harwood, 1932. Photomicrographs of male and female *P. warneri* have not been published previously, and some features are included here (Figs. 1-4). This pinworm was found in the colon and rectum of almost one-fourth of all lizards (75.5 ± 1.0, range 60-99 mm SVL), including 50 (27 percent) of the males and 19 (18 percent) of the females ($X^2 = 2.77$, 1 df, $P < 0.01$). Prevalence also varied according to locale; 50 percent from New Mexico, 37 percent from Texas, and 11 percent from México (a new distributional record) were infected. However, none of the 39 whiptails from Oklahoma was found to harbor the parasite.

Pharyngodon warneri is apparently host specific at the generic level as it has now been reported from eight species of *Cnemidophorus* from Arizona, New Mexico, South Dakota, Texas, Utah, and México (McAllister, 1990*b*, 1990*c*). In addition, *P. warneri* had been reported previously by McAllister et al. (1986) to infect at least one

TABLE 2. Prevalence of helminths infecting different age, sex and size classes of *C. gularis* from New Mexico, Oklahoma, Texas, and México.

Age, sex, and size class	Prevalence
Hatchlings (31-39 mm SVL)	0/8 (0%)
Juveniles (40-59 mm SVL)	9/46 (20%)
Adult females (60-91 mm SVL)	34/88 (39%)
Adult males (60-108 mm SVL)	72/147 (49%)
All immatures (31-59 mm SVL)	9/52 (17%)
All adults (60-108 mm SVL)	106/237 (45%)
All lizards (31-108 mm SVL)	115/289 (40%)

parthenogenetic *C. laredoensis* subgroup (LAR-A—*sensu* Walker, 1986), a clonal complex derived from independent hybridization of gonochoristic species *C. gularis* and *C. sexlineatus* (Walker et al., 1990).

Third-stage larvae of *Physaloptera* Rudolphi, 1819, were found in the stomach of 10 percent of the lizards. This ubiquitous parasite has been reported previously from numerous whiptail lizards from southern and southwestern Texas, including *C. laredoensis* (McAllister et al., 1986), *C. tesselatus* (McAllister, 1990*a*), *C. neomexicanus* (McAllister, 1990*b*), and *C. exsanguis* (McAllister, 1990*c*).

Twenty-five linstowiid tapeworms of the genus *Oochoristica* Lühe, 1898, were collected from the duodenum of five juvenile and five adult whiptails (four males, six females; 62.1 ± 4.4, 45-86 mm SVL). Small prestrobilar forms (USNM 81122, 81124) were found in juvenile whiptails (OUMZ 26084-26085, 25089, 45-52 mm SVL) collected in Carter County, Oklahoma, and a juvenile (SRSU 5009; 58 mm SVL) taken in Taylor County, Texas. Immature adults with distinct genital primordia (USNM 81123) were found in an adult female (SRSU 4359, 86 mm SVL) from Irion County, Texas. Mature worms with gravid proglottids (USNM 81118-81121) infected a juvenile (SRSU 5074, 55 mm SVL) obtained in Brewster County, Texas, three adult females (SRSU 2915, 3285, 3288, 65-86 mm SVL) collected in Pecos County, Texas, and one adult male (UNM 23631, 60 mm SVL) from Eddy County, New Mexico. It was not possible to assign the prestrobilar, immature adults, and at least eight (USNM 81121) of 12 mature worms to species; however, four of the latter (USNM 81118-81120) possessed distinct vitellaria characteristic of *O. bivitellobata* Loewen, 1940.

Unidentified acanthocephalan cystacanths were recovered from the coelomic cavity and muscle fascia of 11 *C. gularis* (eight males, three females; 74.4 ± 2.6, 62-91 mm SVL), including a single lizard from Johnson County, Texas, and two and eight lizards, respectively, from the states of Coahuila and Tamaulipas, México. Cystacanths have been reported previously from *C. neomexicanus, C. tigris*, and *C. uniparens* (see McAllister, 1990*b*).

TABLE 3. Variation in prevalence of infection in *C. gularis* from various regions of New Mexico, Oklahoma, Texas, and México.

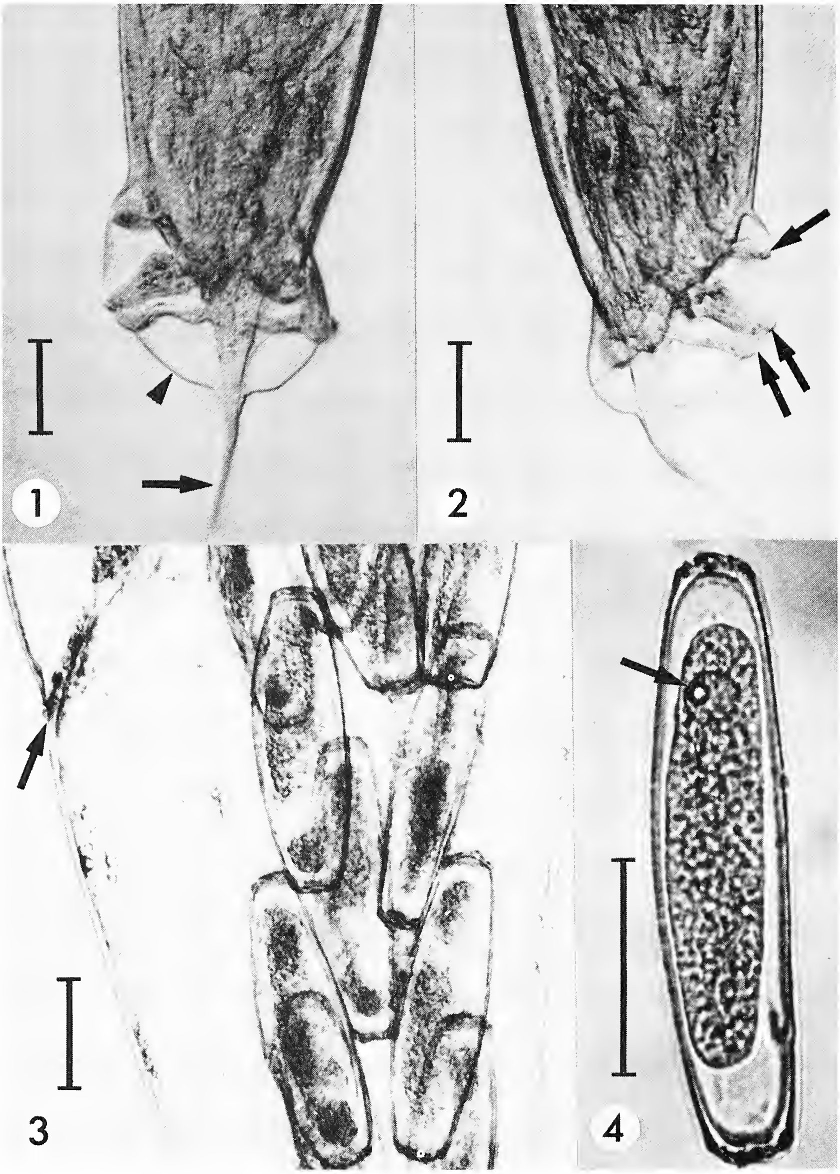
Region	Prevalence
Southeastern New Mexico	7/14 (50%)
South-central Oklahoma	4/17 (24%)
Southwestern Oklahoma	4/22 (18%)
North-central Texas	8/33 (24%)
South-central Texas	3/13 (23%)
Southern Texas	35/42 (83%)
Coastal Texas	0/2 (0%)
Western Texas	4/5 (80%)
Big Bend/Trans-Pecos Texas	28/47 (60%)
Northern México	22/94 (22%)

Pharyngodon kirbii Specian and Ubelaker, 1974, was originally described from the plateau spotted whiptail, *C. scalaris* (syn. *septemvitattus*) from Brewster County, Texas (Specian and Ubelaker, 1974*a*). Only two lizards in the present study were infected with this nematode, including an adult female (SRSU 5090, 92 mm SVL) obtained on 1 June 1980, 34 km. NE Alpine, Brewster County, and an adult female (SRSU 2388, 76 mm SVL) taken on 5 August 1971, northwest of Shafter Lake in Andrews County. The former site is located *ca.* 116 kilometers northwest of the type locality of *P. kirbii.*

Hannum (1942) reported *Pharyngodon papillocauda* from *C. gulae* (*sic*) in the vicinity of Tucson, Arizona. Read and Amrein (1953) also noted the parasite in the same host without further comment. However, this must be in error given that the range of the host extends to the west only as far as southeastern New Mexico. At least seven other species of *Cnemidophorus* are known to occur in Arizona (Stebbins, 1985); inasmuch as no host voucher was mentioned in the original description of *P. papillocauda*, it is suggested the host be regarded simply as *Cnemidophorus* sp.

A single *Parathelandros texanus* Specian and Ubelaker, 1974, was found in the rectum of a female whiptail (74 mm SVL, SRSU 447) obtained on 5 August 1963 in Jeff Davis County, Texas. This nematode has been reported previously from *Urosaurus texanus* in Arizona (Walker and Matthias, 1973; Specian and Ubelaker, 1974*b*), *C. tesselatus* in Presidio County, Texas (McAllister, 1990*a*), and *Sceloporus merriami, S. undulatus, Cophosaurus texanus, C. inornatus, C. septemvittatus*, and *C. tigris* in Brewster County, Texas (Specian and Ubelaker, 1974*b*).

In summary, all of the helminths noted herein from *C. gularis* have been reported previously to infect several other species of North American whiptail lizards. The most common parasites of species of *Cnemidophorus* appear to be tapeworms of the genus *Oochoristica* and



FIGURES 1-4. Genital organs of male and ova of female *Pharyngodon warneri* from *Cnemidophorus gularis*: 1) posterior end of male showing well-developed genital cone (arrowhead) and tail (arrow); 2) lateral view of male showing arrangement of caudal papillae (arrows); 3) posterior end of female showing ova in utero and anus (arrow); 4) a bioperculate ovum in multicellular stage showing nucleus (arrow). Scale bars = 50 μm.

oxyurid and spirurid nematodes, *Pharyngodon warneri* and *Physaloptera* sp., respectively. Interestingly, both the biparental species, *C. sexlineatus* and *C. gularis*, and their diploid parthenogen, *C. laredoensis*, harbor *P. warneri*. Because *P. warneri* has a direct life cycle and exhibits little host specificity toward either the paternal (*C. sexlineatus*) or maternal (*C. gularis*) parental species, it is not possible to discern whether *C. laredoensis* has a closer genetic identity to *C. gularis* or to delineate coevolutionary patterns in these three species of *Cnemidophorus*.

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REMAINDERS OF POWER SERIES II

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Abstract.—This is an extension of "Remainders of Power Series" (McCall et al., 1979). Let p (n) be a strictly increasing sequence of natural numbers; regard p (n) thin if $\lim_{n\to\infty} [p(n+1) - p(n)] = \infty$. For a power series $\sum_{k=0}^{\infty} a_k z^k$, let $\sigma_n(z) = |\sum_{k=n}^{\infty} a_k z^k|$. Suppose that $\lim_{n\to\infty} |a_n|^{1/n} = R^{-1} \neq 0$ with $0 < |z_1| < R$ and $0 < |z_2| < R$. Let T be a neighborhood of z₂ and pick $0 < \delta < |z_2| / |z_1|$. If $\sigma_{p(n)}(z) < \delta^{p(n)} \sigma_{p(n)}(z_1)$ for all n and for all z in T, then p is thin (note that there is no restriction on the relative size of $|z_1|$ and $|z_2|$). As motivation for the above result, an example is given for the case in which $\limsup_{n\to\infty} |a_n|^{1/n} = R^{-1}$, but $\lim_{n\to\infty} |a_n|^{1/n}$ does not exist. Finally, for the general case, in which $\limsup_{n\to\infty} |a_n|^{1/n} = R^{-1}$ replaces $\lim_{n\to\infty} |a_n|^{1/n} = R^{-1} \neq 0$ in the hypothesis, it is conjectured that (1) forces p (n) to necessarily satisfy either the Fabry Gap Condition or to be not thick. The Fabry Gap Condition is $\lim p(n)/n = \infty$. Thick is defined as $\limsup [p(n+1) - p(n)] < \infty$. *Key words*: power series; growth of remainders; gap conditions; Chebyshev. *Mathematics subject classification (1985 revision)*: primary, 30810; secondary, 30B30, 30C99.

This research and the first "Remainders of Power Series" (RPS) paper (McCall et al., 1979) arose from the $\delta = 1$ version of the following problem. Let $f(z) = \sum_{k=0}^{\infty} a_k z^k$ have radius of convergence R and let $\sigma_n(z) = |\sum_{k=n}^{\infty} a_k z^k|$. Suppose that $0 < |z_1| < z_2| < R$ and either $T = \{z_2\}$ or T is a neighborhood of z_2. Further, let $0 < \delta < |z_2| / |z_1|$. If p (n) is a strictly increasing sequence of positive integers such that

$$\sigma_{p(n)}(z) < \delta^{p(n)} \sigma_{p(n)}(z_1) \tag{1}$$

for all z in T and for all n, what is the nature of p?

Quick answer.—The sequence p exhibits gaps. The specific answer seems to depend on whether $\lim_{n\to\infty} |a_n| 1/n = R^{-1}$ or $\limsup_{n\to\infty} |a_n| 1/n = R^{-1}$.

Remark 1.—If we also allow $|z_2| \leq |z_1|$, then this can be referred to the Extended RPS Problem. It seems that any answer to the RPS Problem produces an answer to the Extended RPS Problem.

A reason for thinking that the original problem might have an interesting answer is that for fixed n, the means

$$M_\infty(r, \sigma_n) = \max_{|z|=r} \sigma_n(z)$$

$$M_p(r,\sigma_n) = \{\frac{1}{2\pi} \int_{\sigma}^{2\pi} [\sigma_n(re^{i\theta})]^p \, d\theta$$

increase as r → R (Duren, 1970:8-10); that is, on the average, the approximation to f by the partial sums of its power series gets worse as $|z| = r$ approaches R.

Further, the following example for the RPS Problem from (McCall et al., 1979:246-249) suggests that p should be thin or exhibit gaps. Here p is lacunary.

Example 1.—($R=1$, $z_1=\frac{1}{4}$. $z_2=-\frac{1}{2}$, T is the disc $|z+\frac{1}{2}| < \frac{1}{4}$, $\delta=1$, and $p(n) = 4^n$). Let $Q_k(z) = (1/b_k)\, z^{p(2k-1)}\, (z-\frac{1}{2})^{p(2k)}$ where b_k equals the maximum of the coefficients in the binomial expansion of $(z-\frac{1}{2})^{p(2k)}$. Form the power series $f(z) = \sum_{n=0}^{\infty} a_n z^n \sum_{k=1}^{\infty} Q_k(z)$. Then $\sigma_p(2n-1)(z) = |\sum_{k=n}^{\infty} Q_k(z)|$ and

$$\sigma_p(2n\text{-}1)(z) < \frac{1}{3}\sigma p(2n\text{-}1)(z_1) \tag{2}$$

for all n and all z in T. Note that once we have (2) for $z_1 = \frac{1}{4}$, we see that it also holds for any $z_1 = r$ ($r \geq \frac{1}{4}$). Also the above power series exhibits overconvergence.

Thinness also is suggested by Theorem 1 from the original paper (McCall et al., 1979:241-243). Here $T = \{z_2\}$. This result indicates that if $\lim_{n\to\infty} |a_n|^{1/n} = R^{-1}$ with $0 < |z_1|, |z_2| < R$ and $0 < \delta < |z_2| / |z_1|$, then the set $S = \{p(1), p(2), —\}$ for which (1) holds cannot contain an infinite tail set, that is, there is no N such that for all $n \geq N$, $p(n)$ lies in S. Because there is no restriction on the relative size of $|z_1|$ and $|z_2|$, this also is an illustration of Remark 1.

This paper deals exclusively with T a neighborhood of z_2 and gives answers to the extended PRS Problem. The next section is preliminary. It discusses the various types of gap sequences considered. The third section gives an example for $\limsup_{n\to\infty} |a_n|^{1/n} = R^{-1}$ that stems from the one above.
It is meant to serve as additional motivation for the theorem of the fourth section. This theorem indicates that for the case $\lim_{n\to\infty} |a_n|^{1-n} = R^{-1}$ ($R \neq \infty$), $p(n)$ must satisfy $\lim_{n\to\infty} [p(n+1 - p(n)] = \infty$. A $p(n)$ satisfying this condition is termed thin. The paper concludes with a conjecture for the general case $\limsup_{n\to\infty} |a_n|^{1/n} = R^{-1}$.
The conjecture is that in this case $p(n)$ must be either not thick or $p(n)$

must satisfy the Fabry Gap Condition. Thick means $\limsup_{n\to\infty} [p(n+1) - p(n)] < \infty$. The Fabry Gap Condition is $\lim_{n\to\infty} p(n)/n = \infty$.

GAP SEQUENCES

Three distinct gap conditions are discussed, as also is a subadditive condition needed for the example in the next section. Throughout the discussion, it is assumed that p (n) is a strictly increasing sequence of positive integers.

Definition 1.—The sequence p is thin if $\lim_{n\to\infty} [p(n+1) - p(n)] = \liminf_{n\to\infty} [p(n+1) - p(n)] = \infty$.

Examples (*thin sequences*).—A) A lacunary sequence is thin. Inasmuch as lacunary means that there is an $\alpha > 1$ such that for all n, $p(n+1)/p(n) > \alpha$, we find $p(n) > \alpha^{n-1} p(1)$. Thus, $p(n+1) - p(n) > \alpha\, p(n) - p(n) > (\alpha-1)\, \alpha^{n-1} p(1)$, which goes to infinity as n→∞. B) Let k be a fixed positive integer and set $p(n) = n^k$. This p (n) is thin, but not lacunary.

Because the proof of the theorem is by contradiction, we state what p is not thin means. If p is not thin, then there exists an $M > 0$ such that for each positive integer k, we can find an n_k for which

$$p(n_k+1) - p(n_k) < M + 1/k \leq M + 1. \tag{3}$$

For notational convenience later in the paper, I use $t(2k) = p(n_k)$ and $t(2k+1) = p(n_k+1)$. Thus, when we state lemmas involving $t(2k+1) - t(2k)$, we are really thinking of (3). The following is a weaker gap condition.

Definition 2.—The sequence p (n) satisfies the Fabry Gap Condition if $\lim_{n\to\infty} p(n)/n = \infty$. Dienes (1931:372-373) showed that every thin sequence satisfies the Fabry Gap Condition. The example $p(2n) = n^2$, $p(2n+1) = n^2 + 1$ shows that the Fabry Gap Condition does not imply thinness. An even weaker gap condition is what I term "not thick."

Definition 3.—The sequence p (n) is thick if $\limsup_{n\to\infty} [p(n+1) - p(n)] < \infty$.

It is easy to see that if p (n) is thick, then there is an $M > 0$ such that $p(n+1) < nM + p(1)$. Thus a thick sequence is a kind of modified arithmetic sequence.

Not thick means there is a sequence of n_k's such that $\lim_{k\to\infty} [p(n_k+1) - p(n_k)] = \infty$. Thus not thick, like the Fabry Gap Condition, means that both p (n) has gaps and, at the same time, there is not necessarily a gap between each consecutive pair. Further, every sequence p (n) that satisfies the Fabry Gap Condition is also not thick; just use $p(n+1) \leq nM + p(1)$ to show thick implies not Fabry. The following example shows that p (n) can be not thick without satisfying the Fabry Gap Condition.

Example.—Because $\sum_{k=1}^{n-1} [p(k+1) - p(k)] + p(1)$ it suffices to define the differences, $p(k+1) - p(k)$. For this set $p(k+1) - p(k) = n$ when $k=n^2$, n a positive integer; otherwise set $p(k+1) - p(k) = 1$.

Finally, for the example of the next section we need a special type of thin sequence; one that satisfies the subadditive condition,

$$p(n) + p(n-1) < p(n+1) \tag{4}$$

for all n.

Let p (n) be a lacunary sequence, $p(n+1)/p(n) > \alpha > 1$ for all n, with $\alpha > \frac{1+\sqrt{5}}{2}$. Then p (n) satisfies (4). To see this, consider $\frac{\alpha-1}{\alpha^2}$ -1, which is a decreasing function of α for $\alpha > 0$. Because $\alpha = \frac{1+\sqrt{5}}{2}$ is a zero for this function, we have $\frac{\alpha+1}{\alpha^2} < 1$ for all $\alpha > \frac{1+\sqrt{5}}{2}$. Thus

$$\begin{aligned} p(n) + p(n-1) &< \alpha [\alpha p(n) + p(n)] \\ &< \left(\frac{\alpha-1}{\alpha^2}\right) p(n+1) \\ &< p(n+1) \end{aligned}$$

whenever $\alpha > \frac{1+\sqrt{5}}{2}$. The most useful case is $p(n) = \ell^n$ (ℓ an integer and $\ell \geq 2$).

Another example for (4) is the sequence 1, 1, 3, 5, 9, 15—.Here $p(1) = p(2) = 1$ and $p(n+1) = p(n) + p(n-1) + 1$.

AN EXAMPLE FOR THE EXTENDED RPS PROBLEM

We will deal with the R=1 case first. The other cases require simple modifications of this one. Except for $R=\infty$, we have $\limsup_{n\to\infty} |a_n|^{1/n} = R^{-1}$, but not $\lim_{n\to\infty} |a_n|^{1/n} = R^{-1}$.

Now let p (n) be a strictly increasing sequence of positive integers satisfying (4), $p(n) + p(n-1) < p(n+1)$ and set $d(n) = p(2n) - p(2n-1)$. Further, let $z_1 = r$ ($r \geq ¼$), $z_2 = -½$ and T the neighborhood of z_2 consisting of those z for which $|z + ½| < ¼$. Then there exists a power series $\sum_{n=0}^{\infty} a_n z^n$, with radius of convergence R=1 such that

$$\sigma_{p\,(2n-1)}(z) < (1/3)^{d\,(n)}\sigma_{p\,(2n-1)}(z_1) \tag{5}$$

for all n and for all z in T.

Comment.—Let $p\,(n) = \ell^n$ (ℓ an integer, $\ell \geq 2$). Then $p\,(2n) - p\,(2n\text{-}1) = (\ell\text{-}1)\,p\,(2n\text{-}1)$ and (5) reads

$$\sigma_{p\,(2n-1)}(z) < \delta^{p\,(2n-1)}\,\sigma_{p\,(2n-1)}(z_1) \tag{6}$$

where $\delta = (1/3)^{\ell^{-1}}$. This is the example for the Extended RPS Problem.

Construction.—Let b_k be the largest coefficient in the binomial expansion of $(z + ½)^{p\,(2k)}$ and set

$$Q_k(z) = (1/b_k)\,z^{p\,(2k-1)}\,(z+½)^{p\,(2k)}.$$

Then form the power series

$$f(z) = \sum_{n=0}^{\infty} a_n z^n = \sum_{k=0}^{\infty} Q_k(z).$$

Condition (4) implies that each a_n is either zero or comes from the coefficient of a z^n in the expanded form of some $Q_k(z)$. Dividing by b_k in each $Q_k(z)$ makes the maximum value of the a_n's, equal to one and forces $\limsup_{n\to\infty} |a_n|^{1/n}=1$.

We need two lemmas.

Lemma 1.—For all k and for all z with $|z+½| < ¼$, we have

$$|Q_{k+1}(z)| < (¼)\,|Q_k(z)|.$$

Lemma 2.—For all k and for all z with $|z+½| < ¼$, we have

$$|Q_k(z)| < (1/3)^{d(k)}\,Q_k(r),$$

where $r \geq ¼\,[d(k) - p\,(2k) - p\,(2k\text{-}1)]$.

The proof modulo these lemmas goes as follows. For $|z + ½| < ¼$ we have

$$\sigma_{p(2n-1)}(z) \leq \sum_{k=n}^{\infty} |Q_k(z)|$$

$$< [\sum_{k=n}^{\infty} (¼)^{k-n}]\,|Q_n(z)|$$

by Lemma 1

$$= (4/3)\,|Q_n(z)|$$

$$< (4/3)\,(1/3)^{d(n)}\,Q_n(r)$$

by Lemma 2

$$< (4/3)\,(1/3)^{d(n)}\,\sigma_{p\,(2n-1)}(r)\ .$$

Proof of Lemma 1.—For $|z+\tfrac{1}{2}| < \tfrac{1}{4}$, we have

$$|Q_{k+1}(z)| < (1/b_k)\,|z|^{p(2k-1)}\,|z+\tfrac{1}{2}|^{p(2k)} \cdot |z+\tfrac{1}{2}|^{p(2k+2)-p(2k)}$$

$$= |Q_k(z)|\,(\tfrac{1}{4})^{p(2k+2)-p(2k)}$$

$$< (\tfrac{1}{4})\,|Q_k(z)|\,.$$

Proof of Lemma 2.—For $|z+\tfrac{1}{2}| < \tfrac{1}{4}$, we have

$$\frac{|Q_k(z)|}{Q_k(\tfrac{1}{4})} = |z|^{p(2k-1)}\,|z+\tfrac{1}{2}|^{p(2k)}\,4^{p(2k-1)} \cdot (4/3)^{p(2k)}$$

$$< (3/4)^{p(2k-1)}\,(\tfrac{1}{4})^{p(2k)} \cdot 4^{p(2k-1)} \cdot (4/3)^{p(2k)}$$

$$= 3^{p(2k-1)-p(2k)}\,.$$

Because $Q_k(\tfrac{1}{4}) \leq Q_k(r)$ for all $r \geq \tfrac{1}{4}$, the lemma is proved.

An example for $0 < R < \infty$ can now be produced by taking $z_1 = rR$ ($r \geq \tfrac{1}{4}$), $z_2 = -R/2$ and considering the power series $\sum_{n=0}^{\infty} a_n (z/R)^n$.

Now for $R = \infty$, pick a sequence $\{A_k\}_{k=1}^{\infty}$ with $A_{k+1} \geq A_k$, $A_1 \geq 1$, and $A_k \to \infty$. Then replace division by b_k in the original definition of $Q_k(z)$ with division by $c_k = A_k^{s(k)} \cdot b_k$, where $s(k) = p(2k) + p(2k-1)$. With this modification, the series $f(z) = \sum_{n=0}^{\infty} a_n z^n \sum_{k=1}^{\infty} Q_k(z)$ gives the desired result, with $z_1 = r$ ($r \geq \tfrac{1}{4}$), $z_2 = -\tfrac{1}{2}$ and T consisting of those z for which $|z + \tfrac{1}{2}| < \tfrac{1}{4}$. The only thing that needs to checked is that the radius of convergence $R = \infty$. But for $0 \leq j \leq p(2n)$, the $[j + p(2k-1)]$ the root of $a_{j+p(2k-1)}$ is less than or equal to $1/A_k$ because $p(2k) + p(2k-1)$ divided by $_{j+p(2k-1)}$ is greater than or equal to one. Inasmuch as $1/A_k \to 0$ as $k \to \infty$, $R = \infty$.

Remark 2. ($R = 1$ case).—Because the series $\sum_{k=1}^{\infty} Q_k(z)$ converges outside the unit circle, our example is overconvergent.

THE SEQUENCE p (n) IS THIN

We first give a full statement of the theorem.

Theorem.—Let $\lim_{n\to\infty} |a_n|^{1/n} = R^{-1} \neq 0$ with $0 < |z_1|, |z_2| < R$ and T a neighborhood of z_2. Pick $0 < \delta < |z_2|/|z_1|$. If (1) $\sigma_{p(n)}(z) < \delta^{p(n)}\,\sigma_{p(n)}(z_1)$ for all n and for all z in T, then p is thin.

Remark 3.—Let E be an arc of the circle $|z| = r_2$ where $r_2 = |z_2|$ and also let z_2 be the center of E. Then if E is small enough, $E \subset T$. The actual proof depends on (1) holding for all z on E.

Proof.—We give a proof for the case R = 1 only. The proof will be by contradiction. We start the argument with (7) below. The derivation of (7) is postponed until the end of the proof. All other "dirty work" is to be found in the three lemmas stated at the end of this section. We have

$$\left|\sum_{k=p(n)}^{p(n+1)-1} a_k z^k\right| \le [\delta^{p(n+1)} + \delta^{p(n)}]\,\sigma_{p(n)}(z_1) + \delta^{p(n+1)} \left|\sum_{k=p(n)}^{p(n+1)-1} a_k z_1^{\,k}\right| \tag{7}$$

If we pick $\epsilon > 0$ such that $(1+\epsilon)\,|z_1| < 1$, and n such that for $k \ge p(n)$, we have $|a_k|^{1/k} < 1+\epsilon$. Then the right hand side (RHS) of (8) below is greater than or equal to the RHS of (7) above. This establishes

$$\left|\sum_{k=p(n)}^{p(n+1)-1} a_k z^k\right| \le \left[\frac{(1+\epsilon)\,|z_1|\,p(n)}{1-(1+\epsilon)\,|z_1|}\right]\ [2\,\delta^{p(n+1)} + \delta^{p(n)}] \tag{8}$$

Because (8) holds for any z in E and $R^{-1} \ne 0$ allows us to divide by $a_{p(n+)-1}$, we find

$$|a_{p(n+1)-1}|\,|z_2|^{p(n)} \max_{z\in E} \left|\sum_{k=0}^{p(n+1)-p(n)-1} (a_{k+p(n)}/a_{p(n+1)-1}) z^k\right|$$
$$\le \left[\frac{(1+\epsilon)\,|z_1|\,p(n)}{1-(1+\epsilon)\,|z_1|}\right]\ [2\,\delta^{p(n+1)} + \delta^{p(n)}]. \tag{9}$$

In turn, the left hand side (LHS) of (9) is greater than or equal to $|a_{p(n+1)-1}|\,|z_2|^{p(n)} \min_{q\in Q} \max_{z\in E} q(z)$, where Q consists of all those polynomials of degree $p(n+1) - p(n)-1$ with leading coefficient one. We denote thin MIN MAX by $M_{p(n+1)-p(n)-1}$ for now. We assume that p (n) is not thin, so there exists $t(2k) = p(n_k)$ and $t(2k+1) = p(n_k+1)$ with the property that $t(2k+1) - t(2k) \le M \le \infty$ for all k. Applying all this to (9) gives

$$|a_{t(2k+1)-1}|\,|z_2|^{t(2k)}\,M_{\Delta(k)} \le \left[\frac{(1+\epsilon)\,|z_1|^{t(2k)}}{1-(1+\epsilon)\,|z_1|}\right] \cdot [2\,\delta^{t(2k+1)} + 8^{t(2k)}], \tag{10}$$

where $\Delta(k) = t(2k+1) - t(2k) - 1$. The final step is to take the t(2k) the root of each side of (10) and let $k \to \infty$. We claim this gives $|z_2| \le \delta |z_1|$, which is a contradiction of the way we chose δ, $0 < \delta < |z_2|/|z_1|$.

To get $|z_2|$ from the LHS of (10) in the above step, we need the t(2k)th roots of both $a_{t(2k+1)-1}$ and $M_{\triangle}(k)$ to converge to one as $k \to \infty$. On the RHS of (10), it suffices to show that $[2\,\delta^{t(2k+1)} + \delta^{t(32k)}] < C\delta^{t(2k)}$, where the constant C is independent of k. These facts are the content of the lemmas at the end of this section.

The only other thing that remains is to establish (7), which is

$$(7) \qquad \left|\sum_{k=p(n)}^{p(n+1)-1} a_k z^k\right| \le [\delta^{p(n+1)} + \delta^{p(n)}]\sigma_{p(n)}(z_1) + \delta^{p(n+1)} \left|\sum_{k=p(n)}^{p(n+1)-1} a_k z_1^k\right| .$$

For (7) we begin with using (1) to get

$$\sigma_{p(n)}(z_1) \ge \sigma_{p(n+1)}(z_1) - \left|\sum_{k=p(n)}^{p(n+1)-1} a_k z_1^k\right| \qquad (11)$$

for all z in $E \subset T$.

Now

$$\delta^{-p(n+1)}\sigma_{p(n+1)}(z) \ge \delta^{-p(n+1)} \left|\sum_{k=p(n)}^{p(n+1)-1} a_k z^k\right| - \delta^{-p(n+1)}\sigma_{p(n)}(z)$$

$$\ge \delta^{-p(n+1)} \left|\sum_{k=p(n)}^{p(n+1)-1} a_k z^k\right| - \delta^{p(n)-p(n+1)}\sigma_{p(n)}(z_1) \qquad (12)$$

where we have used (1) again. Inequalities (11) and (12) imply (7).

We now return to the facts discussed previously. The first lemma will deal with taking the t(2k) th root of $M_{\triangle}(k)$. However, before stating the lemma we need to discuss $M_n = \underset{q \in Q_n}{\mathrm{MIN}}\ \underset{z \in E}{\mathrm{MAX}}\ |q(z)|$.

E is taken to be an arc of some circle $|z| = r$, $r > 0$, and Q_n consists of all those polynomials of degree n and leading coefficient one. It is well known that the MIN MAX above is actually obtained and that $\lim_{n\to\infty} M_n^{1/n}$ exists and equals $\rho = \rho\,(E)$, the Chebyshev constant for E (Hille, 1962:265-266). Further, $\rho > 0$ (Ahlfors, 1973:31).

Lemma 1.—If $t\,(2k+1) - t\,(2k) \le M < \infty$ for all k and $\triangle(k) = t\,(2k+1) - t\,(2k)-1$, then the t (2k) th root of $M_{\triangle}(k)$ converges to one as $k \to \infty$.

Proof.—Inasmuch as E is a subset of the circle $|z| = r$, we have $\underset{q \in Q_n}{\mathrm{MIN}}\ \underset{z \in E}{\mathrm{MAX}}\ |q(z)| \le \underset{q \in Q_n}{\mathrm{MIN}}\ \underset{|z| = r}{\mathrm{MAX}}\ |q(z)|$.

From Hille (1962:267), it is known the RHS equals r^n, thus $M_n \le r^n$. Also, because ρ (E) > 0, it is known there is an $\epsilon > 0$ such that $\epsilon \le M_n^{1/n}$ for all n. Thus $\epsilon^{\Delta(k)} \le M_{\Delta(k)} \le r^{\Delta(k)}$ for all k and our result will follow if we show Δ (k)/t (2k)$\rightarrow 0$ as $k \rightarrow \infty$. But the hypothesis on t (2k) = p (n_k) and t (2k+1) = p (n_k+1) and the fact that p is an increasing sequence of positive integers say that

$$0 \le \Delta\,(k) \le M\text{-}1.$$

Now dividing by t (2k) and letting $k \rightarrow \infty$ proves the lemma.

Lemma 2.—If $\delta > 0$ and t (2k+1) − t (2k) $\le M < \infty$ for all k, then $2\,\delta^{t(2k+1)} + \delta^{t\,(2k)} \le C\,\delta^{t\,(2k)}$, where C is a constant independent of k.

Proof.—The result is true for $\delta \le 1$ without the not thin condition, t (2k+1) − t (2k) $\le M < \infty$. For $\delta > 1$, the not thin condition is applied to get $2\,\delta^{t\,(2k+1)} + \delta^{t\,(2k)} \le 2\,\delta^{t(2k)+M} + \delta^{t\,(2k)} = [2\delta^M+1]\,\delta^{t\ 2k)}$, ($C = 2\,\delta^M + 1$), which establishes the lemma.

Lemma 3.—If t (2k+1) − t (2k) $\le M \le \infty$ for all k, then

$$\lim_{k \rightarrow \infty} |\, a_{t\,(2k+1)\text{-}1}|^{1/t\,(2k)} = 1.$$

Proof.—Rewriting the exponent, we have

$$1/t\,(2k) = [1/t\,(2k+1)\text{-}1]\,[\frac{t\,(2k+1)\text{-}1}{t\,(2k)}].$$

Because $\lim_{k \rightarrow \infty} |a_n|^{1/n} = 1$, we know that the [t (2k+1)-1] th root of $a_{t\,(2k+1)\text{-}1}$ converges to one as $k \rightarrow \infty$. Thus we need only show $\lim_{k \rightarrow \infty} [\frac{t\,(2k+1)\text{-}1}{t\,(2k)}] = 1$. But $0 \le t\,(2k+1) - t\,(2k) - 1 \le M - 1$, so $0 \le \frac{t\,(2k+1)\text{-}1}{t\,(2k)} - 1 \le \frac{M\text{-}1}{t\,(2k)}$. Letting $k \rightarrow \infty$ gives the desired result.

The theorem just proved requires $\lim_{n \rightarrow \infty} |a_n|^{1/n} = R^{-1}$ where $R \neq \infty$. For the general case, the following conjecture can be stated.

Conjecture.—Let $\limsup_{n \rightarrow \infty} |a_n|^{1/n} = R^{-1}$ with $0 < |z_1|, |z_2| < R$ and T a neighborhood of z_2. Pick $0\ \delta < |z_2|/|z_1|$. If $\sigma_{p(n)}\,(z) < \delta^{p(n)}\,\sigma_{p(n)}$ (z_1) for all n and for z in T, see equation (1), then p is not thick.

Remark.—It could be that the correct answer is that p satisfies the Fabry Gap Condition.

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POLLEN EVIDENCE FOR HISTORIC VEGETATIONAL CHANGE, HUECO BOLSON, TEXAS

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Abstract.—Pollen analysis of a coppice dune northeast of El Paso, Texas, shows a decrease from 46 to 16 percent grass pollen, base to top, in accord with historical records, which document the replacement of desert-grass rangeland by mesquite and creosote during the past 100 years. The pollen record supports other evidence indicating that grass populations in this area declined in response to grazing pressure. *Key words*: pollen analysis; historic vegetation; coppice dunes; arid rangeland.

The past 100 years of vegetational history in southern New Mexico have been documented by a comparison of old land survey records from the General Land Office with present-day conditions, and by the analysis of repeated baseline vegetation plots at Jornada Experimental Range. These records show an historic decrease in black grama (*Bouteloua eriopoda*) grassland and increase in honey mesquite, *Prosopis glandulosa* (Gardner, 1951; Buffington and Herbel, 1965; York and Dick-Peddie, 1969; Gile, 1975; Gross and Dick-Peddie, 1979; Hennessy et al., 1983). Wind erosion and coppice dune formation occurred concurrent with the spread of mesquite and creosote and the decrease in grass cover in southern New Mexico. Whereas black grama is vulnerable to drought and historically has been slow to recover from years of low rainfall (Gibbens and Beck, 1988), the spread of mesquite is attributed to cattle grazing (Fisher, 1977). Extensive accumulations of coppice dunes in the Hueco Bolson area of Trans-Pecos Texas are continuous with the New Mexico dunes and may have experienced a similar history. Pollen analysis of the dune sand may provide a new means of evaluating historical changes in local vegetation.

Pollen samples were collected in 1986 from the excavated face of a small coppice dune in the Hueco Bolson on the Fort Bliss Military Reservation northeast of El Paso, Texas. The Hueco Bolson is an arid basin at about 1200 meters elevation between the Franklin and Hueco mountains. Annual precipitation is about 220 mm, most originating from convectional storms during the months July through October (Whalen, 1978). The study dune, formed around a small honey mesquite tree, has a height of about 1.2 meters above the surrounding surface and a basal diameter of about three meters. Faint stratification planes in the weakly consolidated sand were visible on the excavated face of the coppice dune.

Methods

Samples were taken at 5-15, 25-35, 50-60, 70-80, and 90-100 centimeters below the top of the dune crest. A surface sample consisting of 20 pinches of surficial sand within a 20-meter

TABLE 1. Additional palynologic data from Hueco Bolson coppice dune.

	Sample depth (centimeters)					
	Surface	5-15	25-35	50-60	70-80	90-100
Diagram key*	S	A	B	C	D	E
Pollen count	426	448	537	516	411	456
Unknown pollen (%)	4.9	3.3	1.9	5.2	3.6	0.9
Indeterminable (%)	1.4	9.6	6.5	7.4	6.1	2.2
Corroded (%)	2.3	12.5	9.3	6.0	7.8	9.6
Degraded (%)	16.4	31.9	45.1	43.4	28.2	14.5
Spike count	11	34	45	39	32	13
Pollen conc/gram	182000	3940	3670	5170	3720	11600
Charcoal/gram	88200	1660	2980	3720	2160	14400
Charcoal:pollen	0.48	0.42	0.81	0.72	0.58	1.24

* from Figure 1.

radius of the dune was also collected. The weighed, dry samples, about 60 to 80 grams each (Table 1), were treated with HCl, HF, HCl, and hot water prior to heavy liquid separation (zinc chloride, sg 2.0). The light fraction was washed in dilute HCl, treated to a second HF, boiled in an acetolysis solution for eight minutes, and stained with safranin O. Prior to the initial HCl wash, two *Lycopodium* spore tablets (11,267 ± 298 spores per tablet; batch 201890) were introduced to each weighed sample.

During pollen counting, the preservation class of each pollen grain was noted. Charcoal and charred particles greater than 25 μm (long axis) were tabulated. The concentrations of pollen and charcoal were determined from *Lycopodium* spike counts.

POLLEN ANALYTICAL RESULTS

The pollen assemblages from the coppice dune are dominated by Chenopodiineae, Asteraceae (Compositae), and Poaceae (Gramineae) pollen, with minor but persistent amounts of *Pinus, Juniperus, Prosopis, Ephedra*, and Brassicaceae (Cruciferae). *Tidestromia, Eriogonum*, and *Boerhaavia* pollen are present as well and are shown in the pollen diagram (Fig. 1). The most significant change in the pollen assemblage is a major shift in percentage of Poaceae (Gramineae) from 40 percent at the base to 16 percent at the top of the dune (and 10 percent in the modern surface sample).

Pollen Concentration and Preservation

The pollen content of the dune sand is comparatively high, ranging from 3600 to 11,000 grains per gram of dry sediment processed (Table 1). Pollen preservation in the dune is moderately good: an average of nine percent of the pollen grains are corroded (exine etched), and an average of 32 percent of the grains are degraded (exine layers fused). In this study, 18 samples from late Holocene sediments (radiocarbon dated 690 to 4230 years BP) near the coppice dune locality were also analyzed for pollen. All of the prehistoric samples contain pollen, averaging 960 grains per gram; 80 percent of the pollen grains, however, are deteriorated

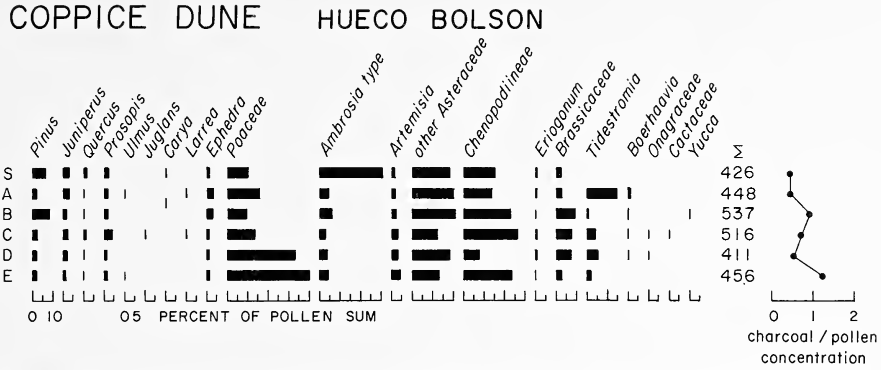

FIGURE 1. Pollen diagram from coppice dune, Hueco Bolson, northeast of El Paso, Texas; additional data in Table 1.

(corroded plus degraded). The advanced state of grain deterioration and low pollen concentration in the late Holocene material indicate that the pollen assemblages are not reliable for vegetational or environmental reconstruction. The pollen content of the prehistoric deposits contrasts sharply with the well-preserved, abundant pollen in the coppice dune, indicating that pollen grain deterioration progresses rapidly in the arid Hueco Bolson environment.

Charcoal Content

Charcoal and charred particles greater than 25 μm (long axis) range from 1600 to 14,000 per gram in the coppice dune. The ratio of charcoal-pollen concentrations may be an index to regional range fires. If so, the decrease in charcoal-pollen ratios base to top may document a diminished fire frequency in the Hueco Bolson during the period of dune sand deposition, coinciding with a decrease in grasses in the local vegetation. These results must be viewed as tentative, however, because the charcoal trend is largely dependent upon the lowermost sample, which could have a comparatively higher content due to reworking of charcoal from an adjacent prehistoric archaeological site.

DISCUSSION AND CONCLUSION

Grasses have been an important component of the northern Chihuahuan Desert vegetation of southern New Mexico for the past several millennia. Pollen diagrams from Gardner Spring near Las Cruces (Freeman, 1972) and the Garnsey bison kill site near Roswell (Hall, 1984, 1985) show that Poaceae pollen frequencies have been about 20 to 30 percent for the past 5000 years. (Both lower and higher amounts of Poaceae have been found in studies in the El Paso area—Cully and Clary, 1980; Horowitz et al., 1981; the greater variability may be due to poor preservation of the pollen assemblages noted by these workers.) In the Hueco Bolson, the 40 percent Poaceae pollen at the base of the coppice dune indicates a vigorous desert-grassland vegetation at the time the dune began to form. Other plant taxa in the pollen diagram do not exhibit significant trends. This does not necessarily mean that other changes in plant species composition have not occurred. In arid lands, pollen grains from a few wind-pollinated plant species are generally over-represented and dominate pollen assemblage counts even though insect-pollinated taxa may be stronger components of the vegetation. Persistent frequencies of *Prosopis* suggest that mesquite was present during the deposition of the coppice dune. Independent dating of the dunes was not attempted in this study, but land survey records and other documents indicate that many of the New Mexico dunes formed in the late 19th and early 20th centuries (Gile, 1975). The Hueco Bolson dunes are probably historic in age as well. In the first analysis of a coppice dune, Dean (1988) found moderately well-preserved pollen. Holocene sediments in this arid region, however, have not produced reliable pollen assemblages (Cully and Clary, 1980; Clary, 1988; Dean, 1988; this study). Pollen records from the extensive coppice dune field may provide new information on aspects of vegetation change during the past 100 years.

The recent decrease in grasses, as documented by both range literature and pollen analysis, may be related to change in climate to greater aridity, or to strong grazing pressure from the expanding late 19th century cattle industry, or both. From the perspective of a broader time scale, the middle Holocene (6000 to 4000 years ago) of the Southwest and southern Great Plains was characterized by a climate hotter and dryer than that of today (Hall, 1985, 1988). The Gardner Spring pollen diagram, from analysis of alluvial deposits east of Las Cruces, documents the last phase of the severe arid period (Freeman, 1972). Poaceae pollen frequencies from this period are 15 to 20 percent, comparable to pollen deposition in the southwest plains rangeland today (Hall, 1990). Although the 10-16 percent Poaceae in the upper coppice dune and adjacent surface is at the low end of the scale of grassland pollen assemblages, the magnitude of change from 40 percent represents a dramatic decline in grasses that is without parallel in the Holocene record. Although independent paleoclimatic information from this region is sparse, there is no indication from Holocene studies in adjacent areas of a decline in Poaceae at a magnitude even close to that shown in the Hueco Bolson coppice dune pollen diagram. In this regard, the pollen record is compatible with the grazing pressure explanation for grassland decline in southern New Mexico and adjacent Texas.

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PRODUCTION OF EXTRACELLULAR CELLULOLYTIC ENZYMES BY *FUSARIUM OXYSPORUM* F.SP. *LYCOPERSICI*

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Abstract.—The components of the extracellular cellulases of *Fusarium oxysporum* f. sp. *lycopersici* and the effect of different carbon sources on the induction of these enzymes were investigated. In this work, the stronger inducer for endoglucanase, cellobiohydrolase and B-glucosidase was carboxymethyl cellulose, while the highest production of xylanase was found in those cultures with xylan as the carbon source. The production of endoglucanase was induced by all carbon sources tested and it appears that the test fungus produces endoglucanase in a constitutive manner. *Key words*: extracellular cellulases; enzymes; *Fusarium*.

Several species of saprophytic fungi are known to produce extracellular enzymes that can decompose cellulosic plant residues. A few of these species such as *Aspergillus fumigatus* (Stewart et al., 1983), *Chaetomium cellulolyticum* (Dubeau et al., 1986), and *Trichoderma harzianum* and *Trichoderma reesei* C30 (Robinson, 1984; Saddler et al., 1985) produce sufficient cellulolytic enzymes to degrade cellulose and hemicellulose when grown in media containing cellulose derivatives or crystalline cellulose as the carbon source. It has been shown (Ortega, 1980; Ortega and Baca, 1983) that some species of *Fusarium (F. solani, F. roseum* var. *Graminearum, F. oxysporum)* produce cellulolytic enzymes when grown in media containing a cellulosic substrate as the carbon source and cellulase inducer.

Direct penetration of susceptible hosts by phytopathogenic fungi has been regarded as a mechanical process. However, it has been stated (Strobel and Mathre, 1970; Agrios, 1978) that extracellular enzymes produced by pathogenic fungi may help in the softening and disintegration of the host's cell wall to facilitate the penetration of the pathogen.

The main objectives of this work were to determine the components and assess the activities of the extracellular cellulolytic enzyme of *F. oxysporum* f. sp. *lycopersici*, and to determine the effects of carbon source on the production of these enzymes by the fungus.

Materials and Methods

Maintenance of the Fungus

Stock cultures of *F. oxysporum* f. sp. *lycopersici* were maintained in potato dextrose agar (Difco, B13) test tubes at 4°C.

Preparation of Inoculum

The fungus was previously grown in 250 milliliter flasks with 125 milliliters of a medium containing 0.02 percent $MgSO_4 \cdot 7H_2O$, 0.01 percent $Ca(NO_3)_2 \cdot 4H_2O$, 0.1 percent Peptone, 0.2 percent yeast extract, and 2.0 percent glucose in Na-citrate buffer at pH 4.8.

Composition of Growth Medium for the Production of Cellulases

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 parts per million $Fe(NO_3)3.9H_2O$; 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 as carbon source and cellulase inducer. The carbohydrates used separately in the growing media were sodium carboxymethyl cellulose (Hercules, Inc. type 7HF), microcrystalline cellulose (Sigma Chemical Co., type 50), D-cellobiose (Aldrich Chemical Co.), and Xylan (Aldrich Chemical Co). The control cultures had glucose as carbon source. The pH of the growing medium was adjusted to 4..8 with citric acid.

Enzyme Production

Flasks (250 milliliter) containing 125 milliliters of sterile growth medium were inoculated with five milliliters of mycelium inoculum that had been harvested after four days of growth. The inoculum was washed twice in distilled water and used to inoculate the cellulolytic medium. Flasks were incubated on an orbital shaker at 100 revolutions per minute and 26°C for seven days. Culture fluids were harvested after seven days of growth by centrifuging (4500 rpm, 30 minutes, 10°C). The cell-free supernatant was used for the determination of extracellular activity of the enzymes. All tests were replicated three times.

Enzyme Assays

Endoglucanase (CM-cellulase, Carboxymethyl cellulase, EC 3.2.1.4).—Endoglucanase activity was assayed by viscometric technique (Ortega and Baca, 1983). The viscometric data were then analyzed by a nonlinear method described previously (Ortega and Chance, 1988). The reaction mixture consisted of nine milliliters of 0.8 percent sodium carboxymethyl cellulose (Hercules Co.) in 0.01 M potassium phosphate buffer, (pH 4.5) and one milliliter of enzyme. The viscosity tests were made at 40°C. The activity of endoglucanase was expressed as mg of substrate reacted per minute per milliliter.

Cellobiohydrolase (EC 3.2.1.91).—Extracellular cellobiohydrolase was assayed with the method described by Tanaka et al. (1988). The substrate was a suspension of 50 mg/ml microcrystalline cellulose (type 50 by Sigma Chemical Co.) in 0.05M sodium acetate buffer, pH 4.8. The reaction mixture consisted of nine milliliters of cellulose suspension and one milliliter of enzyme. The reaction tubes were incubated at 40°C for two hours. After centrifugation, the amount of reducing sugars in the supernatant fluid was determined by the phenol-sulfuric acid method of Dubois et al. (1956).

B-Glucosidase (ED 3.2.1.21).—Extramycelial B-glucosidase was determined as described by Stenberg and Mandels (1982). B-glucosidase activity was determined by incubating 1 ml of enzyme with 10 mg of D-cellobiose (Aldrich Chemical Co.) in one milliliter of 0.05 M sodium citrate buffer (pH 4.8) at 50°C for 30 minutes. The reactions were stopped by immersing the test tubes in boiling water for five minutes. Glucose (or equivalent) resulting from the reaction was determined by the oxidase-peroxidase test (Sigma Chemical Co.).

Xylanase (EC 3.2.1.32).—The activity of extracellular xylanase was determined as described by Saddler et al. (1985). The reaction mixture consisted of 10 milligrams of oat spelts xylan (Aldrich Chemical Co.) in one milliliter of 0.05M sodium citrate buffer (pH 4.8) and one milligram of enzyme.

The activities of cellobiohydrolase, B-glucosidase, and xylanase were expressed as micromoles of reducing sugars reacted per minute, glucose and xylose, respectively. All enzyme activity tests as well as protein determinations were replicated three times.

Protein Determination

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

Results and Discussion

Endoglucanase

Maximum endoglucanase activity of 0.89 milligrams per milliliter was recorded in the culture fluid when *F. oxysporum* f. sp. *lycopersici* was grown in media containing CMC (Table 1). This activity was twice as much of that measured when the test fungus was grown in the control medium. The amount of total protein measured in the fluids of both cultures (CMC and control), corresponds approximately to the endoglucanase activities recorded in these cultures (Table 1). Most probably, the endoglucanase recorded in the control medium is a component of the complex of cellulolytic enzymes that is produced constitutively. Bhat and Wood (1989) found multiple endoglucanase forms produced by *Penicillium pinophilum* when the fungus was grown in a medium containing microcrystalline cellulose (Avicel) as the carbon source.

Lesser production of endoglucanase was measured when the test fungus was grown in cultures containing other cellulase inducers. Apparently, most of the cellulolytic enzyme produced in cultures with cellobiose as carbon source was endoglucanase. These cultures had 800 μg/ml of total protein.

Cellobiohydrolase

Production of cellobiohydrolase was induced in those cultures containing CMC, microcrystalline cellulose and xylan. Maximum production of cellobiohydrolase (0.80 IU/ml) was measured in the CMC culture with 500 ug/ml of total protein (Table 1). When the test fungus was grown in media containing microcrystalline cellulose, the production of this enzyme was 0.47 IU/ml. This amount corresponds approximately to the amount of total protein (300 μg/ml) measured in these cultures. The lowest production of cellobiohydrolase (0.12 IU/ml) was recorded in fluids from cultures that had xylan as the carbon source. However, fluids from these cultures had the highest amount (1650 μg/ml) of total protein per milliliter measured in this work. Apparently, cellobiohydrolase was not produced in the cultures containing cellobiose or in the control cultures.

B-Glucosidase

Maximum production of B-glucosidase (0.52 IU/ml) was measured in cultures that had CMC as carbon source and enzyme inducer (Table 1). When the fungus was grown in media containing microcrystalline cellulose as the carbon source, the production of this enzyme was 0.36 IU/ml. The lowest production of B-glucosidase was recorded in the cultures with cellobiose as the carbon source. This enzyme was not detected in the fluids obtained from the control and those cultures that had xylan as the inducer and carbon source.

TABLE 1. Average (three replications) effect of different carbon sources on the production (IU/ml.min) of extracellular cellulolytic enzymes by *Fusarium oxysporum* f. sp. *lycopersici*.

Carbon source and cellulase inducer	Enzymes				
	Endo-glucanase[1]	Cellobio-hydrolase	B-glucosidase	Xylanase	Total protein[2]
CMC	0.89	0.80	0.52	1.16	500
Microcrystalline cellulose	0.05	0.47	0.36	0.55	300
Cellobiose	0.48	nd	0.04	nd	800
Xylan	0.22	0.12	nd	3.44	1650
Control	0.45	nd	nd	nd	280

[1] mg/ml.min.
[2] μg/ml.
nd = none detected.

Sternberg and Mandels (1982) reported that the production of B-glucosidase by *Trichoderma reesei* was enhanced when some glucosides were added to cultures of the fungus that already had a carbon source. The stronger inducer found in these studies was methyl-B-glucosidase.

Xylanase

Production of xylanase was induced in the cultures that had CMC, microcrystalline cellulose and xylan as carbon sources (Table 1). Maximum production of this enzyme (3.44 IU/ml) was found in the fluids of the culture with xylan. The production of xylanase recorded in the cultures that had CMC (1.16 IU/ml) was only about one third of the enzyme produced in the cultures with xylan. The amount of total protein measured in the fluids from the cultures with CMC (500 μg/ml) is also about one third of the total protein found in the cultures where xylan was the carbon source (1650 μg/ml). This enzyme was not found in the control cultures or in the cultures where cellobiose was the carbon source.

Stewart et al. (1983) reported that the production of xylanase by *Aspergillus fumigatus* was much larger when the fungus was grown on delignified hay and grass residues than when grown on purified celluloses. Dubeau et al. (1986) found that several lignocellulosic substrata induce the production of xylanase in *Chaetomium cellulolyticum*. The best inducer for the production of the enzyme found in these studies was wheat straw in solid state fermentation.

ACKNOWLEDGMENT

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GENERAL NOTES

FIRST RECORD OF *BRANCHINECTA PACKARDI* PEARSE (CRUSTACEA: ANOSTRACA) FROM MEXICO

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On 4 June 1987, 19 specimens of the fairy shrimp, *Branchinecta packardi,* were collected approximately 16 kilometers west of the municipality of Salinas in the west-central part of the state of San Luis Potosí, México. They were taken from an ephemeral pool in a shallow arroyo beneath a concrete bridge 100 meters east of kilopost 115 on Highway 49 near the border of the state of Zacatecas. The location is at an approximate elevation of 3000 meters and is within 100 kilometers of the Continental Divide to the west. Although this report represents the first published record of the genus for central México as well as the southernmost locality of record for the species, the presence of *Branchinecta* from this region was not unexpected. In the first report of the genus for México, Belk and Lindberg (1979) proposed that the occurrence of *B. lindahli* on Isla de Guadalupe strongly suggested its presence on mainland México 290 kilometers to the east. In his coverage of the branchiopod fauna of México, Central America, and the West Indies, Hartland-Rowe (1982) predicted the occurrence of members of the genus *Branchinecta* in this region. These investigators were proven correct by Belk's (1983) more recent report of *B. lindahli* from the Baja Peninsula of western México.

Branchinecta packardi was earlier thought by Lynch (1964) to have a somewhat restricted distribution. Based upon then known collections, he (1964:476) stated that *B. packardi* "apparently has a rather limited distribution which is practically confined to the Great Plains region east of the Rocky Mountains." After reviewing both published records as well as specimens in the National Museum of Natural History, Belk (1975) reported the occurrence of this species from Alberta and Saskatchewan in Canada south through the Great Plains to Texas. Although this report of *B. packardi* from San Luis Potosí represents a considerable extension of the known geographic range, it is not thought to represent an extension of this species into an ecologically new habitat. Considering the elevation, annual rainfall, and the proposal by Johnston (1977) that this area of the Chihuahuan Desert may well have been a grassland prior to more recent agricultural activities, the occurrence of *B. packardi* from the high plateau of central México is not considered ecologically significant.

Of the 19 specimens collected, 18 were males. The single female was mature and measured 13 mm in total length. It exhibited dorsolateral lobes only on segments XI and XII and lacked the small conical lobes noted by Lynch (1964) to occur on segments II and III in varying percentages of the specimens he examined. Because only one female was present in the collection and the statement by Lynch (1964) that "all of the species of *Branchinecta* are quite variable", the variation mentioned above is not considered to be of taxonomic importance at this time. Five males and the single female of *B. packardi* are deposited in the National Museum of Natural History (USNM 239268) as are five males in the Instituto de Biologío de la Universidad Nacional Autónoma de México (EM 10733). Collected along with the specimens of *B. packardi* from the pool were specimens of *Streptocephalus texanus.* Appreciation is extended to Dr. Michael Carlo of Angelo State University for his review of the manuscript.

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A LATE HOLOCENE HERPETOFAUNA FROM MONTAGUE COUNTY, TEXAS

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Holocene herpetofaunas are poorly known in Texas or from elsewhere in North America. Reported herein is a small late Holocene herpetofauna collected in 1961 by W. W. Dalquest and C. W. Hibbard from a bank section of Dye Creek, approximately 4 kilometers east of the Dye Community, and 1.3 kilometers North of the Cook E. T. Triangulation Station, Montague County, Texas. The herpetofauna consists of at least two frogs, one turtle, one lizard, and six snakes, which add information about the late Holocene herpetological life of north-central Texas. There is a radiocarbon date of 1350 ± 150 years BP determined from a sample of human fashioned charcoal believed to be contemporary with the Dye Creek vertebrates (Dalquest and Hibbard, 1965). In the following annotated herpetofaunal list, catalog numbers are from the Midwestern State University Collection of Fossil Vertebrates.

Rana cf. *pipiens* Schreber complex.—A left ilium (12545; Fig. 1A). This ilium has a smooth vastus prominence and gently sloping ilial crest as in the *Rana pipiens* complex (Holman, 1984). Within this complex, the species *Rana blairi* and *Rana sphenocephala* presently occur in Montague County (Dixon, 1987).

Bufo speciosus Girard or *B. cognatus* Say.—A left ilium (12549; Fig. 1B). The ilial prominence of *Bufo speciosus* and *Bufo cognatus* is higher than in all other similar-sized extant species of *Bufo*, but I am unable to separate the species on the basis of ilia. Both species occur in or near Montague County today (Dixon, 1987).

Kinosternon flavescens.—A vertebral, three marginals, and a left hypoplastron (12550) These elements of a small turtle are identical to those of living *Kinosternon flavescens.*

Ophisaurus cf. *attenuatus* (Cope).—A trunk vertebra (12551). This vertebra is identical to *Ophisaurus* in being short and wide, with the posterior portion of the neural spine thick and extending anteriorly as a thin sheet of bone, and in having the bottom of the centrum flat (Etheridge, 1961). The fossil is similar in size and structure to trunk vertebrae of *Ophisaurus attenuatus.*

Thamnophis sp. indet.—A trunk vertebra (12552). This small natricine vertebra is referred to *Thamnophis* rather than *Nerodia* or *Regina* based on its small size, elongate shape, and

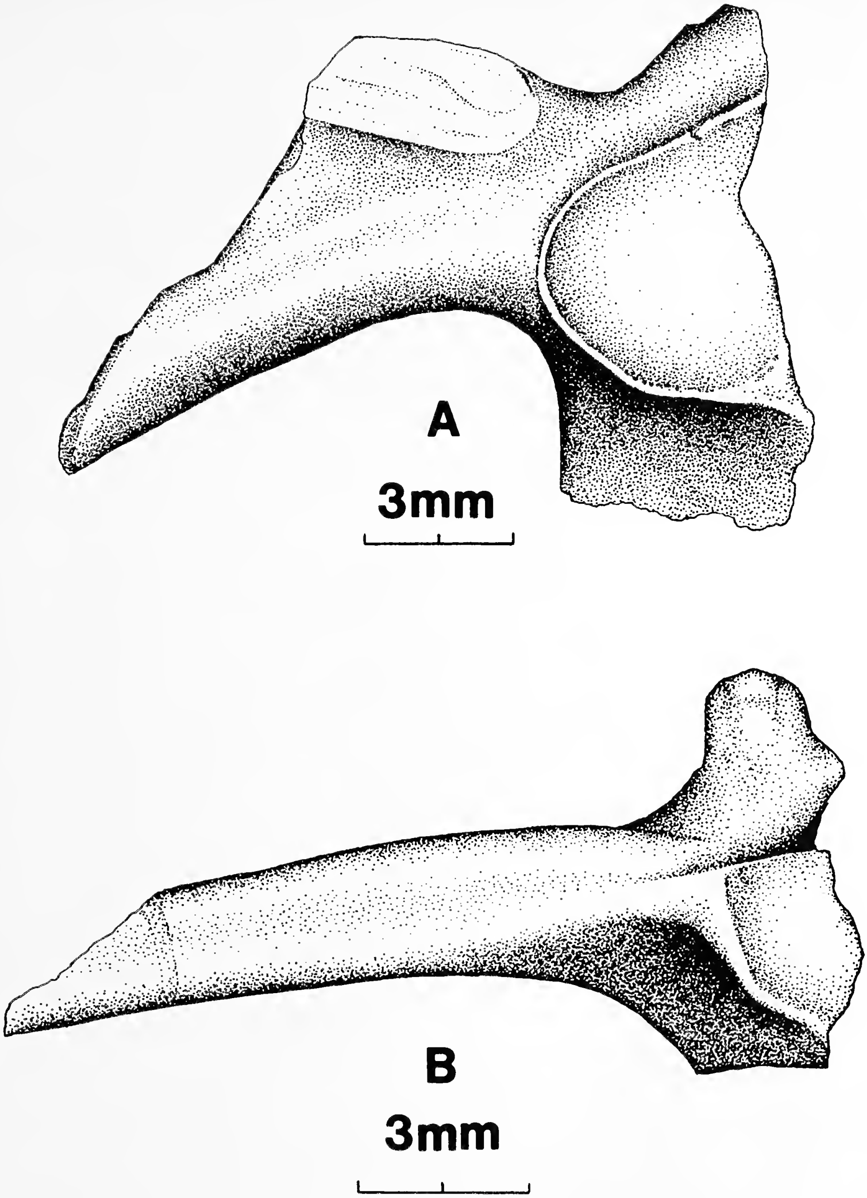

FIGURE 1. Ilia of *Rana* cf. *pipiens* complex (A; 12545), and *Bufo speciosus* or *B. cognatus* (B; 12549), each shown in lateral view.

moderately short, posteriorly directed hypapophysis (Brattstrom, 1967; Parmley, 1988*a*). The fossil is too fragmentary for specific identification.

Elaphe guttata (Linnaeus) or *Elaphe obsoleta* (Say).—A trunk vertebra (12553). This vertebra has a higher neural arch and weaker subcentral ridges than those of species of *Lampropeltis* of similar size. Based on characters discussed in Parmley (1986*a*, 1986*b*), the vertebra represents either *Elaphe guttata* or *Elaphe obsoleta*. Both species presently occur in Montague County (Dixon, 1987).

Heterodon sp. indet.—A trunk vertebra (12554). This vertebra is undoubtedly referable to *Heterodon* based on its depressed neural arch and wide, obsolete hemal keel, but it is too fragmentary for specific identification. *Heterodon nasicus* and *Heterodon platyrhinos* presently occur in Montague County (Dixon, 1987).

Pituophis melanoleucus (Daudin).—Fifty-six trunk vertebrae (12555). Vertebrae of adult *Pituophis melanoleucus* are rather distinctive in being large, with high neural spines, vaulted neural arches, weak subcentral ridges, and arched zygosphenes viewed anteriorly.

Lampropeltis getulus (Linnaeus).—A trunk vertebra (12547). This vertebra is identical to those of *Lampropeltis getulus* in having the following characteristics: a depressed neural arch; long, low and dorsally thickened neural spine; and strongly developed, bowed subcentral ridges with deep subcentral ridge concavities (Parmley, 1990).

Coluber sp. indet. or *Masticophis* sp. indet.—Three trunk vertebrae (12548). I am unable to distinguish vertebrae of *Masticophis* from those of *Coluber* (Parmley, 1988*b*). The fossil vertebrae are indistinguishable from those of living *Coluber* and *Masticophis* in being longer than wide; they have long, thin neural spines, well-developed epizygapophyseal spines, vaulted neural arches, and uniformly narrow hemal keels. The species *Coluber constrictor* and *Masticophis flagellum* occur in Montague County today (Dixon, 1987).

The Dye Creek herpetofauna consists of four taxa indicating the proximity of aquatic conditions (*Rana pipiens* complex, *Bufo speciosus* or *B. cognatus, Kinosternon flavescens, Thamnophis* sp.), and six kinds typical of uplands (*Ophisaurus attenuatus, Elaphe guttata* or *E. obsoleta, Heterodon* sp., *Pituophis melanoleucus, Lampropeltis getulus, Coluber* sp. or *Masticophis* sp.). As a unit, the herpetofauna offers no clues to suggest late Holocene ecological conditions were any different than at the present, as all of the taxa occur in, or near Montague County today (Dixon, 1987). This contrasts with the Dye Creek mammalian fauna, which suggests slightly dryer, less mesic conditions for the creek area approximately 1300 years ago (Dalquest and Hibbard, 1965). For example, Dalquest and Hibbard suggested prairie must have extended 50 to 100 miles to the east of its present extent in north-central Texas to allow grasshopper mice (*Onychomys leucogaster*) to live at Dye Creek. Nonetheless, such a discrepancy is not unexpected considering the fact that living herpetological representatives of the Dye Creek fauna presently can be found in semiarid grasslands to the west of Montague County (in Wichita County) where the grasshopper mouse also occurs (Dalquest and Horner, 1984).

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NOTEWORTHY RECORDS OF THREE SPECIES OF RODENTS FROM HONDURAS

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Examination of specimens housed in the Texas Cooperative Wildlife Collection, Texas A&M University, has revealed noteworthy range extensions of three rodents from Honduras.

Heteromys desmarestianus fuscatus J. A. Allen, 1908.—This spiny pocket mouse has been recorded from central and eastern Honduras (Goodwin, 1942; Hall, 1981; Benshoof et al., 1984). Two females were collected on 23 June 1983 from Lancitilla, Department of Atlantida. This is the first record of *H. d. fuscatus* in the northern part of the country and extends the known range approximately 210 kilometers northwestward from Las Mairins on the Río Mairin Tingni (Benshoof et al., 1984).

Oryzomys fulvescens fulvescens (Saussure, 1860).—The pygmy rice rat has been recorded from eastern Honduras at Patuca, Department of Gracias a Dios, and Sabana Grande, Department of Francisco Morazán (Hall, 1981). A female *O. f. fulvescens* was taken 2.4 mi. SW Dulce Nombre de Clumí, Department of Olancho. This locality fills the gap between Patuca and Sabana Grande and is the first to be reported from east-central Honduras.

Hoplomys gymnurus truei J. A. Allen, 1908.—This rat has been recorded from Río Maririn Tingni, Department of Gracias a Dios (Benshoof et al., 1984), and 78 mi. ENE Danlí on the Río Coco and 40 km. E Catacamas, Department of Olancho (Pine and Carter, 1970). A male *H. g. truei.* was obtained 2.4 mi. SW Dulce Nombre de Culmí, Department of Olancho. This specimen represents the westernmost locality record for the species in Honduras and extends the known range approximately 100 kilometers southwest from Río Mairin Tingni (Benshoff et al., 1984) and 40 kilometers northwest from the locality east of Catacamas reported by Pine and Carter (1970).

I would like to thank Dr. David J. Schmidly for allowing me to examine specimens in the Texas Cooperative Wildlife Collection, and Dr. J. Knox Jones, Jr., for his critical review and comments on the manuscript.

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FIRST REPORTED OCCURRENCE OF THE FILARIOID NEMATODE, *LITOMOSOIDES WESTI*, IN *GEOMYS PERSONATUS*

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Filarioid nematodes of the genus *Litomosoides* have been reported to occur in species of several genera of mammals in the Nearctic and Neotropical regions (Burnham, 1953; West, 1962; Forrester and Kinsella, 1973; Gardner and Schmidt, 1986). *L. thomomydis* occurs in disjunct populations within the range of the pocket gopher, *Thomomys talpoides*, in southern Colorado (Miller and Ward, 1960). *Litomosoides westi* has been reported in both *Geomys bursarius* of the Great Plains region and *T. bottae* from the eastern foothills of the Rocky Mountains in Colorado (Gardner, 1983; Gardner and Schmidt, 1986).

In the course of investigations of the biology of *Geomys personatus* in southern Texas, nematodes identified as *L. westi* were collected from the pleural cavities of three adults. The nematodes were recovered from two female *G. p. megapotamus* collected on 12 May 1988 from 3 mi. N and 4 mi. E Hebbronville, Duval County, and a male *G. p. davisi* taken on 14 May 1988 at a place 2.5 mi. N and 4 mi. E San Yancio, Zapata County. This is the first record of *L. westi* from *G. personatus* and represents a considerable extension of the known range of this nematode. Additional collections of parasites from species of other genera of geomyids in the Southwest and in México and Central America are needed to define more precisely the range of hosts in which these filarioid nematodes occur.

Specimens of *G. personatus* are deposited in the Texas Cooperative Wildlife Collection (TCWC) at Texas A&M University. Specimens of *L. westi* from these gophers are deposited as voucher specimens in the Nematology Collection, Department of Nematology, University of California, Davis.

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FIRST RECORD OF *PEROMYSCUS GYMNOTIS* (MURIDAE) FROM EL SALVADOR, WITH SECOND RECORDS FOR *CHOERONISCUS GODMANI* AND *DIAEMUS YOUNGI* (PHYLLOSTOMIDAE)

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Recent field studies in El Salvador by one of us (Owen) resulted in a collection of small mammals that has been deposited in The Museum of Texas Tech University. Three species in the collection document noteworthy records, one the first report of the peromyscine rodent *Peromyscus gymnotis* from the country, and the others the second Salvadorian records for *Choeroniscus godmani* and *Diaemus youngi*, bats of the American family Phyllostomidae.

Peromyscus gymnotis Thomas, 1894.—This species originally was named and described on the basis of material from Guatemala. Osgood (1909) arranged *gymnotis* as a subspecies of *P. mexicanus*. Later, Hooper (1968) expressed doubt that *gymnotis* was conspecific with *mexicanus* but did not formally change the nomenclature. Musser (1971), however, elevated *gymnotis* to species rank, listing the Chiapian *allophylus* (Osgood, 1904) as a synonym. These decisions were accepted by Huckaby (1980) and Carleton (1989). *P. gymnotis* is one of the smaller members of the *mexicanus* species group.

Huckaby (1980) and Hall (1981) published records of *gymnotis* from southeastern Chiapas and from localities in southwestern Guatemala. Elevations cited by these authors ranged from 65 feet at Astillero, Departmento de Escuintla, Guatemala, to 5500 feet at Finca Helvetia, Departamento de Quezaltenango, Guatemala. Jones and Yates (1983) reported *gymnotis* from 12 localities along the length of western Nicaragua, almost to the Costa Rican border. Elevations for their Nicaraguan material ranged from 35 to 1000 meters. On the basis of known locality and habitat data, Jones and Yates (1983) suggested that the geographic distribution of *gymnotis* also includes El Salvador, southern Honduras, and northwestern Costa Rica. Carleton (1989) cautioned that specimens of gymnotis may be found in samples previously thought to represent *mexicanus* from the Isthmus of Tehuantepec and from El Salvador.

During the period from October 1989 to February 1990, 21 *P. gymnotis* (12 males and nine females), the first to be reported from El Salvador, were collected at a finca about 3-6 mi. NW San Luis Talpa, Departamento de La Paz, near the Pacific coast and at an elevation of about 50 meters. Specimens were taken in second growth tropical vegetation consisting of scattered trees and brush.

Where the distributions of *gymnotis* and *mexicanus* approach each other in Nicaragua, Jones and Yates (1983) observed that the latter is found at higher, inland localities. These authors also noted that the two species are not known to occur sympatrically in Nicaragua (or elsewhere), which also appears to be true in El Salvador.

On 28 December 1988, 29 specimens of *P. mexicanus* were trapped on Volcán de Santa Ana, Departamento de Santa Ana, El Salvador. This locality, at approximately 1800 meters elevation, is about 72 kilometers from San Luis Talpa. All *Peromyscus* taken at this higher, inland site were *mexicanus*, whereas all *Peromyscus* obtained at the coastal lowland site near San Luis Talpa were *gymnotis*.

Our data for *gymnotis* and *mexicanus* in El Salvador thus are consistent with the pattern described for the species by Jones and Yates (1983) in Nicaragua and by Huckaby (1980) in Chiapas. *Peromyscus gymnotis* appears to be endemic to the coastal Pacific lowlands and adjacent areas of intermediate elevation. It is replaced by *mexicanus* at higher, usually more inland localities.

Choeroniscus godmani (Thomas, 1903).—Previously, this bat was known from El Salvador by two specimens reported from Volcán de San Miguel, Departamento de San Miguel (Burt and Stirton, 1961). Although Burt and Stirton did not cite elevational data, the fact that their specimens were taken on a volcano suggests that they came from a moderately high locality (the elevation of Volcán de San Miguel is 2153 meters). On 31 January 1990, Owen netted a specimen of *C. godmani* at La Hacienda Escuintla, Departamento de La Paz. This record extends the known range of *C. godmani* in El Salvador into the tropical lowlands.

Diaemus youngi (Jentink, 1893).—Greenbaum and Jones (1978) reported the first record of this vampire for El Salvador from 3 mi. NW La Herradura, Departamento de La Paz. On 27 May 1989, Owen netted a specimen at a nearby site, about 1 mi. N La Herradura. It was taken in the front yard of a campesino's hut near a tree where chickens sometimes roost at night. The campesino reported that his chickens sometimes had signs of bleeding from the legs and feet in the morning, possibly indicating they had been preyed upon by *D. youngi* inasmuch as this species has been observed to bite the legs and tarsi of chickens (Sazima and Uieda, 1980). Many nights of bat netting in similar habitat, but far removed from chicken roosts, failed to yield a single specimen of this vampire. The specimen reported by Greenbaum and Jones (1978) was obtained 14 years earlier than the one reported here. These data suggest that *D. youngi* maintains a rare but constant presence in the lowland tropics of El Salvador, with localized distribution related to the presence of suitable avian prey.

We thank Dr. Julio Cesar Castro for permission to camp and trap on his finca, "La Soledad," near San Luis Talpa.

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ECOLOGICAL IMPLICATIONS OF THE RED-EARED TURTLE TRADE

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Red-eared turtles (*Trachemys scripta elegans*) are almost certainly the most commonly traded reptile in the pet industry. The subspecies is produced on commercial ranches in the United States, particularly in Louisiana. Thorough descriptions of these operations and marketing procedures are given in Warwick and Holford (1984), Warwick (1984, 1985*a*, 1985*b*, 1986). The industry claims an annual production of four to five million (Warwick, 1986) to six to seven million (Warwick and Steedman, 1988) turtles. There are approximately 50 principal ranches in the United States. Numerous aspects of production in the pet turtle industry attract attention from a wide variety of sectors. Concern is particularly strong in connection with: 1) public health and safety, because there are serious epidemiological problems (Lamm et al., 1972; Cohen et al., 1980; Tauxe et al., 1985; Gangarosa, 1985), which resulted in a national ban on sales of turtles 10 centimeters or less in length in 1975, and in Canada in 1976 (Iceland apparently instituted a ban on imports of turtles due to health risks in 1962); 2) humane considerations because stress and early mortality are frequent occurrences at all points in the trade; 3) conservation concerns, inasmuch as breeding operations are not closed-cycle and as many as 100,000 adult *T. s. elegans* may be collected from free-ranging populations annually in order to maintain breeding stocks (Warwick, 1986); 4) threats to the natural ecology of importing nations from released and escaped pets—viable and potentially viable introduced populations of turtles have been reported, in particular for South Africa (Newberry, 1984), Malaysia (E. Moll, correspondence, 1989), and Japan (I. Uchida, correspondence, 1990). West Germany ceased importation of the turtles because of ecological threats of their introduction (D. Jelden, personal communication).

In addition, there is evidence of an extensive market in wild-caught *T. s. elegans* for human consumption, particularly in Far Eastern countries, which may account for an estimated 765,000 turtles per year (Warwick and Steedman, 1988). Alteration of habitat due to land development, mortality arising from traffic, supplies for biological teaching and research, and other factors, undoubtedly also adversely affect natural populations.

Table 1 gives available information on exports of red-eared turtles from the United States from 1985 to 1988. *T. s. elegans* is not listed under international trade agreements and, as a consequence, methodological monitoring of commercialism is not mandatory although numerous organizations and individuals attempt to formulate reliable data. Data on all countries, even of limited nature, are unavailable and existing data are incomplete. In addition, Table 1 probably does not represent all trading nations. These data, therefore, almost certainly offer a highly conservative account of the extent of international trade. Known ports of export of *T. s. elegans* from the United States (supplied by U. S. Fish and Wildlife Service) are: Atlanta, Chicago, Dallas/Fort Worth, Detroit, Los Angeles, Miami, New Orleans, New York, San Francisco, Seattle, and Tampa.

Qualitative and quantitative data on free-living populations of *T. s. elegans* are lacking. Population surveys in southern and central Louisiana, within areas both accessible and inaccessible to commercial hunters, showed a considerable variance in numbers, with the animal only minimally represented at known sites of exploitation (Warwick, 1986). Comparative assessments between harvested and nonharvested areas are particularly lacking. Ranch operators, professional hunters, and biologists who have worked in the habitat of *T. s. elegans* have provided qualitative reports that suggest there has been a widespread depletion of natural populations of this turtle. D. Jackson (correspondence, 1989) pointed out the susceptibility of *T. s. elegans* to capture due to its nesting and

TABLE 1. Countries known to be recent or current importers of hatchling *T. s. elegans* from the United States in four recent years. Derived from material compiled by TRAFFIC (USA) from unedited computerized data provided by the United States Fish and Wildlife Service, and from data compiled by the authors. Unknown numbers of turtles also have been exported to French Polynesia, Guyana, Hungary, Malta, Reunion Island, and Toga.

Country	1985	1986	1987	1988
Argentina				3,000
Australia[1]	1,000	1,858		
Austria	3,500[2]	8,000	9,500	2,000
Belgium	6,000[2]	13,500	15,000	55,500
Canada[1]	8	18	314	
Chile			10,000	6,000
China			15,000	
Denmark	3,020[2]	6,030	5,020	11,546
West Germany	63,709[2]	7,771	55,593	74,560
France	163,305[2]	206,840	191,193	419,490
East Germany	19,600	86,984	6,650	9,525
Greece			7,000	
Honduras		1,000	2,000	
Hong Kong	94,000[2]	160,426	380,000	229,700
Ireland	1,000	5,275		1,775
Israel[1]	6,000[2]		1,950	
Italy	11,050[2]	50	100	161,266
Japan	1,036,200[2]	282,200	232,800	402,201
Korea			77,000	275,000
Martinique		500		
Mexico		8,004	49,000	53,500
Netherlands	13,000[2]	24,500	3,000	4,000
Panama			400	
Singapore	15,100[2]	5,000		20,000
Spain	52,500[2]	164,460	127,100	247,250
Sweden			62	
Switzerland			500	
Taiwan	145,000[2]	100,000	71,700	
Trinidad and Tobago	6,000[2]	2,000	2,000	1,000
United Kingdom	33,700[2]	28,500	17,712	33,750
West Indies	1,000	1,000		
Yugoslavia				5,500
Zambia				5,000
Exports to unknown destinations	26,000			
Totals	1,700,692	1,113,916	1,280,540	2,021,563

These data are based on exports declared to Customs; therefore, they probably do not reflect the actual volume of trade.

[1] Imports probably for scientific research, because trade bans for pet purposes are now in force.

[2] Figures given in personal communication with M. Anderson by Division of Law Enforcement, U. S. Fish and Wildlife Service, are higher than recorded in general export data.

terrestrial activities and its omnivorous diet and basking habits, which render the subspecies easily trapped. W. Parker (correspondence, 1989) noted that this turtle is vulnerable to rapid elimination of individual populations, due to its typical occurrence in definable bodies of water. R. Seigel (correspondence, 1989) reported on interviews with trappers and wildlife officials and cited unquestioned decline in abundance of *T. s. elegans* in southern Louisiana, primarily as a result of collection for the meat and pet trades, and that certain areas where the species was once common now are virtually devoid of turtles. R. Conant (correspondence, 1989) considered the subspecies seriously threatened in certain parts of eastern and central North America, mentioning a marked reduction in the size of populations.

While there are numerous areas wherein *T. s. elegans* remains abundant, and casual observations of the red-eared turtle are commonplace throughout much of its distribution, it may be overly optimistic to assume that such sightings imply unstressed populations. In many areas where these turtles were once abundant they now are uncommon or rare. Sizes of turtles in well-collected as opposed to uncollected habitats probably are highly significant, because population structure data show remarkably few large adult females in the former. Turtle collectors seek out such specimens for captive-breeding stock and the culinary market.

J. Congdon (correspondence, 1989) cited data from extensive field research on three species of turtles in Michigan (including *T. s. elegans*) over 15 years, and in modeling population responses to increase in mortality of adult or juvenile turtles, is convinced that harvesting of individuals past their first year of life can have severe adverse impact on almost any population. In addition, Congdon also noted that demographics of turtles suggest they are not capable of sustaining historic populations under even modest levels of increased loss. S. Minton (correspondence, 1989) reported that no more than 18 percent of hatchlings reach sexual maturity; while females may have a reproductive lifespan of 10 years, less than one percent of natural populations are believed to achieve this level. H. Fitch (correspondence, 1989) and W. Parker (correspondence, 1989) implied that late maturation of the subspecies (six to nine years for females) and highly irregular reproductive success are also important considerations.

The status of this turtle in the wild probably is often under valued, and depletion of natural populations almost certainly has broader implications affecting local ecology. Because large females constitute the primary reproductive stock, depletion of this sector of a population is highly significant and well may result in a compromised ability to recover from population stresses. Small- and medium-sized turtles are more vulnerable to predation than are larger turtles. Assuming, for example, that the collective energy requirement of major predators, for example, the American alligator, *Alligator mississippiensis*, remains reasonably unchanged, at least in the short- and medium-terms, a larger number of smaller turtles may be taken by predators to substitute for unavailability of larger turtles. Large-scale collection even for short periods, therefore, may lead to both short- and long-term population reduction. It is probably of considerable ecological importance that large populations of *T. s. elegans* remain intact, because reasonably dense natural congregations seem to be the biological optimum. Population decline also offers potentially serious consequences for cohabiting chelonians, and other fauna, because reduction in availability of red-eared turtles as a major prey animal probably places undue pressure on several species that are known to exist in much smaller populations or within restricted ranges.

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USE OF CAST NETS FOR COASTAL STREAM FISH SURVEYS

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Cast nets are commonly and effectively used by recreational fishermen for capture of schooling bait fish on the Gulf Coast. In some shallow coastal streams, cast nets also can enable a single investigator to conduct a rapid, quantified survey of a fish community. Because each cast is a discrete replicate sample of the fish community, cast net data meet statistical criteria for comparisons among locations or times. Stream surface area sampled is defined by the diameter of the net and the number of casts, allowing unit effort control in these comparisons. Discrete macrohabitats can be targeted, and species associations can be recognized by catch compositions for individual casts.

For survey data to be ecologically meaningful, however, bias and other limitations inherent in the sampling apparatus must be understood. For impact surveys (that is, a comparison upstream and downstream of an anthropogenic influence), age-class structure and species richness are two important community measures that could be effected by sampling bias. This note reports cast net data for size classes, and species richness as a function of sampling effort, for two southern Texas streams. The work was undertaken to develop a rapid method of surveying fish for impact studies to compliment existing procedures for other stream components, for example the "rapid bioassessment" of benthic communities developed by Shackleford (1988) and others. The work was not intended to replace more intensive methods traditionally utilized to produce complete faunal descriptions.

Netting was conducted on Petronila Creek, Nueces County, and San Fernando Creek, Kleberg County, Texas. Both are low-gradient coastal streams with agricultural watersheds, a shallow pool structure, and a soft substrate. The streams have base flows of approximately 0.028-0.142 cubic meters per second, and both are influenced by waste water discharges. Thirty casts were made over about 200 meters of stream at each of several stations (San Fernando Creek) using a net 1.83 meters (six feet) in diameter of 0.635-

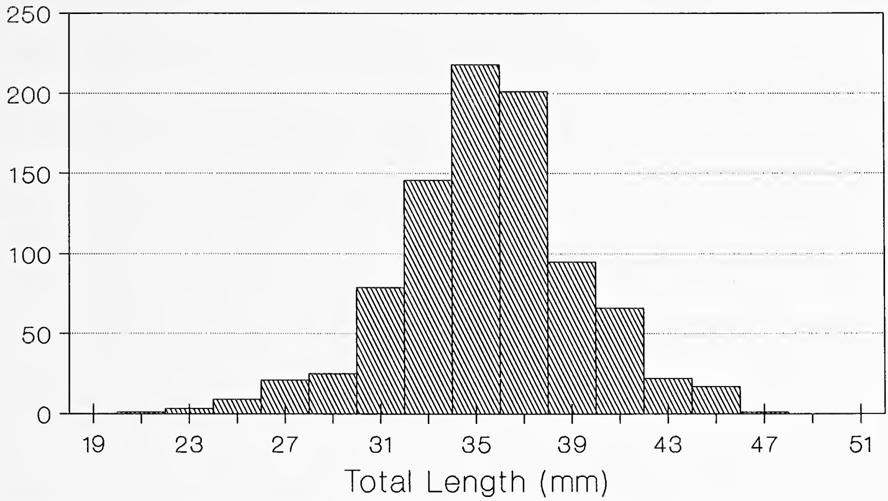

FIGURE 1. Size frequency distribution for 903 *Cyprinodon variegatus* taken with 10 casts in Petronila Creek, Nueces Co., Texas, using 0.635-centimeter (quarter inch) mesh.

centimeter (quarter inch) mesh (the smallest commercially available mesh size). Fish were identified, measured and weighed separately for each cast, and were not returned to the stream.

A total of 1205 fish was captured with 120 casts at four San Fernando stations (mean, 10.04 fish per cast; station means, 2.6-14.8 fish per cast). Fish were caught in 108 of 120 casts (90 percent), with the mean number of species caught per cast ranging from 1.33 to 3.03 at the four stations. The net was effective in capturing fish greater than about 25 mm in total length. The size-class distribution for *Cyprinodon variegatus* (Fig. 1) was a normal distribution for fish larger than this minimal size, but because I had no data on the actual size-class distribution of this species in the stream, the precise lower size limit for effective capture is unknown. the upper size limit for effective capture would require alternative collecting methods for deep water habitats where larger individuals would be found.

The cumulative number of species captured at a location increased asymptotically with sampling effort (Fig. 2). Data from four stations on San Fernando Creek showed 20 casts captured an average of 88.9 percent of the species present in the 30-cast sample. Dominant species could be characterized with relatively little effort; for example at a typical station, five casts were sufficient to identify six of the 10 species taken with 30 casts. These six species represented 97.4 percent of total fish numbers and 73.4 percent of fish biomass in the entire 30-cast sample at that location.

Replication of casts provided estimates of within-site variability required for statistical testing for among-station differences. Both ANOVA and the Kruskal-Wallis nonparametric ANOVA calculated for the San Fernando data revealed significant location differences ($P < 0.05$) in catch data that could be attributed to known habitat differences among stations or to impact on water quality resulting from waste water discharges. These results increased the usefulness of cast netting for impact analyses in these streams (Bowman et al., 1990; Shipley, 1991).

Statistical use of cast net data has several limitations. First, parametric procedures require normally distributed data and homogeneous variance among stations, and, therefore, most casts must catch fish. Cast net data easily meet assumptions for distribution-free tests like the Kruskal-Wallis Test, but these procedures are less powerful. However, parametric and nonparametric tests yielded the same results in most comparisons in this study.

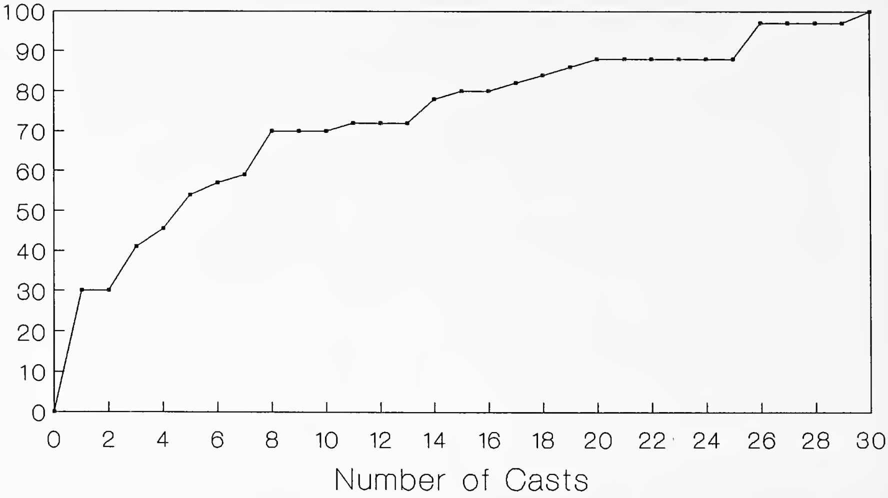

FIGURE 2. New species added as a function of sampling effort. Data are expressed as a percent of total species caught with 30 casts at each location, and are a composite of four stations on San Fernando Creek, Kleberg Co., Texas. The mean number of species representing 100 percent was 9.5.

Second, impact studies may be designed to detect significant location effects (for example, upstream and downstream of an outfall), but such effects by themselves cannot determine impact. Inasmuch as the cast is the replicated unit, parameters being tested are per-cast means (that is, number of species per cast, number of individuals per cast, or biomass per cast). The treatment itself cannot be replicated, because this would require several streams with similar influences. Therefore, results must be considered in relation to other stream data and professional judgement, lest the investigator be guilty of "pseudoreplication" (Hurlbert, 1984).

Not all potential sources of variability were characterized by cast net results. Slender species (for example, *Menidia*) or small species (for example, *Gambusia*), were probably under-sampled by 0.635-centimeter mesh, although some individuals as small as 15 mm in total length were collected. Other variables that could influence net efficiency include proficiency of the investigator and net visibility (monofilament as opposed to white nylon, sunlight conditions, stream turbidity). Similarity, effectiveness of the cast net in streams other than the shallow, low-gradient streams studies likely would be reduced. Further trials utilizing rotenone or other reference comparisons would be beneficial in the future. In spite of these limitations, results of this study indicated that cast nets can be effective for rapid community comparisons. For streams with appropriate physiography, the method is best suited for studies limited to a single investigator, for environments so polluted that wading is not desirable, or for studies requiring a high degree of quantification per unit field effort.

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INDEX TO VOLUME 42 (1990), 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 the titles or as key words.

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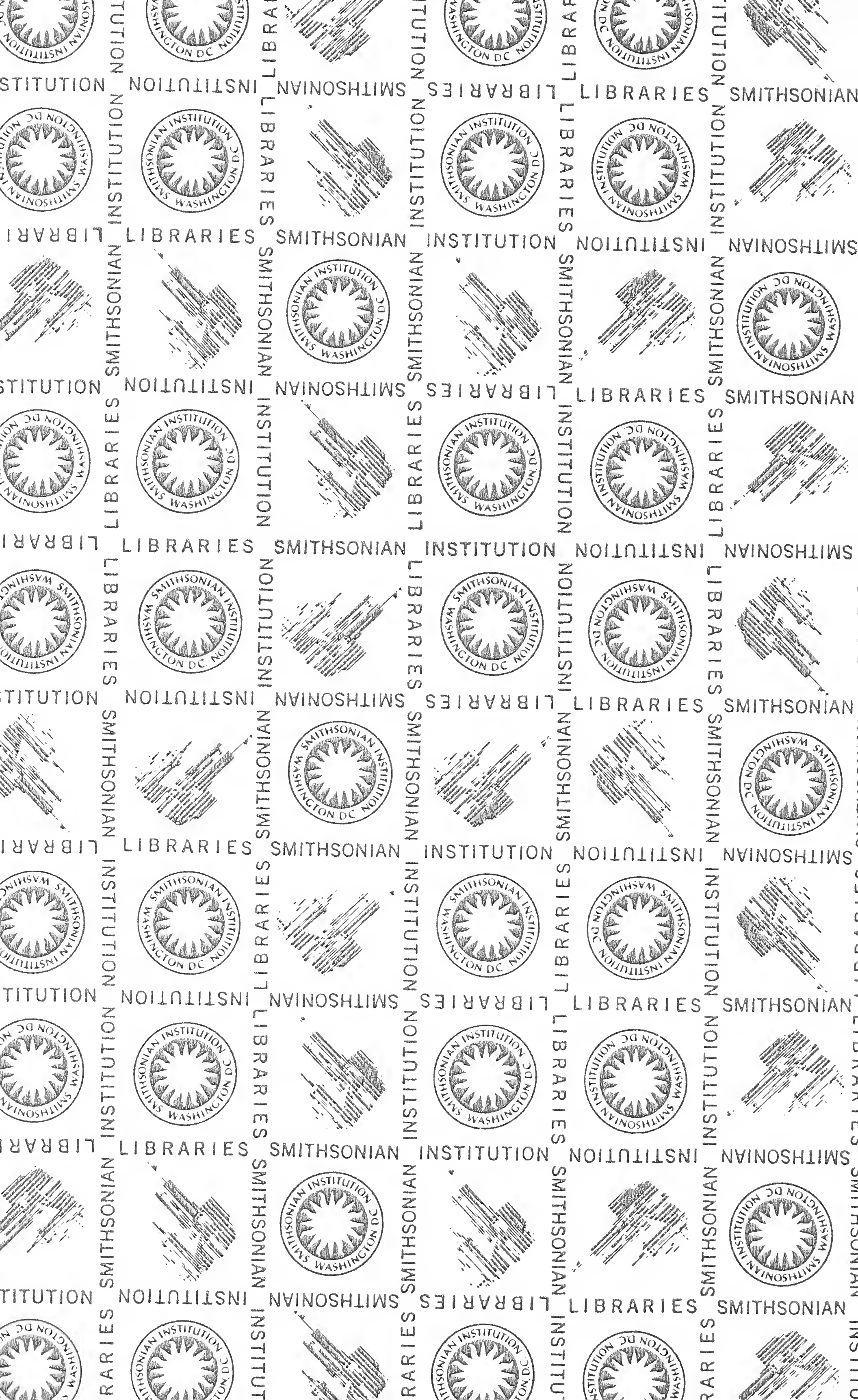
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